Eawag
Das Wasserforschungsinstitut
des ETH-Bereichs

"Projet Lac" synthesis report

Diversity, distribution and community composition of fish in perialpine lakes

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eawag
aquatic research

Impressum

Herausgeber
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Schweizerische Eidgenossenschaft
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Bundesamt für Umwelt BAFU
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Dieser Expertenbericht wurde vom Bundesamt für Umwelt (BAFU) durch eine Finanzhilfe gemäss Art. 12 Bundesgesetz über die Fischerei BGF unterstützt. Weitere Partner und Finanzgeber des "Projet Lac" sind auf Seite 105 bei den Verdankungen aufgelistet. Für den Inhalt ist allein der Herausgeber verantwortlich.

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Zitierung
Alexander T., Seehausen O. (2021). Diversity, distribution and community composition of fish in perialpine lakes – "Projet Lac" synthesis report. Eawag: Swiss Federal Institute of Aquatic Science and Technology. 282 pages.
ISBN 978-3-906484-76-1

Layout
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Fotos und Abbildungen
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Bild Titelseite
Verborgen am Grund vom Lago Maggiore ein Cagnetta *(Salaria fluviatilis)*. Um die Diversität der Fische und deren Dynamik besser zu verstehen, haben die Forschenden im Projet Lac begonnen, die Fische direkt in ihrer Umgebung zu beobachten.
Foto: Ole Seehausen

Zusammenfassung

Das Projet Lac war ein grosses Projekt der Eawag und der Universität Bern zur erstmaligen quantitativen Erfassung ganzer Fischgemeinschaften in grossen und tiefen Seen in und um die europäischen Alpen mit standardisierten Probenahmeverfahren. Ab 2010 wurden insgesamt 35 Seen in der Schweiz, Italien, Frankreich, Deutschland und Österreich untersucht und über 106 Fischarten erfasst. Dieser Bericht fasst die wichtigsten Ergebnisse zusammen, vergleicht die Fischgemeinschaften der einzelnen Seen, untersucht ihre Beziehung zu Umweltparametern und gibt einen Überblick über die Faktoren, welche die biologische Vielfalt und die Struktur der Gemeinschaften in diesem wichtigen Ökosystem beeinflussen.

Stichworte: See, Fische, Biodiversität, Schutz, Endemismus, Umweltveränderung, Monitoring, Fischerei, Biogeographie, Klimawandel

Résumé

Le Projet Lac était un grand projet de l'Eawag et de l'Université de Berne visant à recenser pour la première fois de manière quantitative des communautés entières de poissons dans les grands et profonds lacs des Alpes européennes et de leurs environs, à l'aide de méthodes d'échantillonnage standardisées. A partir de 2010, 35 lacs au total ont été étudiés en Suisse, en Italie, en France, en Allemagne et en Autriche et plus de 106 espèces de poissons ont été recensées. Ce rapport résume les principaux résultats, compare les communautés de poissons des différents lacs, examine leur relation avec les paramètres environnementaux et donne un aperçu des facteurs qui influencent la diversité biologique et la structure des communautés dans cet écosystème important.

Mots-clés: lac, poisson, biodiversité, protection, endémisme, changement environnemental, surveillance, pêche, biogéographie, changement climatique

Riassunto

Il Projet Lac era un progetto su larga scala dell'Eawag e dell'Università di Berna per la prima indagine quantitativa di intere comunità di pesci in laghi grandi e profondi nelle Alpi europee e dintorni, utilizzando metodi di campionamento standardizzati. A partire dal 2010, un totale di 35 laghi in Svizzera, Italia, Francia, Germania e Austria sono stati studiati e sono state registrate oltre 106 specie di pesci. Questo rapporto riassume i risultati principali, confronta le comunità di pesci di ogni lago, esamina la loro relazione con i parametri ambientali e fornisce una panoramica dei fattori che influenzano la biodiversità e la struttura della comunità in questo importante ecosistema.

Parole chiave: lago, pesce, biodiversità, conservazione, endemismo, cambiamento ambientale, monitoraggio, pesca, biogeografia, cambiamento climatico

Abstract

Projet Lac was a large project conducted by Eawag and the University of Bern to quantitatively survey, for the first time, whole-lake fish communities in the large and deep lakes in and around the European Alps using multiple, standardised sampling methods. Starting in 2010, in total 35 lakes were investigated across Switzerland, Italy, France, Germany and Austria, with more than 106 fish species recorded. This report brings together key findings, compares fish communities among lakes, investigates their relationship to environmental parameters, and provides an overview of drivers of biodiversity and community structure in this important ecosystem.

Keywords: lake, fish, biodiversity, conservation, endemism, environmental change, monitoring, fisheries, biogeography, climate change

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1. Zusammenfassung

Einzigartige Fischgemeinschaften in Alpenrandseen

Die grossen und tiefen Seen im europäischen Alpenraum bilden ein einzigartiges Ökosystem, das in Europa Seltenheitswert hat und geografisch von anderen, ähnlichen Ökosystemen getrennt ist. Die Fischartengemeinschaften der Schweizer Alpenrandseen zeichnen sich durch eine besondere Vielfalt aus. Dies, weil die Schweiz im Einzugsgebiet der vier grossen Flüsse Rhein, Rhone, Po und Donau liegt, die zu drei verschiedenen Süsswasser-Ökoregionen in Europa gehören.[1] Viele kälteangepasste, endemische Arten mit kleinem Verbreitungsgebiet leben in nur einem See, bzw. in benachbarten Seen gemeinsamen geologischen Ursprungs. Dort haben sie sich nach dem Rückzug der pleistozänen Eisschilde entwickelt. Diese Arten haben zwar eine geographisch eng eingegrenzte Verbreitung, kommen jedoch in den jeweiligen Seen zahlreich vor und sind für die Berufs- und Freizeitfischerei von grosser Bedeutung. Gleichzeitig sind sie für den Artenschutz von globaler Bedeutung und reagieren empfindlich auf menschliche Eingriffe. Die Fische der Alpenrandseen bilden eine wichtige Naturressource für die Erhaltung der Biodiversität, das Funktionieren der Ökosysteme und die menschliche Nutzung.

Zweck der standardisierten Probenahmen

Im Laufe der Jahrhunderte haben aufmerksame Fischerinnen und Fischer, begeisterte Naturforschende, Seenutzer sowie Wissenschaftlerinnen und Wissenschaftler eine Fülle von Erkenntnissen über die Fischartengemeinschaften in den Alpenrandseen gesammelt. Bislang beschränkten sich die Beobachtungen und Forschungsprojekte zumeist auf einen oder wenige Seen, bzw. Seehabitate oder eine oder wenige Fischarten. Zudem wurden die Daten nur selten in einem breiteren ökologischen oder biogeografischen Zusammenhang analysiert. So liegen beispielsweise für alle grossen Seen Fischereistatistiken vor, die Angaben zu Anzahl und Art der gefangenen Fische liefern (einige Datensätze reichen mehrere Jahrhunderte zurück). Die ersten kontinuierlich erhobenen und seeübergreifenden Statistiken zum kommerziellen Fischfang, wurden um das Jahr 1900 am Genfersee und am Bodensee erhoben. Die Analyse dieser Datensätze liefert heute wertvolle Erkenntnisse zu den Veränderungen der Seen und der Fischerei im letzten Jahrhundert. Da Fischereistatistiken jedoch nur Aufschluss über bestimmte Fischarten in einem See, bzw. nur zu grossen Individuen dieser kommerziell interessanten Arten geben, liefern sie auch nur eine beschränkte und potenziell verzerrte Information zu der Fischartengemeinschaft eines Sees. Ein nachhaltiges Fischereimanagement, das auf den Erhalt der Fischgemeinschaften in den Seen abzielt, erfordert eine fundierte Kenntnis des aktuellen Zustands der Fischdiversität mit einer genauen Bestandesaufnahme der vorkommenden Arten und Populationen sowie ihrer relativen Häufigkeiten.

Ziele des «Projet Lac»

Ziel des Projektes «Projet Lac» war es, die bestehenden Informationslücken zur Verbreitung und Häufigkeit der Fischarten in allen Alpenrandseen durch quantitative Erhebungen zu schliessen. Dazu wurden mehrere standardisierte Probenahme-Methoden – kombiniert mit aktualisierter Fischtaxonomie, modernen Identifikationsmethoden und den neuesten Erkenntnissen über die Artenabgrenzung – verwendet. Mit Probenahmen in allen Seeteilen liess sich die Verteilung der Fische zum Erhebungszeitpunkt (Spätsommer – Frühherbst) beschreiben. Dies gibt Aufschluss über den ökologischen Zustand eines Sees. In allen Seen wurden dieselben Probenahmen-Methoden verwendet, so dass die Fischgemeinschaften verglichen werden konnten. Diese Erhebungen sind dank der präzisen Dokumentation der verwendeten Methodik reproduzierbar. Obwohl der Zustand der Seen zum Zeitpunkt der Aufnahmen bereits deutliche menschliche Einflüsse aufweist, fungiert die erste quantitative Erhebung auch als ein Referenzzustand, um diesen mit zukünftigen Daten vergleichen zu können. Damit kann festgestellt werden, wie die Fischgemeinschaften auf veränderte Umweltbedingungen (z.B. Klimawandel) oder auf spezifische Massnahmen (z.B. Renaturierung von Seeufern) reagieren.

Neu entdeckte und wiederentdeckte Vielfalt

Im Rahmen des «Projet Lac» wurden 35 Seen in der Schweiz und an mit dem Ausland benachbarten Grenzseen zu Italien, Frankreich, Deutschland und Österreich (in den beiden letztgenannten Ländern nur der Bodensee) untersucht. Dabei wurden über 106 Fischarten nachgewiesen. Mit beinahe 20 Prozent aller in Europa bekannten Fischarten (525 Arten[2]) gehört die Schweiz, die nur 0,4 Prozent der europäischen Landfläche ausmacht, zu den Regionen mit der höchsten Diversität an Fischarten. Auf der Grundlage dieser Erhebungen konnten 15 phänotypisch und/oder genetisch unterschiedliche, mehrheitlich endemische Fischtaxa erstmals nachgewiesen und dokumentiert werden. Dabei wurden auch fünf Fischarten gefangen, deren Vorkommen in der Schweiz bislang nicht bekannt war. Zwei Arten wurden nördlich der Alpen nachgewiesen, deren Vorkommen bisher nur von südlich der Alpen bekannt war. Bei den Probenahmen wurden zudem vier endemische Fischarten wiederentdeckt, die als ausgestorben galten, darunter der Bodensee-Tiefseesaibling (*Salvelinus profundus*).

Ausserordentlich hohe Anzahl endemischer Fischarten

Die meisten nachgewiesenen, einheimischen Fischarten gehören zur Familie der Lachsfische (*Salmonidae*, einschl. *Coregoninae*: 44 Arten), gefolgt von der Familie der Karpfenfische (*Cyprinidae*: 27 Arten). Diese beiden Fischfamilien sind in Europa generell am stärksten verbreitet, allerdings mit einem umgekehrten Dominanzverhältnis (236 Karpfenfischarten und 98 Lachsfischarten)[2]. Die meisten für den Artenschutz besonders wertvollen 41 endemischen Arten gehören zur Familie der Lachsfische, hierbei handelt es sich vor allem um unterschiedliche Felchen- (*Coregonus* spp) und Saiblingsarten (*Salvelinus* spp). Diese haben sich seit dem Ende der Eiszeit lokal entwickelt. Zudem wurden 31 in einigen Seen als gebietsfremd (ursprünglich aus Mitteleuropa) oder exotisch (aus Asien oder Nordamerika eingeführt oder eingeschleppt) eingestufte Fischarten nachgewiesen. Die meisten gehören ebenfalls zur Familie der Lachsfische (11 Arten) und der Karpfenfische (8 Arten). Die übrigen nachgewiesenen, nicht in der Schweiz heimischen Arten, verteilten sich auf 16 weitere Familien; sieben davon waren nur durch eine vertreten, z.B. die *Lotidae* mit der Trüsche (*Lota lota*) und die *Siluridae* mit dem Wels (*Silurus glanis*). Die «Projet-Lac»-Daten im Vergleich mit anderen Veröffentlichungen zeigen, dass viele Arten extrem selten vorkommen und dass ein Grossteil davon bei den «Projet-Lac»-Erhebungen gar nicht nachgewiesen wurden.

Verteilung der Fische innerhalb der Seen

Die meisten endemischen Fischarten wurden entweder in den Offen- oder Tiefenwasserhabitaten von nährstoffarmen Seen nachgewiesen. Die grösste Anzahl an Fischarten dagegen wurde in der flachen Uferzone gefangen. Das Verhältnis von Gesamtartenreichtum (die sog. Alpha-Diversität) und Reichtum an endemischen Arten war folglich zwischen Freiwasser und Ufer umgekehrt. In den litoralen Habitaten (Uferzone) wurde die grösste Anzahl Fischarten im Mündungsbereich von Bächen und Flüssen verzeichnet. Je nach Habitattyp im Uferbereich finden sich unterschiedliche Arten bzw. Altersstadien einer Art, was die grosse Bedeutung von vielfältigen Uferhabitaten für die Fischdiversität in einem See unterstreicht.

In wärmeren Uferbereichen und am Grund der oberen Wasserschichten war die Häufigkeit der Fische bzw. deren Biomasse am grössten. In nährstoffarmen Seen war der Unterschied bezüglich der Fischbiomasse zwischen Ufer und Tiefenwasser weniger ausgeprägt: Sogar in den tiefsten Schichten dieser Seen wurden noch Fische gefangen. In sehr nährstoffreichen Seen wurden ab 30 m Tiefe praktisch keine Fische mehr gefangen, weil während der Sommer-Schichtung dort der Sauerstoff komplett fehlte. Der Klimawandel hat in einigen Seen, z.B. im Untersee des Zürichsees, solche Trends verschärft: Wegen des wärmeren Oberflächenwassers im Winter wird das Zeitfenster verkürzt, in dem die vertikale Durchmischung zu einer Sauerstoffanreicherung im Tiefenwasser führt. In anderen Seen, die nach der Eutrophierung (Nährstoffbelastung) des letzten Jahrhunderts wieder nährstoffärmer sind, sind die Tiefenwasserarten wegen des Sauerstoffmangels zur Zeit der Eutrophierung ausgestorben. Die Tiefwasserbereiche dieser Seen sind deshalb heute nur spärlich von Fischen besiedelt, obwohl sie erneut als Lebensraum genutzt werden können.

Felchenarten und Egli in den meisten Seen dominant

Verschiedene Felchenarten (*Coregonus* spp) wiesen die höchste Fischbiomasse in den Kiemennetzfängen auf und waren in den meisten grossen Alpenrandseen dominant. Darin zeigt sich ihre Bedeutung für ein funktionierendes Seeökosystem. In Seen mit höheren Phosphorkonzentrationen war die Verbreitung und Biomasse von Felchen tendenziell geringer und diejenige des Egli/Flussbarsches (*Perca fluviatilis*) höher. Die höhere Biomasse der Felchen in nährstoffarmen Seen basiert zumeist auf kleineren Felchenarten. In den Kiemennetzfängen in den flachen, bodennahen Bereichen der meisten Seen waren Egli/Flussbarsch, Rotauge (*Rutilus* spp), Alet (*Squalius* spp) und Rot-/Schwarzfeder (*Scardinius* spp) dominant. Egli/Flussbarsche und Rotaugen waren in den ufernahen Bereichen vieler kleineren und auch mehreren grösseren Seen reichlich vorhanden; häufig wurde dort eine höhere Nährstoffkonzentration gemessen. Ausnahmen bildeten der Lago Maggiore, wo im offenen Wasser der Süsswasserhering (*Alosa agone*) dominierte, und die Alpenseen von Sils und Poschiavo, wo standortfremde Seesaiblinge (*Salvelinus umbla*), einheimische und eingeführte Forellen (*Salmo* spp) und die exotische Kanadische Seeforelle (*Salvelinus namaycush*) vorherrschten.

Fischartenzusammensetzung durch Biogeografie, Isolation und Seegrösse bestimmt

Die Zusammensetzung der in jedem See vorkommenden einheimischen Arten war eng mit der geografischen Lage des Sees assoziiert, d. h. dem zugehörigen Flusseinzugsgebiet, sowie der Lage des Sees ob nördlich oder südlich der Zentralalpen, alpin, perialpin oder voralpin. Seen innerhalb der gleichen Flusseinzugsgebiete (Rhein, Rhone, Po) weisen generell eine ähnlichere Zusammensetzung der einheimischen Fischgemeinschaften auf. Die Unterschiede in der Artenzusammensetzung zwischen den Einzugsgebieten gehen auf die verschiedenen pleistozänen Rückzugsgebiete zurück, in denen manche Arten die letzten Eiszeiten überlebten. Die südlichen perialpinen Seen im Einzugsgebiet des Po wurden überwiegend von Fischen wiederbesiedelt, die in den stromabwärtsliegenden Teilen des Einzugsgebiets nahe der Adria Zuflucht gefunden hatten. Die nördlichen Voralpenseen wurden von Arten verschiedenster Herkunft besiedelt – ein Hinweis auf die Verbindung zu den eiszeitlichen

Tieflandrefugien der drei grossen Flusseinzugsgebiete (Rhein, Rhone und Donau). Elf Gattungen waren mit verschiedenen, nördlich und südlich der Alpen heimischen Arten vertreten. Diese Arten waren selten eng miteinander verwandt, sondern hatten jeweils enger verwandte Arten in anderen Regionen von Europa: Darin spiegeln sich die unterschiedlichen Evolutionswege dies und jenseits der Alpen wider, die wahrscheinlich durch die Trennwirkung der Alpen und nicht durch die pleistozänen Gletscherzyklen bedingt sind. Die wenigen einheimischen Fischarten in den geografisch isolierten Alpenseen (Sils und Poschiavo) gehörten zu Abstammungslinien, die sich an das Leben in kaltem Wasser angepasst hatten.

Die grossen Seen im Einzugsgebiet des Rheins weisen – im Gegensatz zu jenen der Rhone und des Po – zahlreiche endemische Arten auf. Wahrscheinlich ist dies auf die Grösse vieler Seen im Rheineinzugsgebiet und das verbreitete Vorkommen der Gattungen *Coregonus* und *Salvelinus* zurückzuführen. Diese Taxa sind nach dem Rückzug der pleistozänen Gletscher mit als erstes in die Seen eingewandert und daraus haben sich viele neue Arten (Neoendemiten) entwickeln können. Die meisten nicht einheimischen und exotischen Arten wurden hingegen in den südlichen, perialpinen Seen des Po-Einzugsgebiets gefunden.

Die tendenziell tiefen und wärmeren grossen Seen liegen auf geringerer Meereshöhe, meistens im Einzugsgebiet von Rhein- und Po- und beherbergen zahlreichere Fischarten. Grössere Seen bieten eine grössere Vielfalt an unterschiedlichen Lebensräumen (ökologische Nischen), in denen mehr Arten nebeneinander koexistieren können. Sofern die Seen tief genug sind um im Sommer Kaltwasserrefugien zu bieten, welche mit genügend Sauerstoff bis zum Grund versorgt sind, können Fische durch ökologische Spezifikation sich an diese extremen Umgebungen anpassen und neue Arten gehen daraus hervor. Grössere Seen können auch grössere Populationen von den meisten Arten beherbergen. Damit sinken die Risiken, dass Schwankungen in der Jahrgangsstärke (demografische Stochastik) oder Umweltveränderungen zum lokalen (und bei endemischen Arten möglicherweise globalen) Aussterben führen. Die Seen im Einzugsgebiet des Rheins und des Po gehören zu gut vernetzten See- und Flusssystemen, während jene im oberen Rhone- und Donaulauf eher isoliert sind. So bilden sich grössere Meta-Gemeinschaften von an den See angepassten Fischarten und -populationen. Dies wiederum trägt zu einer häufigeren Besiedlung und den Fortbestand in diesen Seen bei. In Übereinstimmung mit den Vorhersagen der Insel-Biogeographie ist die Arten-Areal- Beziehung (beschreibt Anzahl Arten, die auf einer Fläche vorkommen kann) für gebietsfremde Arten gering, für einheimische grösser und für endemische am höchsten. Würde man hier noch die historisch belegten ausgestorbenen Arten miteinbeziehen, wäre der Zusammenhang noch stärker.

Weitere wichtige natürliche und anthropogene Faktoren

Als weitere wichtige Einflussfaktoren für die Fischgemeinschaften sind neben der Biogeografie, der Insel-Biogeografie, der Seemorphologie und den Nährstoffen auch die Temperatur, das Vorkommen von gebietsfremden Arten, die Vernetzung mit einmündenden Fliessgewässern und das Fischereimanagement zu nennen. Saisonale Wassertemperaturzyklen beeinflussen die räumliche Verteilung der Fische im Jahresverlauf, auch bezüglich Wassertiefe. Die stärkere Erwärmung des Oberflächenwassers infolge des Klimawandels beeinträchtigt in einigen Seen die vertikale Durchmischung und verursacht bzw. verschärft somit den Sauerstoffmangel im Tiefenwasser. In der Folge ist der Transport von Nährstoffen aus dem Tiefenwasser an die Oberfläche reduziert und begünstigt so die Ausbreitung von Phytoplankton-Arten, welche für das Zooplankton nicht nutzbar oder unverdaulich sind. Dies wirkt sich auf die Fischgemeinschaften aus, weil sich der potenziell besiedelbare Lebensraum im See reduziert (Wasservolumen), Refugien im Kaltwasserbereich nicht nutzbar sind und die Auswahl an Fischnährtieren verändert wird.

Standortfremde und exotische Fischarten konkurrieren mit einheimischen Arten um dieselben Nahrungsressourcen. Wenn standortfremde Fische sich mit verwandten einheimischen Arten fortpflanzen (Hybridisierung), gehen die genetischen und ökologischen Eigenschaften der einheimischen Arten potenziell verloren. So bleibt das Aufkommen einer standortfremden Art womöglich unentdeckt und führt zu einer heimlichen Verdrängung der einheimischen Art, bzw. zur Bildung einer Hybridpopulation. Zu den häufigsten exotischen oder standortfremden Arten in den beprobten Seen gehören der Eurasische Kaulbarsch (*Gymnocephalus cernua*) und der Sonnenbarsch (*Lepomis gibbosus*), das Rotauge (*Rutilus rutilus*) und verschiedene Felchenarten (*Coregonus* spp) in den südlichen perialpinen Seen. Häufig vorkommende gebietsfremde Wirbellose wie die Zebramuschel (*Dreissena polymorpha*), die Quagga-Muschel (*Dreissena bugensis*) und die Asiatische Körbchenmuschel (*Corbicula fluminea*) führen in vielen Seen zu grossflächigen Veränderungen am Seegrund und damit verändert sich das Habitat der Fische und ihrer Nahrung. Dadurch wird möglicherweise das Nahrungsnetz des Sees verändert – mit noch weitgehend unbekannten, aber weitreichenden Folgen für die einheimischen und gebietsfremden Arten.

Die grössenselektive, kommerzielle Fischerei beeinflusst die Grössenzusammensetzung von Fischpopulationen, weil selektiv die grössten Individuen gefangen werden. Die sehr unterschiedlichen direkten und indirekten Auswirkungen dieser grössenselektiven Fischerei betreffen nicht nur die Population der befischten Arten, sondern das gesamte Seeökosystem. Durch die intensive Befischung werden die meisten grossen Individuen der Zielart gefangen. Infolge dessen nimmt der Prädationsdruck auf deren Beute ab und/oder die Populationen, welche um dieselbe Beutearten konkurrieren, profitieren davon und nehmen in der Anzahl zu bzw. verteilen sich anders im See. Die intensive Fischerei führt bei der befischten Population womöglich auch zu evolutionären Veränderungen von Wachstums- und Life-History-Merkmalen. Dies wiederum kann Auswirkungen auf das Zusammenspiel der Arten im Ökosystem haben.

Schliesslich beeinflussen der Zustand der in die Seen einmündenden Flüsse deren aquatische Durchgängigkeit, und die Vernetzung der Seen die entsprechenden Fischgemeinschaften in den Seen. Viele Seefischarten steigen in die Flüsse auf, um dort zu laichen oder nutzen die Flüsse als Wanderkorridore um zu den Laichplätzen zu gelangen. Andere Fischarten laichen in den Deltabereichen der Seen, wo die einmündenden Fliessgewässer Geschiebe ablagern, das als Laichhabitat fungiert. Begradigte und verbaute Zuflüsse sowie Veränderungen der Flussdeltas schaden deshalb auch den Fischgemeinschaften in den Seen.

Empfehlungen zum Erhalt der Fischvielfalt in den Seen

In Anbetracht der vielen Bedrohungen für die Vielfalt der Seefische und der vielen anthropogenen Einflüsse des Menschen auf die Fischgemeinschaften, stehen die Bewirtschafter vor der schwierigen Herausforderung, die negativen Einflüsse abzumildern und gleichzeitig die nachhaltige Nutzung der Seenfischerei zu ermöglichen. Aus den Auswertungen der aus dem «Projet Lac» gewonnen Daten und weiterer Forschungsarbeiten lassen sich verschiedene Empfehlungen zur Bewahrung der Fischvielfalt in den Seen herleiten. Die Wiederherstellung der Schlüsselfaktoren des Seeökosystems (z.B. litorale und profundale Habitate, Wasserqualität und Nährstoffe) und die Wiederherstellung eines möglichst naturnahen Fluss-See-Netzwerkes, schaffen die besten Voraussetzungen für den Schutz und die Erhaltung der einheimischen Fischarten. Effektives Monitoring und der Erhalt der Fischbiodiversität setzen eine fundierte Dokumentation und Kenntnis zu Artenvielfalt, Ökologie und Verbreitung, Taxonomie, Evolutionsverhältnisse sowie Wechselwirkungen zwischen den Arten voraus. Die taxonomische Beschreibung bislang unbeschriebener Fischarten ist für die Bewirtschaftung und den Erhalt wichtig und notwendig. Dies auch um die Öffentlichkeit über die Existenz dieser Arten zu informieren und somit zu sensibilisieren. Sobald diese Informationen wissenschaftlich bestätigt sind, müssen sie in die Gesetzgebung einfliessen und als Rechtsgrundlage für den Erhalt und den Schutz dieser Arten dienen, auch um eine Verschleppung dieser Arten ausserhalb ihres natürlichen Verbreitungsgebiets zu verhindern. Zudem müssen die direkten anthropogenen Auswirkungen auf die Umwelt und die Genetik der Fischpopulationen, z. B. schlechte Wasserqualität, nicht-nachhaltige Fischerei und Fischbesatz erkannt und mit entsprechenden Massnahmen korrigiert werden. Schliesslich bildet das kontinuierliche Monitoring mit quantitativen, standardisierten Methoden und objektiven, aussagekräftigen Beurteilungen, die auf ökologischen, taxonomischen und genetischen Informationen basieren, eine wichtige Grundlage für ein schlüssiges, adaptives Management dieser wertvollen Naturressource.

1. Résumé

L'ichtyofaune unique des lacs périalpins

Les grands lacs profonds situés au pied des Alpes constituent un écosystème unique, rare à l'échelle de toute l'Europe et géographiquement isolé d'autres écosystèmes similaires. En Suisse, l'ichtyofaune de ces lacs périalpins est particulièrement riche car le pays alimente les bassins hydrographiques de quatre cours d'eau majeurs: le Rhin, le Rhône, le Pô et le Danube, qui appartiennent à trois écorégions d'eau douce d'Europe.[1] On trouve dans ces lacs un grand nombre d'espèces endémiques adaptées au froid, avec de très petites aires de répartition. Ces espèces se retrouvent dans un lac seulement ou dans des lacs voisins ayant la même origine géologique, où elles ont évolué après le retrait de la couverture glaciaire du Pléistocène. Malgré l'exiguïté de leurs aires de répartition, beaucoup de ces espèces comptent parmi les plus abondantes dans leurs lacs respectifs et sont importantes pour la pêche commerciale et récréative. Parallèlement, il s'agit d'espèces d'intérêt pour la conservation à l'échelle mondiale, très sensibles aux perturbations anthropiques. L'ichtyofaune des lacs périalpins est donc une richesse naturelle d'importance pour la conservation de la biodiversité, le fonctionnement écosystémique et l'activité humaine.

Pourquoi faut-il des échantillonnages standardisés?

Les observations faites au fil des siècles par des pêcheurs, des naturalistes, des usagers des lacs et des chercheurs ont permis de constituer un vaste ensemble de connaissances sur l'ichtyofaune des lacs périalpins. Cependant, ces observations et ces études étaient généralement consacrées à un ou quelques lacs, à un ou quelques habitats lacustres ou bien à une ou quelques espèces de poissons. Les données ont rarement été analysées dans un contexte écologique ou biogéographique plus large. Par exemple, on dispose pour tous les grands lacs de statistiques sur le nombre et l'espèce de poissons capturés par les pêcheurs, dont certaines comprennent des séries de données datant de plusieurs siècles. Les statistiques systématiques des captures commerciales de poissons portant sur l'ensemble d'un lac remontent aux alentours de 1900 pour les plus anciennes (Lacs Léman et de Constance). Leur analyse fournit des renseignements précieux sur l'évolution des lacs et de la pêche au siècle dernier. Néanmoins, les statistiques de la pêche se rapportent uniquement à un petit sous-ensemble d'espèces présentes dans les lacs et seulement aux spécimens de grande taille, ce qui donne lieu à une représentation étroite et potentiellement biaisée de la composition de l'ichtyofaune de ces lacs. Or, pour pratiquer une gestion et une conservation éclairées des peuplements pisciaires lacustres, il faut une description complète de l'état de la diversité ichtyologique dans l'ensemble de la région, accompagnée d'un inventaire des espèces et des différentes populations indiquant leur abondance relative au sein des lacs et par comparaison avec les autres lacs.

Objectifs du Projet Lac

Le but du Projet Lac est de collecter ces informations manquantes en procédant à une étude quantitative (inventaire) des peuplements pisciaires dans chacun des lacs périalpins au moyen de méthodes d'échantillonnage standardisées, combinées avec une taxonomie ichtyologique actualisée, des outils d'identification modernes et une conception récente de la délimitation entre les espèces. L'échantillonnage de tous les compartiments de chaque lac a permis de décrire la distribution des poissons durant la période d'inventaire (de la fin de l'été au début de l'automne), ce qui fournit des informations sur le fonctionnement écologique des lacs étudiés. L'application du même protocole d'échantillonnage dans tous les lacs offre la possibilité de comparer les peuplements d'un lac à l'autre. De plus, ces inventaires pourront être reproduits ultérieurement puisque les méthodes d'échantillonnage ont été documentées avec précision. Bien que l'état des lacs soit déjà loin de ce qu'il était avant de subir l'impact de l'activité humaine intensive, cette première étude quantitative fournit un état des lieux de référence avec lequel les données futures pourront être comparées afin de déterminer comment l'ichtyofaune continue de réagir aux changements environnementaux, comme les changements climatiques, ou aux mesures de renaturation, comme par exemples des rives lacustres.

Découverte et redécouverte de la diversité

Dans le cadre du Projet Lac, 35 lacs ont été étudiés en Suisse, en Italie, en France, en Allemagne et en Autriche (le lac de Constance seulement pour ces deux derniers pays). Au total, plus de 106 espèces de poissons ont été recensées. La Suisse abrite 20 % de toutes les espèces pisciaires connues en Europe (au nombre de 525[2]) sur un territoire représentant 0,4 % de la superficie terrestre du continent, ce qui en fait l'une des régions ayant l'ichtyofaune la plus riche. Les échantillons récoltés pour le projet ont permis de mettre en évidence quinze taxons distincts par leur phénotype ou leur génotype qui n'avaient pas été documentés auparavant et dont la plupart sont endémiques. Le projet a également révélé la présence de cinq espèces de poissons déjà décrites mais jamais observées en Suisse et de deux espèces au nord des Alpes auparavant observées seulement au sud des Alpes. L'échantillonnage de tous les compartiments des lacs a en outre permis de redécouvrir quatre taxons endémiques que l'on pensait disparus, dont l'omble des abysses (*Salvelinus profundus*) du lac de Constance.

Espèces endémiques extraordinairement nombreuses

La majorité des espèces de poissons natives recensées appartenait appartient à la famille des salmonidés (y compris les corégones ; 44 espèces), suivie de la famille des cyprinidés (27 espèces). La prédominance de ces deux familles reflète la situation dans l'ensemble de l'Europe, mais avec une importance relative inversée (236 espèces de cyprinidés et 98 espèces de salmonidés sont recensées à l'échelle de l'Europe)[2]. Particulièrement précieuses en matière de conservation, les 41 espèces endémiques inventoriées sont elles aussi majoritairement issues de la famille des salmonidés: il s'agit avant tout de différentes espèces de corégones (*Coregonus* spp) et d'ombles (*Salvelinus* spp) qui ont évolué localement après la fin de l'ère glaciaire. Parmi les espèces recensées, 31 sont considérées comme étrangères à la région dans quelques lacs au moins (déplacements à l'intérieur de la région d'Europe centrale) ou comme exotiques (introductions depuis l'Asie ou l'Amérique du Nord). Là encore, il s'agit principalement de salmonidés (onze espèces) et de cyprinidés (huit espèces). Les autres espèces inventoriées sont réparties entre 16 autres familles, dont sept sont représentées par une seule espèce. C'est le cas de la lotte (*Lota lota*), pour la famille des lotidés, ou du silure (*Silurus glanis*), pour la famille des siluridés. En comparant l'abondance des espèces révélée par le Projet Lac avec les données historiques, il apparaît que de nombreuses espèces sont devenues extrêmement rares dans les lacs étudiés et qu'une partie non négligeable d'entre elles n'a pas été observée lors des inventaires du Projet Lac.

Distribution de l'ichtyofaune à l'intérieur des lacs

La plupart des espèces ichtyologiques endémiques ont été recensées en eau libre ou dans la zone profonde des lacs à faible teneur en nutriments. Par contre, les captures les plus diversifiées ont été effectuées dans la zone littorale, peu profonde et près des rives du lac. La diversité des espèces en général (appelée aussi diversité alpha) et la diversité des espèces endémiques sont donc inversées entre ces deux habitats majeurs. Dans la zone littorale, c'est à l'embouchure des affluents que l'on a inventorié les plus grands nombres d'espèces. Différentes espèces mais aussi différentes cohortes d'âge d'une même espèce étaient associées à différents habitats littoraux, soulignant l'importance d'habitats littoraux bien structurés et proches de l'état naturel dans chaque lac. L'abondance et la biomasse de poissons les plus élevées ont également été constatées dans la zone littorale plus chaude et dans les habitats benthiques en eau peu profonde. La diminution de la biomasse avec la profondeur était plus progressive dans les lacs à faible teneur en nutriments, où des captures ont été effectuées jusque dans les très grandes profondeurs. Les lacs ayant une teneur très élevée en nutriments (suite à l'eutrophisation) étaient désertés au-delà de 30 m de profondeur en raison de l'absence complète d'oxygène durant la stratification estivale. Le réchauffement climatique exacerbe ces effets ou provoque des effets similaires dans certains lacs, comme le bassin inférieur du lac de Zurich, car l'élévation de la température des eaux de surface en hiver raccourcit la période durant laquelle le brassage vertical permet de recharger les eaux profondes en oxygène. D'autres lacs qui ont récemment surmonté des problèmes graves d'eutrophisation au siècle dernier ont perdu les espèces adaptées à la vie en eau profonde. Bien que leur zone pélagique soit redevenue habitable, elle reste faiblement peuplée.

Corégones et perches prédominants dans la majorité des lacs

Dans la plupart des grands lacs périalpins, les corégones (*Coregonus* spp) dominent la biomasse pisciaire, comme l'ont établi les prises au filet maillant, ce qui reflète leur probable importance dans le fonctionnement des écosystèmes lacustres. Si l'on compare les différents lacs, l'abondance et la biomasse des corégones tendent à être plus faibles et celles des perches (*Perca fluviatilis*), plus élevées dans les lacs à forte teneur en phosphore. Dans les lacs à faible teneur en nutriments, la biomasse plus élevée des corégones est plutôt due à des espèces de petite taille. Dans la plupart des lacs, les prises au filet maillant effectuées près du fond en eau peu profonde ont mis en évidence une prédominance des perches, suivies des gardons (*Rutilus* spp), des chevesnes (*Squalius* spp) et des rotengles (*Scardinius* spp). Les perches et les gardons sont abondants loin du littoral dans de nombreux petits lacs ainsi que dans plusieurs grands lacs, souvent en association avec des concentrations élevées en nutriments. Le lac Majeur fait exception, avec des eaux libres dominées par l'alose feinte (*Alosa agone*). Il en va de même des lacs alpins de Sils et de Poschiavo, où prédominent un omble étranger à la région (*Salvelinus umbla*), des truites natives ou introduites (*Salmo* spp) ainsi qu'une espèce exotique, la truite des lacs canadiens (*Salvelinus namaycush*).

Composition de l'ichtyofaune conditionnée par la biogéographie, l'isolement et la taille des lacs

La composition des espèces indigènes présentes dans chacun des lacs est étroitement corrélée à la situation géographique du lac, c'est-à-dire à son bassin hydrographique et à sa position par rapport aux Alpes (au nord ou au sud des Alpes centrales, en zone alpine, périalpine ou préalpine). Les lacs situés dans le bassin hydrographique d'un même cours d'eau, que ce soit le Rhin, le Rhône ou le Pô, présentent en général des peuplements ichtyologiques très similaires. Les différences observées parmi les bassins hydrographiques reflètent la connectivité de ceux-ci avec les différentes aires où les espèces se sont réfugiées durant les périodes glaciaires du Pléistocène. Les lacs périalpins du sud des Alpes situés dans le bassin hydrographique du Pô ont été recolonisés principalement par des espèces qui avaient trouvé refuge dans les zones de basse altitude du bassin hydrographique de la mer Adriatique. Les lacs périalpins du nord, quant à eux, ont été colonisés par des espèces aux origines multiples, ce qui reflète leur connexion avec les refuges de basse altitude qu'offraient les trois grands bassins hydrographiques concernés (Rhin, Rhône et Danube) durant l'ère glaciaire. Au total, onze genres sont représentés par différentes espèces indigènes du nord et du sud des Alpes. Ces espèces sont rarement proches génétiquement les unes des autres; en revanche, elles présentent des liens de parenté assez étroits avec des espèces établies ailleurs en Europe. Cela reflète des millions d'années d'évolution divergente de part et d'autre de la chaîne alpine, évolution probablement due à l'orogenèse des Alpes plutôt qu'aux cycles glaciaires du Pléistocène. Les lacs isolés géographiquement au cœur des Alpes (Sils et Poschiavo) abritaient peu d'espèces pisciaires indigènes, la plupart appartenant à des lignées adaptées à la vie en eau froide.

Beaucoup d'espèces endémiques ont été trouvées dans les grands lacs du bassin du Rhin, ce qui n'a pas été le cas dans le bassin du Rhône ni dans celui du Pô. Cela tient probablement au fait qu'un nombre élevé de lacs situés dans le bassin hydrographique du Rhin sont de grande taille et que les genres *Coregonus* et *Salvelinus* sont très répandus dans les lacs de ce bassin. Or, on sait que ces taxons ont étendu leur aire de répartition pour occuper des niches vacantes, évoluant pour former de nombreuses nouvelles espèces (espèces néoendémiques) après le retrait de la couverture glaciaire du Pléistocène. À l'inverse, c'est dans les lacs de l'espace périalpin méridional situés dans le bassin hydrographique du Pô que l'on a recensé le plus grand nombre d'espèces étrangères à la région ou exotiques.

Les grands lacs, qui sont généralement plus profonds, plus chauds et situés à des altitudes inférieures, en majorité dans les bassins du Rhin et du Pô, présentent une plus grande diversité ichtyologique. En effet, ils abritent une plus grande variété de niches écologiques, si bien que davantage d'espèces peuvent y coexister. Ils offrent également des conditions favorables à la spéciation, pour autant qu'ils soient suffisamment profonds pour fournir de vastes refuges en eau froide durant l'été, qu'ils soient oxygénés jusque dans leurs plus grandes profondeurs et qu'ils contiennent des espèces capables d'exploiter ces environnements extrêmes. Les grands lacs ont également l'avantage de pouvoir abriter des populations importantes de plusieurs espèces, ce qui réduit la probabilité que la stochasticité démographique ou les changements environnementaux ne conduisent à des extinctions locales (voire globales, s'agissant d'espèces endémiques). Enfin, les lacs situés dans les bassins du Rhin et du Pô font partie d'un réseau hydrographique plus vaste que les lacs situés dans les systèmes supérieurs du Rhône et du Danube, lesquels sont plus isolés. Cela permet la formation de vastes métacommunautés d'espèces et de populations pisciaires adaptées aux conditions locales, ce qui contribue à accroître le taux de colonisation et de persistance des espèces dans ces lacs. Conformément aux prévisions du modèle de la biogéographie insulaire, les corrélations observées entre espèces et surface sont faibles pour les espèces non natives, fortes pour les espèces natives et très fortes pour les espèces endémiques, ces résultats étant amplifiés si l'on prend en compte les extinctions documentées historiquement.

Autres facteurs naturels et anthropiques importants

La biogéographie, y compris insulaire, la morphologie des lacs et leur teneur en nutriments ne sont pas les seuls aspects ayant une influence majeure sur les peuplements ichtyologiques. L'étude a également mis en évidence l'action de facteurs comme la température, les espèces étrangères à la région ou exotiques, la connectivité entre les cours d'eau et la gestion de la pêche. Les cycles saisonniers de la température de l'eau provoquent des changements dans la distribution verticale et horizontale de l'ichtyofaune tout au long de l'année. Le réchauffement de l'eau en surface dû aux changements climatiques freine le brassage vertical de certains lacs, causant ou exacerbant un déficit en oxygène des eaux profondes, ralentissant la remontée des nutriments et contribuant à la prolifération de phytoplancton non appétent ou indigeste pour le zooplancton. Ce phénomène a un impact sur les communautés ichtyologiques car il réduit le volume habitable du lac, limite les refuges en eau froide disponibles l'été et modifie la disponibilité des proies.

Les espèces étrangères à la région et exotiques peuvent entrer en concurrence avec les espèces indigènes, ces dernières subissant parfois une forte prédation. Les poissons non natifs sont également susceptibles de s'hybrider avec des espèces natives parentes, ce qui peut aplanir les différences génétiques et écologiques entre les espèces. De ce fait, il est possible qu'une introduction se produise sans être détectée, entraînant l'éviction cryptique d'une espèce par une autre espèce ou par l'installation d'une population hybride. Les espèces étrangères à la région ou exotiques particulièrement communes recensées dans les lacs étudiés étaient la grémille (*Gymnocephalus cernua*) et la perche soleil (*Lepomis gibbosus*) ainsi que le gardon (*Rutilus rutilus*) ainsi que plusieurs espèces de corégones (*Coregonus* spp) pour ce qui concerne les lacs périalpins méridionaux.

Des invertébrés non indigènes abondants comme la moule zébrée (*Dreissena polymorpha*), la moule quagga (*Dreissena bugensis*) et le corbicule asiatique (*Corbicula fluminea*) modifient le fond de beaucoup de lacs sur de vastes étendues, ce qui se répercute sur l'habitat des poissons et de leurs proies. Cela peut altérer le réseau trophique et avoir des conséquences importantes, mais largement inconnues, pour les poissons indigènes et non indigènes.

La pêche commerciale pratique une sélection selon la taille: en prélevant les individus les plus gros de l'espèce cible, elle influe de manière directe ou indirecte sur la composition des populations non seulement des espèces cibles, mais aussi des autres espèces au sein de l'écosystème lacustre. Lorsqu'elle est intensive et prélève la plupart des individus de grande taille des espèces cibles, la pêche peut atténuer l'effet de régulation de la prédation exercée par ces espèces sur les organismes qu'elles consomment, favoriser la croissance des effectifs d'espèces concurrentes ou encore modifier la distribution spatiale de celles-ci. La pêche intensive peut ainsi entraîner un changement dans la croissance et dans des traits de l'histoire de vie de la population cible, avec des répercussions probables sur l'interaction et la coexistence entre les espèces.

Enfin, l'état des cours d'eau environnants, leur connectivité longitudinale et leurs connexions avec les lacs influent également sur les communautés pisciaires lacustres. Certaines espèces lacustres utilisent les cours d'eau comme habitat de frai ou comme voies de migration vers les zones de frai. D'autres espèces de poissons fraient dans les lits de gravier en eau profonde constitués ou entretenus par les affluents. La canalisation et l'endiguement des cours d'eau ainsi que l'altération de leur embouchure ont donc des conséquences négatives pour les peuplements pisciaires lacustres.

Recommandations concernant la conservation et la diversité de l'ichtyofaune lacustre

Face aux menaces multiples qui pèsent sur la diversité de l'ichtyofaune lacustre et aux nombreuses activités humaines qui modifient les peuplements pisciaires, les gestionnaires ont un défi de taille à relever: il leur faut atténuer ces menaces et ces changements tout en permettant une exploitation durable des lacs et de leur ichtyofaune. L'analyse des données collectées pour le Projet Lac dans le contexte d'autres études a conduit à formuler plusieurs recommandations concernant la gestion de la diversité ichtyologique des lacs. C'est dans la renaturation d'éléments clés de l'écosystème lacustre (p. ex. habitats littoraux et pélagiques, qualité de l'eau, nutriments) que résident les meilleures chances de protéger et de renforcer les espèces de poissons indigènes. Pour monitorer, gérer et conserver la biodiversité ichtyologique, il faut la documenter correctement et comprendre la diversité, l'écologie et la distribution des espèces, la taxonomie, l'évolution ainsi que la diversité intraspécifique. La description taxonomique des espèces non encore décrites est importante pour la gestion et la conservation ; elle est également nécessaire pour que ces espèces soient reconnues et que le public prenne conscience de leur existence et de leur valeur. Toutes ces données, après validation par la communauté scientifique, sont à intégrer dans la législation sous la forme de bases légales régissant la conservation et la protection des espèces. Elles doivent également servir de fondement à des mesures visant à éviter que des poissons soient introduits en dehors de leur aire de répartition d'origine. Il est indispensable en outre de comprendre et de gérer de manière appropriée l'impact direct des activités humaines sur l'écologie et la génétique des peuplements pisciaires (diminution de la qualité de l'eau, pêche et repeuplements non durables). Enfin, il est essentiel de mettre en place un monitorage continu utilisant des méthodes quantitatives standardisées combinées à des évaluations objectives et informatives basées sur des données écologiques, taxonomiques et génétiques afin de pratiquer une gestion adaptative de ces précieuses ressources naturelles qui se fonde sur des informations probantes.

1. Riassunto

Comunità ittiche uniche dei laghi perialpini

I laghi profondi e di grandi dimensioni che circondano le Alpi costituiscono un ecosistema unico, raro in Europa e geograficamente isolato da altri ecosistemi simili. Le comunità ittiche di questi laghi perialpini sono particolarmente variegate in Svizzera, dato che il Paese racchiude le acque di quattro grandi bacini fluviali, Reno, Rodano, Po e Danubio, appartenenti a tre diverse ecoregioni d'acqua dolce europee [1]. Molte delle specie che vivono in questi laghi sono adattate alle acque fredde, endemiche e caratterizzate da un areale molto limitato, poiché vivono solamente in un lago o in laghi limitrofi dall'origine geologica comune dove si sono evolute dopo il ritiro delle calotte glaciali del Pleistocene. Nonostante la distribuzione limitata, molte di queste specie sono tra le più abbondanti nei rispettivi laghi e sono importanti per la pesca commerciale e sportiva. Allo stesso tempo, la loro conservazione è di interesse globale e sono molto vulnerabili alle perturbazioni di origine antropica. I pesci dei laghi perialpini sono quindi risorse naturali importanti per la conservazione della biodiversità, il funzionamento dell'ecosistema e le attività umane.

Perché è necessario un campionamento standardizzato?

Sull'arco di secoli, la ricerca scientifica e le attente osservazioni di pescatori, naturalisti e utenti hanno costituito un ricco bagaglio di conoscenze riguardo le comunità ittiche dei laghi perialpini. Tuttavia tali osservazioni e progetti di ricerca si focalizzavano generalmente su uno o pochi laghi o ambienti lacustri, oppure su una o poche specie ittiche. Inoltre, raramente i dati erano stati analizzati in un contesto ecologico o biogeografico più ampio. Ad esempio, le statistiche sul numero e sul tipo di pesci pescati da pescatori sono disponibili per tutti i grandi laghi, con alcune serie di dati che risalgono a secoli fa. Le prime statistiche sistematiche sulla pesca commerciale riferite a interi laghi risalgono al 1900 circa e concernono i laghi Lemano e Bodanico. Le analisi di queste statistiche forniscono conoscenze preziose su come i laghi e la pesca siano cambiati durante il secolo scorso. Tuttavia, le statistiche sulla pesca si riferiscono solo a un piccolo sottoinsieme di specie ittiche e in esse vengono rappresentati soltanto gli individui più grandi, fornendo così una prospettiva limitata e potenzialmente distorta di una determinata popolazione. Una gestione e una conservazione consapevoli delle comunità ittiche lacustri richiedono una descrizione accurata dello stato attuale della diversità ittica nella regione, incluso un inventario preciso delle specie e delle popolazioni come pure della loro abbondanza relativa tra e all'interno dei laghi.

L'obiettivo di Projet Lac

L'obiettivo di Projet Lac era di fornire queste informazioni mancanti tramite un'indagine quantitativa delle comunità ittiche dei laghi che circondano le Alpi utilizzando diversi metodi di campionamento standardizzati in combinazione con una tassonomia dei pesci aggiornata, strumenti di identificazione moderni e le conoscenze più recenti sulla delimitazione delle specie. Il campionamento di tutte le parti di ogni lago ha permesso di descrivere la distribuzione dei pesci al momento dell'indagine (fine estate – inizio autunno), il che fornisce informazioni sul funzionamento ecologico del lago. L'impiego degli stessi protocolli di campionamento ha consentito di confrontare tra loro le comunità ittiche di diversi laghi. La documentazione precisa dei metodi di campionamento permette di ripetere le indagini in futuro. Nonostante le condizioni dei laghi siano già molto diverse da quelle che si presentavano prima dei principali impatti antropici, questa prima serie di indagini quantitative fornisce lo uno stato di riferimento. Esso potrà essere utilizzato in futuro per confrontare i dati al fine di determinare il modo in cui le comunità ittiche continuano a rispondere alle mutate condizioni ambientali, come i cambiamenti climatici, o alle azioni di rinaturazione degli ambienti, come per esempio le rive dei laghi.

Una diversità appena scoperta e riscoperta

Nell'ambito del Projet Lac sono stati studiati 35 laghi in Svizzera, Italia, Francia, Germania e Austria (negli ultimi due Paesi solo il lago Bodanico) e rilevate 106 specie di pesci. Con quasi il 20 per cento di tutte le specie ittiche conosciute in Europa (525 specie [2]), la Svizzera, il cui territorio rappresenta circa lo 0,4 per cento della superficie terrestre europea, è uno dei Paesi con le più alte densità di ricchezza di specie ittiche in Europa. I campioni del progetto hanno costituito la base per documentare quindici taxa fenotipicamente e/o geneticamente distinti mai documentati in precedenza, la maggior parte dei quali endemici. Inoltre, il progetto ha rivelato la presenza di cinque specie ittiche descritte ma che non si sapeva fossero diffuse in Svizzera e di due specie a nord delle Alpi che in precedenza erano conosciute solo a sud delle Alpi. Il campionamento completo dei laghi ha inoltre evidenziato quattro taxa di pesci endemici che si credevano estinti, compreso il salmerino nano del lago di Costanza (Salvelinus profundus).

Un numero eccezionalmente alto di specie ittiche endemiche

La maggior parte delle specie ittiche indigene appartiene alla famiglia dei salmonidi (*Salmonidae* incluse le *Coreginae*; 44 specie), seguita dai ciprinidi (*Cyprinidae*; 27 specie). La prevalenza di queste due famiglie rispecchia la situazione generale dell'Europa, anche se la ricchezza relativa delle due specie è invertita (in Europa ci sono 236 specie di ciprinidi e 98 di salmonidi)[2]. Anche le 41 specie endemiche, particolarmente preziose dal punto di vista della conservazione, appartengono alla famiglia dei salmonidi: si tratta principalmente di diverse specie di coregoni (*Coregonus* spp.) e salmerini (*Salvelinus* spp.) che si sono evolute localmente dopo la fine dell'era glaciale. Sono state recensite 31 specie estranee alla regione, perlomeno in alcuni laghi (spostate all'interno dell'Europa centrale), o esotiche (introdotte dall'Asia o dal Nord America). Anch'esse provengono principalmente dalle famiglie dei salmonidi (11 specie) e dei ciprinidi (8 specie). Le rimanenti specie recensite appartengono a 16 famiglie, sette di cui rappresentate da una sola specie, ad esempio la bottatrice (*Lota lota*), della famiglia delle lotidae, e il siluro (*Silurus glanis*), della famiglia delle *Siluridae*. Le distribuzioni dell'abbondanza di molte specie relative a numerosi laghi e il confronto dei dati raccolti da Projet Lac con altri dati pubblicati hanno rivelato che molte specie sono estremamente rare nei laghi perialpini e che una quota significativa di tali specie non sono state riscontrate nel corso delle indagini di Projet Lac.

La distribuzione dei pesci nei laghi

La maggior parte delle specie ittiche endemiche sono state rilevate in habitat pelagici o bentonici profondi di laghi a basso contenuto di nutrienti. D'altro lato, il maggior numero di specie ittiche è stato generalmente catturato nella zona litorale poco profonda vicino alle rive dei laghi. La ricchezza complessiva delle specie (conosciuta anche come diversità alfa) e delle specie endemiche erano quindi invertite tra questi principali habitat all'interno di un lago. Tra gli habitat litorali, il maggior numero di specie è stato registrato nelle insenature di torrenti e fiumi. Diverse specie, ma anche individui della stessa specie a diversi stadi di sviluppo, sono stati associati ad habitat litorali diversi, sottolineando l'importanza di una gamma diversificata di habitat litorali prossimi al naturale in ogni lago.

Anche la maggior abbondanza e biomassa ittica sono state rilevate nella zona litorale, più calda, e negli habitat bentonici poco profondi. La diminuzione della biomassa ittica nelle parti più profonde dei laghi è stata più graduale nei laghi a basso contenuto di nutrienti, dove sono stati catturati pesci anche nelle zone più profonde. I laghi con tenori di nutrienti molto elevati erano di fatto privi di pesci al di sotto dei 30 metri di profondità a causa della completa assenza di ossigeno durante la stratificazione estiva. Il riscaldamento climatico sta aggravando o causando effetti simili in alcuni laghi, come quello di Zurigo, poiché le acque superficiali invernali più calde accorciano il periodo in cui un mescolamento verticale può rifornire d'ossigeno le acque profonde. Altri laghi, recentemente ripresisi da gravi problemi legati all'elevata presenza di nutrienti che li hanno caratterizzati nel secolo scorso, hanno perso le specie adattate a vivere nelle acque profonde. La conseguenza è che oggi le parti profonde di questi laghi sono solo scarsamente popolate da pesci, nonostante siano nuovamente in grado di ospitarli.

Nella maggior parte dei laghi dominano le specie di coregone e il pesce persico

Come si è potuto constatare dall'utilizzo di reti da posta, le specie di coregone (*Coregonus* spp.) dominano la biomassa ittica dell'intero lago nella maggior parte dei grandi laghi perialpini: questo rispecchia la loro probabile importanza per il funzionamento degli ecosistemi lacustri. Se si confrontano laghi diversi, in quelli con concentrazioni di fosforo più elevate l'abbondanza e la biomassa di coregoni tendono a essere più basse, mentre quelle del persico (*Perca fluviatilis*) più elevate. La biomassa di coregone è più elevata nei laghi a basso contenuto di nutrienti e tende a essere per lo più costituita da specie di coregone più piccole. Nelle catture con reti da posta effettuate nelle acque litorali poco profonde della maggior parte dei laghi sono risultati dominanti il pesce persico, il gardon (*Rutilus* spp.), il cavedano (*Squalius* spp.) e la scardola (*Scardinius* spp.). Il persico e il gardon sono risultati abbondanti nelle acque lontane dalle sponde di molti laghi di piccole dimensioni come pure in diversi laghi più grandi. La loro abbondanza è spesso correlata a elevate concentrazioni di nutrienti. Costituiscono un'eccezione il Lago Maggiore, dove nelle acque libere domina l'agone (*Alosa agone*), e i laghi alpini (laghi di Sils e di Poschiavo), dove prevalgono il *Salvelinus umbla*, estraneo alla regione, come pure le specie di trota indigene o introdotte (*salmo* spp.) e la trota canadese (*Salvelinus namaycush*) una specie esotica proveniente dal Canada. La composizione delle specie ittiche lacustri è influenzata da biogeografia, isolamento e dimensioni del lago.

L'insieme delle specie indigene presenti in ogni lago è strettamente correlato alla sua posizione geografica, in particolare al bacino fluviale cui il lago appartiene e alla posizione del lago in relazione alle Alpi (nord o sud delle Alpi centrali; lago alpino, perialpino o prealpino). Le comunità ittiche indigene sono, in generale, più simili tra i laghi appartenenti ai principali bacini fluviali: Reno, Rodano e Po. Le differenze tra i bacini rispecchiano la loro connettività ai diversi refugia glaciali del Pleistocene, dove le specie sono sopravvissute alle ere glaciali. I laghi perialpini a sud delle Alpi appartenenti al bacino idografico del Po sono stati generalmente ricolonizzati da specie ittiche rifugiatesi sui rilievi più bassi del bacino del mare Adriatico. I laghi perialpini a nord delle Alpi sono stati colonizzati da specie di origini diverse, il che rispecchia i loro legami con i refugia glaciali di pianura dei tre principali bacini fluviali (Reno, Rodano e Danubio). Undici generi sono rappresentati da diverse specie originarie dei versanti a nord e a sud delle Alpi. Solo in rari casi tali generi erano strettamente imparentati: piuttosto, i loro parenti più vicini si trovavano spesso altrove in Europa. Questo è dovuto a milioni di anni di evoluzione divergente sui due versanti della catena montuosa iniziata probabilmente con l'orogenesi delle Alpi e non con i cicli glaciali del pleistocene. I laghi geograficamente isolati delle Alpi (laghi di Sils e di Poschiavo) contengono poche specie ittiche indigene, la maggior parte delle quali appartiene a linee evolutive adattatesi alla vita in acque fredde.

Molte specie endemiche sono state rinvenute nei grandi laghi appartenenti al bacino fluviale del Reno; poche sono state invece quelle catturate nei bacini del Rodano e del Po. Questo fatto è probabilmente dovuto alle grandi dimensioni di molti laghi nel bacino fluviale del Reno come pure alla presenza dei generi *Coregonus* e *Salvelinus* nei laghi di questo bacino. Questi taxa sono infatti noti per essersi diffusi in nicchie vacanti ed evoluti in molte nuove specie (neoendemiche) dopo il ritiro dei ghiacciai del Pleistocene. D'altro canto, il numero più elevato di specie estranee alla regione o esotiche è stato rilevato nei laghi perialpini a sud delle Alpi appartenenti al bacino del Po.

I laghi di dimensioni maggiori, tendenzialmente più profondi, più caldi e situati ad altitudini inferiori e prevalentemente nei bacini del Reno e del Po, supportano un maggior numero di specie ittiche. I laghi più grandi forniscono una maggior varietà di nicchie ecologiche, il che permette la coesistenza di un maggior numero di specie e rende possibile la speciazione ecologica, a condizione che i laghi siano abbastanza profondi da permettere l'esistenza di grandi refugia estivi con acque fredde, che siano ossigenati fino al fondale e che contengano linee evolutive di pesci che possano sfruttare ambienti così estremi. Inoltre, i laghi più grandi ospitano popolazioni più grandi della maggior parte delle specie, il che significa che c'è una minor possibilità che la stocasticità demografica o le fluttuazioni ambientali ne causino l'estinzione locale (o, nel caso di specie endemiche, globale). Infine, i laghi nel bacino del Reno e in quello del Po fanno parte di una rete più ampia di laghi e fiumi rispetto ai laghi nei bacini del Reno superiore e del Danubio, che sono più isolati. Questo risulta in metacomunità di specie ittiche adattatesi ai laghi e di popolazioni più grandi, che contribuiscono a una colonizzazione più frequente e a una persistenza in questi laghi. In linea con le previsioni della biogeografia insulare, le relazioni tra specie e area sono deboli per le specie esotiche, più forti per le specie indigene e ancora più strette per le specie endemiche. Se si considerano le specie estinte storicamente documentate, tali relazioni sono ancora più marcate.

Altri fattori naturali e antropogenici importanti

Oltre alla biogeografia, la biogeografia insulare, la morfologia del lago e i nutrienti, ci sono altri fattori importanti che hanno un impatto sulle comunità ittiche, tra i quali la temperatura, le specie esotiche, la connettività con i corsi d'acqua e la gestione della pesca. I cicli stagionali della temperatura dell'acqua provocano cambiamenti nella profondità in cui si trovano i pesci e nella loro distribuzione spaziale durante l'anno. Il riscaldamento delle acque superficiali, quale conseguenza del riscaldamento climatico, indebolisce i processi di mescolamento verticale di alcuni laghi, causando o acutizzando le carenze di ossigeno in profondità, indebolendo il trasporto verso l'alto dei nutrienti e contribuendo alla proliferazione del fitoplancton, che è poco appetibile o digeribile per lo zooplancton. Questo influisce sulle comunità ittiche riducendo il volume abitabile del lago, limitando la disponibilità di rifugi d'acqua fredda durante l'estate e modificando la disponibilità di prede.

Le specie ittiche estranee alla regione o esotiche competono con le specie indigene e le predano. La loro presenza può anche dar luogo a fenomeni di ibridazione con specie indigene imparentate, il che può ridurre le differenze genetiche ed ecologiche tra le specie. In tale contesto, un'introduzione può passare inosservata, con conseguente rimozione criptica di una specie da parte di un'altra specie o la creazione di una popolazione ibrida. Alcune specie esotiche o estranee alla regione particolarmente comuni nei laghi campionati sono l'acerina (*Gymnocephalus cernua*), il persico sole (*Lepomis gibbosus*) come pure il gardon (*Rutilus rutilus*) e diverse specie di coregone (*Coregonus*) nei laghi perialpini a sud delle Alpi. Grandi quantità di invertebrati esotici, come la cozza zebrata (*Dreissena polymorpha*), la Dreissena bugensis e la vongola asiatica (*Corbicula fluminea*) modificano vaste aree del fondale di molti laghi, modificando l'habitat dei pesci e delle loro prede. Questo può alterare la rete alimentare del lago, con probabili conseguenze importanti – ma per lo più sconosciute – per i pesci indigeni e non indigeni.

La pesca commerciale è selettiva in base alle dimensioni del pesce e quindi modifica la composizione delle popolazioni ittiche in funzione della taglia, rimuovendo gli individui più grandi delle specie sfruttate dalla pesca. Questo può avere diversi effetti diretti e indiretti non solo sulla specie bersaglio, ma anche sulle altre specie dell'ecosistema lacustre. La pesca intensiva, che comporta la cattura della maggior parte degli individui di grandi dimensioni delle specie bersaglio, può ridurre l'effetto di controllo della pressione predatoria sugli organismi predati da dette specie e/o favorire la crescita della popolazione o i cambiamenti nella distribuzione spaziale di specie in competizione. La pesca intensiva può anche provocare un cambiamento evolutivo delle caratteristiche di crescita e dell'ontogenia nella popolazione sfruttata dalla pesca, con possibili conseguenze sulle interazioni e sulla coesistenza delle specie.

Infine, anche le condizioni dei corsi d'acqua circostanti, la loro connettività longitudinale e la connessione ai laghi hanno un impatto sulle comunità ittiche. Per molte specie lacustri, i fiumi costituiscono gli habitat in cui deporre le uova o fungono da passaggi per le migrazioni verso i siti di riproduzione. Altre specie ittiche depongono le uova nelle acque profonde dei laghi, sui letti di ghiaia, che sono formati e mantenuti dagli affluenti. La canalizzazione e lo sbarramento dei fiumi come pure le alterazioni dei delta fluviali hanno quindi conseguenze negative per le comunità ittiche lacustri.

Raccomandazioni per la conservazione della diversità ittica lacustre

A fronte delle numerose minacce alla diversità ittica lacustre e alle molte attività antropiche che modificano la comunità ittica, i gestori devono affrontare la difficile sfida di mitigare tali minacce e cambiamenti, pur permettendo l'utilizzo sostenibile dei laghi e dei pesci lacustri. Le analisi dei dati raccolti da Projet Lac nel contesto di altre ricerche portano alla formulazione di diverse raccomandazioni per la gestione della diversità ittica lacustre. Il migliore approccio per proteggere e favorire le specie ittiche indigene consiste nel ripristinare le condizioni prossime allo stato naturale degli aspetti chiave dell'ecosistema lacustre (p.es. habitat litorali e di profondità, qualità delle acque, nutrienti) e della rete che connette laghi e corsi d'acqua. La biodiversità ittica può essere monitorata, gestita e mantenuta in modo efficace solo se viene documentata e compresa a fondo in termini di diversità delle specie, ecologia e distribuzione, tassonomia, relazioni evolutive e diversità all'interno delle singole specie. La descrizione tassonomica di specie ittiche mai descritte in precedenza è importante per la gestione e la conservazione, ed è necessaria per il riconoscimento e la consapevolezza dell'esistenza di dette specie da parte del pubblico. Una volta riconosciute dalla comunità scientifica, queste informazioni devono essere incluse nella legislazione e fungere da base legale per la conservazione e la protezione delle specie e per prevenire lo spostamento di pesci fuori del loro areale d'origine. Per una corretta gestione è anche importante comprendere gli effetti ecologici e genetici delle attività antropiche che influiscono direttamente sulle popolazioni ittiche, come la riduzione della qualità delle acque o la pesca e il ripopolamento non sostenibili. Infine, il monitoraggio continuo con metodi quantitativi standardizzati, combinato con valutazioni obiettive e informative basate su informazioni ecologiche, tassonomiche e genetiche, fornisce una base importante per una gestione adattativa fondata su prove concrete di queste preziose risorse naturali.

1. Summary

Unique fish communities of the perialpine lakes

The large and deep lakes around the European Alps are a unique ecosystem, rare throughout Europe and geographically isolated from other similar ecosystems. The fish communities of these perialpine lakes are particularly diverse in Switzerland as the country contains the waters of four major river catchments: Rhine, Rhone, Po and Danube, belonging to three different Freshwater Ecoregions of Europe [1]. Many species in these lakes are cold-adapted, endemic species with very small ranges, living only in one lake or in neighbouring lakes of shared geological origin, where they evolved after the retreat of the Pleistocene ice sheets. Despite their narrow distributions, many of these species are among the most abundant in their respective lakes and are important for commercial and recreational fisheries. At the same time, they are of global conservation concern and are very vulnerable to anthropogenic perturbation. The fish of the perialpine lakes therefore represent important natural assets for biodiversity conservation, ecosystem functioning and human use.

Why do we need standardised sampling?

A wealth of knowledge on the perialpine lake fish communities has been accumulated over centuries of observations of attentive fishers, naturalists, lake users and through scientific research. However, these observations and research projects were usually focussed on only one or few lakes, on one or few lake habitats, or on one or few fish species, and the data have rarely been analysed in the wider ecological or biogeographical context. For example, statistics on the number and type of fish caught by fishers are available for all large lakes, with some datasets dating back centuries. The earliest consistently collected whole-lake statistics on commercial fish catches begin around 1900, from lakes Geneva and Constance. Analyses of these statistics provide valuable insights into how lakes and fisheries have changed over the past century. However, fisheries statistics relate only to a small subset of fish species in a lake, and only large individuals of those species are represented, hence providing a narrow and potentially biased perspective on a fish assemblage. Informed management and conservation of lake fish communities requires a thorough description of the current state of fish diversity across the region, including an accurate inventory of the species and distinct populations, along with their relative abundances among and within lakes.

Aims of Projet Lac

The aim of Projet Lac was to provide this missing information by quantitatively surveying whole-lake fish communities in the lakes around the Alps using multiple, standardised sampling methods, combined with up-to-date fish taxonomy, modern identification tools, and latest understanding of species delimitation. Sampling all parts of each lake allowed description of the distribution of fishes at the time of the survey (late summer – early autumn), which provides information on the ecological functioning of a lake. The use of the same fish-sampling protocols in every lake meant that fish communities could be compared among lakes. Accurate documentation of the sampling methods means that the surveys can be repeated in the future. Although the condition of the lakes is already far from that of prior to major human impacts, this first round of quantitative surveys also provides a reference state against which future data can be compared to determine how the fish communities continue to respond to changing environmental conditions, such as climate change, or management actions, such as renaturalisation of the lakeshores.

Newly discovered and rediscovered diversity

Through the course of Projet Lac, 35 lakes were investigated across Switzerland, Italy, France, Germany and Austria (only Lake Constance in the latter two countries), with over 106 fish species recorded. With nearly 20% of all known fish species of Europe (525 species [2]), this makes Switzerland, representing around 0.4% of the European land area by surface, one of the regions with the highest densities of fish species richness in Europe. Samples from the project formed the basis for documenting fifteen previously undocumented phenotypically and/or genetically distinct taxa, most of which are endemic. The project also revealed the presence of five described fish species that were not known to occur in Switzerland and two species north of the Alps that were previously only known from south of the Alps. Whole-lake sampling further recovered four endemic fish taxa, which were previously believed to be extinct, including the profundal char (*Salvelinus profundus*) of Lake Constance.

Extraordinary high numbers of endemic fish species

The majority of recorded native fish species belonged to the family of salmon-like fish (Salmonidae inclusive of Coregoninae; 44 species), followed by the family of carp-like fish (Cyprinidae; 27 species). The dominance of these two families mirrors the situation in Europe at large, however the relative richness of the two is inverted (236 species of cyprinids and 98 of salmonids across Europe) [2]. Particularly valuable to conservation, the 41 endemic species were also mostly from the family Salmonidae, primarily different species of whitefish (*Coregonus* spp) and lake char (*Salvelinus* spp) that have evolved locally after the end of the ice age. Thirty-one fish species were recorded as non-native in at least some lakes (moved around within the central European region) or exotic (introduced from Asia or North America). These too were mostly from the salmon-like (11 species) and carp-like (8 species) families. The remaining recorded species were distributed among 16 other families, with seven of these represented by a single species e.g. burbot (*Lota lota*) of the family Lotidae and catfish (*Silurus glanis*) of the family Siluridae. The species-abundance distributions for many lakes and the comparison of Projet Lac data with other published records revealed that many species in these lakes are extremely rare, a significant fraction of which were not encountered in the Projet Lac surveys.

Distribution of fishes within the lakes

Most endemic fish species were recorded either in the open-water or deep-water habitats of the low nutrient lakes. On the other hand, the highest numbers of fish species were generally caught in the shallow littoral zone close to the lakeshore. Overall species richness (also known as alpha diversity) and endemic species richness were thus inverted between these major habitats within a lake. Among the littoral habitats, the highest numbers of species were recorded in the inlets of streams and rivers. Different species, but also different life-stages of the same species, were associated with different littoral habitats, emphasising the importance of a diverse range of littoral habitats close to their natural condition in each lake.

The highest abundance and biomass of fish were also caught in the warmer littoral zone and in shallow benthic habitats. The decreasing fish biomass into the deeper parts of the lakes was more gradual in low-nutrient lakes, with fish even caught in the deepest parts of these lakes. Lakes with very high nutrients were effectively devoid of fish below 30 m depth due to the complete absence of oxygen during summer stratification. Climate warming is exacerbating or causing similar effects in some lakes, such as lower Lake Zurich, as warmer winter surface waters shorten the period over which vertical mixing can replenish deep-water oxygen. Other lakes that have recently recovered from severe nutrient problems in the past century have lost the species adapted to living in the deep-lake habitats. The consequence is that the deep parts of these lakes are today only sparsely populated by fish, despite this zone again being habitable.

Whitefish species and perch dominated most lakes

Whitefish species (*Coregonus* spp) dominated the whole-lake fish biomass, as assessed by gillnetting, in most large perialpine lakes, reflecting their likely importance to the functioning of the lake ecosystems. Comparing among lakes, the abundance and biomass of whitefish tended to be lower, and that of perch (*Perca fluviatilis*) higher, in lakes with higher phosphorus concentrations. The higher whitefish biomass in low nutrient lakes tended to be mostly contributed by smaller whitefish species. Perch dominated gillnet catches in the shallow parts of most lakes close to the lake floor, along with the cyprinids roach (*Rutilus* spp), chub (*Squalius* spp) and rudd (*Scardinius* spp). Perch and roach were abundant in the offshore waters of many smaller lakes, as well as in in several larger lakes, often associated with higher nutrient concentrations. Exceptions were Lake Maggiore, where the open water was dominated by the freshwater clupeid agone (*Alosa agone*) and the Alpine lakes, Sils and Poschiavo, which were dominated by non-native lake char (*Salvelinus umbla*), native and introduced trout (*Salmo* spp) and exotic Canadian lake trout (*Salvelinus namaycush*).

Lake fish species composition shaped by biogeography, isolation and lake size

The set of native species occurring in each lake was closely associated with the geographic position of the lake, namely the river catchment to which the lake belonged and the position of the lake relative to the Alps (north or south of the central Alps; alpine, perialpine or pre-alpine). Native fish communities were generally most similar among lakes within the same major river catchments: Rhine, Rhone, Po. Differences between the catchments reflected their connectivity to the different Pleistocene refugial areas where species survived the ice ages. The southern perialpine lakes in the Po river catchment were mostly recolonised by fish that had taken refuge in the lower elevations of the Adriatic Sea catchment. The northern perialpine lakes were colonized by species from multiple origins, reflecting their links to the lowland, ice-age refuges of the three major river catchments (Rhine, Rhone and Danube). Eleven genera were represented by different species native to the northern and southern sides of the Alps. These were rarely each other's closest relatives, rather each having closer relatives elsewhere in Europe, reflecting millions of years of divergent evolution on either sides of the mountain chain, initiated probably by the orogenesis of the Alps rather than by the Pleistocene glacial cycles. The geographically isolated lakes within the Alps (Sils and Poschiavo) contained few native fish species, most of them belonging to lineages adapted to living in cold water.

Many endemic species were found in the large lakes of the Rhine catchment but only few in each of the Rhone and Po catchments. This is likely due to the large size of many lakes in the Rhine catchment, as well as the widespread occurrence of the genera *Coregonus* and *Salvelinus* among the Rhine catchment lakes, taxa known to have radiated into vacant niches evolving many new species (neoendemics) after the retreat of the Pleistocene glaciers. On the other hand, the highest numbers of non-native and exotic species were recorded in the southern perialpine lakes of the Po catchment.

Larger lakes, which also tended to be deeper, warmer, at lower altitude and mostly in the Rhine and Po catchments, supported more fish species. Larger lakes provide a greater variety of ecological niches, allowing coexistence of a greater number of species, and also provide opportunity for ecological speciation, provided the lakes are deep enough for the existence of large cold water summer refugia, are oxygenated down to the greatest depth, and have lineages of fish that can make use of such extreme environments. Larger lakes also allow larger populations of most species, meaning a lower chance that demographic stochasticity or environmental fluctuations result in their local (and sometimes global when species are endemic) extinction. Finally, the lakes in the Rhine and Po catchments are part of larger networks of lakes and rivers, compared to the lakes in the upper Rhone and Danube systems, which are more isolated. This allows for larger metacommunities of lake-adapted fish species and populations, which will also contribute to more frequent colonization and persistence in these lakes. Consistent with predictions of island biogeography, species-area-relationships were shallow for non-native species, steeper for native species, and steepest for endemic species, and taking historically documented extinctions into account further steepened them.

Other important natural and anthropogenic factors

In addition to biogeography, island biogeography, lake morphology and nutrients, other major factors influencing lake fish communities included temperature, non-native species, river connectivity and fisheries management. Seasonal cycles in water temperature drive changes in the depth and spatial distribution of fishes throughout the year. Warming surface waters resulting from climate change are weakening vertical mixing in some lakes, causing or exacerbating deep-water oxygen deficiencies, weakening upward nutrient transport and contributing to the proliferation of phytoplankton that is unpalatable or indigestible for zooplankton. This influences fish communities by reducing the lake's habitable volume, the limiting availability of summer coldwater refuges and changing the availability of prey.

Non-native and exotic fish species compete with and predate upon native species. Non-native fishes can also hybridise with related native species, potentially eroding genetic and ecological differences between the species. This can cause an introduction to go undetected, resulting in cryptic displacement of one species by another species or by a hybrid population. Particularly common exotic or non-native species among the sampled lakes were Eurasian ruffe (*Gymnocephalus cernua*) and pumpkinseed (*Lepomis gibbosus*), as well as common roach (*Rutilus rutilus*) and several species of whitefish (*Coregonus* spp) in the southern perialpine lakes. Abundant non-native invertebrates such as the zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*) and Asian clam (*Corbicula fluminea*) modify large areas of the lake floor in many lakes, changing the habitat of fish and their prey. This can alter the lake food web, with likely important, but mostly unknown, consequences for native and non-native fishes.

Commercial fishing is size-selective and therefore shapes the size composition of fish populations by selectively removing the larger individuals of targeted species. This can have a wide variety of direct and indirect effects not only on the population of the target species, but also on the other species in the lake ecosystem. Intense fishing, resulting in removal of most large individuals of the target species, can reduce the controlling effect of predation pressure on organisms consumed by the target fish species and/or promote population growth or changes in the spatial distribution of competing species. Intense fishing can also lead to evolutionary change of growth and life history traits in the target population and this may have consequences for species interactions and coexistence.

Finally, the condition of surrounding rivers, their longitudinal connectivity and connections to lakes also influences lake fish communities. Many lake species use the rivers as spawning habitat or as migration passages to spawning grounds. Other fish species spawn in the lakes in deep water gravel beds delivered or maintained by inflowing rivers. Channelization and damming of rivers, as well as modification of river deltas, therefore also has negative consequences for lake fish communities.

Recommendations for conservation of lake fish diversity

In the face of the many threats to lake fish diversity and the many human activities modifying the fish community, managers face the difficult challenge of mitigating these threats and changes, while allowing the sustainable human use of the lakes and lake fish. Analyses of the Projet Lac dataset, in the context of other research, result in several recommendations for management of lake fish diversity. Restoration of key aspects of the lake ecosystem (e.g. littoral and profundal habitats, water quality, nutrients) and lake-river network to near-natural conditions provides the best chance of protecting and supporting native fish species. Fish biodiversity can only be effectively monitored, managed and maintained if properly documented and understood in terms of species diversity, ecology and distribution, taxonomy, evolutionary relationships and within-species diversity. The taxonomic description of undescribed fish species is important for management and conservation, and is necessary for public recognition and awareness of the existence of the species. This information, once recognised by the scientific community, must be included in legislation and serve as a legal basis for species' conservation and protection, and to prevent movement of fish to outside their native ranges. The ecological and genetic effects of human activities that directly affect the fish populations, such as reduced water quality, unsustainable fishing and stocking, are also important to understand and manage appropriately. Finally, ongoing monitoring using quantitative standardized methods, combined with objective and informative assessments based on ecological, taxonomic and genetic information, provide an important foundation for evidence-based adaptive management of these valuable natural assets.

2. General introduction

Lake fish diversity and its management in Switzerland

Lake fish diversity

Biodiversity is the diversity of life at all its levels. From genes and traits within populations, through to different populations within a species, different species, communities (combinations of species) and ecosystems. The importance of biodiversity for human society is widely recognized [3]. It is also clear that the current rates of loss are comparable to those of the largest mass extinctions in the history of the earth [3]. Biodiversity loss is occurring in all habitats, but is particularly dramatic in freshwater ecosystems [4, 5]. Over the last half century, organic pollution, structural habitat modification and invasive species have caused substantial alterations to freshwater ecosystems worldwide [6] translating to large scale changes in communities and losses of biodiversity. Given the ecological, economic, cultural and recreational value of freshwater fish, these changes in fish communities should be a major concern to society [7, 8].

The large and deep perialpine lakes south and north of the central Alps are unique in Europe. These lakes emerged after the retreat of the glaciers at the end of the last glacial maximum around sixteen thousand years ago (i.e. the beginning of the Holocene), forming two separate archipelagos of lakes south and north of the high Alps. Different sets of fish species recolonized the lakes on the southern and northern slopes. Many of the first fish arriving in the newly ice-free lakes on the northern slopes were species adapted to cold water that subsequently went extinct elsewhere in central Europe (associated with the rapid warming of the climate during the Holocene period), and survived only in the deep perialpine lakes. Several of these ice age relict lineages have since diversified into an array of endemic species specifically adapted to the cold water habitats of the deep perialpine lakes [9].

Given that the evolutionary history of a species affects how it can respond and adapt to environmental change, it is critically important to understand both the current state of lake fish communities and their evolutionary history in order to determine how the fish and their environments have been impacted and changed by human activities. Each country also carries an international responsibility to document and preserve its fish fauna. This is particularly the case for the globally unique elements, such as fish species endemic to individual lakes, as well as contributing to conservation of species that are endemic to the region beyond the individual country.

Legal framework

Fish, crayfish and lake ecosystems are managed in Switzerland at the national level primarily through three main pieces of legislation: Federal Act on Fisheries [21st June 1991; Bundesgesetz über die Fischerei], Federal Act on Protection of Waters [24th January 1991; Bundesgesetz über den Schutz der Gewässer] and Federal Act on the Protection of Nature and Cultural Heritage [1st July 1966; Bundesgesetz über den Natur- und Heimatschutz]. These laws provide the principles within which the cantons regulate the management and conservation of fish and use of lake habitats.

Most relevant to lake fish, the purpose of the Federal Act on Fisheries (Art. 1) is to:

a. maintain, improve or, where necessary, restore the natural biodiversity and composition of native fish, crayfish, their prey and their habitats;
b. protect endangered species and forms of fish and crayfish;
c. ensure the sustainable use of fish and crayfish stocks;
d. promote fisheries research.

The Federal Act on Protection of Waters aims generally to protect waterbodies from adverse effects, and specifically, among other goals, to maintain and restore the natural habitats of fish and aquatic invertebrates. Finally, the Federal Act on the Protection of Nature and Cultural Heritage aims, more generally, to support the conservation and sustainable management of indigenous biodiversity and habitats.

Management tools

Examples of management tools implemented by cantons to ensure the sustainable use of fish and crayfish under the Federal Act on Fisheries include regulation of fishing gear for professional and recreational fishers, protection periods, minimum fish length, protected areas, bag limits for recreational fishers, artificial breeding and/or stocking programs. Management strategies vary between cantons and countries and therefore cannot be readily compared among lakes.

Ecological information available to managers

Information used when making decisions in management and conservation of fish include fisheries catch statistics, biological sampling and environmental monitoring. Fisheries catch statistics include the number and/or weight of fish caught by recreational and commercial fishers. Routine monitoring of exploited species, in particular whitefish (*Coregonus* spp), is conducted in several large lakes and involves regular gillnet sampling at a limited number of locations within the lake. Fish growth rates and the age at which the fish reach sexual maturity are also monitored for a few species in several large lakes. In terms of environmental monitoring, the water chemistry of many lakes is monitored on a monthly basis in a depth profile from the water surface to the lake floor at the deepest point of the lake, or at multiple stations in the larger lakes. This involves measuring key properties of the water such as temperature, oxygen and nutrients and provides some information on the ecological state of fish habitats, particularly in open and deep water. Phytoplankton and zooplankton are also monitored on a regular basis in most large lakes. Smaller lakes are generally not monitored for water chemistry nor plankton.

Motivation for Projet Lac

Background

In order to manage lake fish and the lake ecosystem effectively, their current ecological state must be known. Within the European Union, member countries are obliged to determine the state of their lakes and rivers under the Water Framework Directive. In Switzerland, the Federal Act on the Protection of the Environment [Bundesgesetz über den Umweltschutz] requires that before the construction of any facility that could harm the environment, the initial state of the ecosystem must be determined as part of an environmental impact assessment. With regard to aquatic fauna, Swiss cantons are required by the Ordinance of the Federal Act on Fisheries (Art. 10, abs 1) to inform the Federal Office of the Environment (FOEN) on the presence and distribution of endangered species within their jurisdiction (risk status 1 – 3: critically endangered, endangered, vulnerable).

In lakes around the Alps, fulfilling these legal obligations can be difficult. The large surface area and great depth of the lakes make it likely that many lakes host endemic fish species, but they also complicate comprehensive surveys of biodiversity. Indeed, despite the long history of research on fish in perialpine lakes, there had been no comprehensive or standardised sampling of fish in large lakes across the region. The absence of this information impedes conservation-aware ecosystem-level management of fisheries and lake fish habitat, particularly for fish and habitats that are under-represented in other data sources. Comparison of standardised surveys through time can also provide information on the impact of stressors such as climate change, as well as remediation actions such as renaturalisation of lake shores or trophic status.

Aims of Projet Lac

The aim of Projet Lac was to provide information on lake fish and the lake fish habitats by undertaking comprehensive and standardised sampling of fish in the lakes around the Alps. More specifically, the main goals were to:

- Assess and document present-day lake fish diversity.
- Establish a reference state of fish diversity and community composition as a baseline against which future comparisons can be made.
- Identify relationships between environmental variables and species- and population-level diversity by comparing across many lakes.
- In collaboration with the Natural History Museum of Bern build a collection of whole-preserved fish and tissue samples for taxonomic, genetic, ecological and ecotoxicological analyses.

The project also aimed to increase understanding and promote awareness of the ecological and evolutionary mechanisms underlying the fish diversity of the large and deep perialpine lakes.

Aims and geographic focus of this study

The aim of this report is to describe the current state of lake fish diversity and to investigate drivers of differences among the lakes across the region in and around the Western and Central Alps and Jura Mountains. The main objective is to discuss the results of Projet Lac and associated research projects that have investigated samples collected in Projet Lac and/or complemented it with additional sampling, in the context of other earlier work on these and other lakes. This broader perspective provides a more complete overview on the status and major ecological drivers of lake fish communities across the region. Samples from Progetto Fiumi, the sister project of Projet Lac for rivers, are also consulted to understand the distribution of little known fish species throughout the lake-river network [10].

This report focusses on Switzerland because this is the administrative region whose lakes were most intensively sampled and because most of the funding came from Swiss institutions, including federal and cantonal authorities. Some Italian, French and international lakes were also sampled in Projet Lac however, allowing the analysis and discussion of patterns beyond the borders of Switzerland, encompassing the larger perialpine region and more of the three major river catchments: Rhone, Rhine, Po (as well the Danube represented by Lake Sils).

3. Methods

A brief overview of the methods along with key information are provided in the following section. For a full description of the methods, including a discussion of the strengths and limitation of individual fish sampling methods, see Appendix B – Supporting information.

Fish sampling methods

Fish communities were surveyed in 35 lakes north and south of the Alps in Switzerland, eastern France, northern Italy, southern Germany (Lake Constance only) and western Austria (Lake Constance only; Table 21).

Figure 1: Map of lakes surveyed by Projet Lac with major river networks and catchments indicated by background colour. Note that the Aare-Rhine includes the subcatchments of the Reuss and Limat rivers. Data source: Federal Office of Topography swisstopo 2020.

Seventeen surveyed lakes were within Switzerland, one lake was shared between Switzerland and Germany (Lower Lake Constance), one lake shared between Switzerland, Germany and Austria (Upper Lake Constance), one lake shared between Switzerland and France (Lake Geneva) and two lakes were shared between Switzerland and Italy (lakes Lugano and Maggiore). Seven surveyed lakes were exclusively within France and six lakes exclusively within Italy.

Overall, seventeen lakes were sampled in the Rhine river catchment, eight lakes in the Rhone river catchment, nine lakes in the Po river catchment and Lake Sils from the Danube river catchment (Figure 1). Distances among lakes along rivers are shown in Figure 84.

Lakes ranged widely in surface area (0.2 – 582 km^2), maximum depth (10 – 372 m), volume (2 – 79,017 gigaliters) and altitude (65 – 1,797 m above sea level). Each lake was surveyed once. Surveys were conducted between 2010 and 2017, always between August and October.

Sampling was coordinated by Eawag in collaboration with partner institutions, however this report also discusses data received from associated sampling campaigns led by other institutions in collaboration with Eawag. For example, the Italian lakes, Como, Iseo, Idro, Mezzola and Varese, were sampled by the Italian ecological consultancy GRAIA – Gestione e Ricerca Ambientale Ittica Acque srl under contract from Regione Lombardia[1], the sampling of lakes Biel and Sarnen was led by the ecological consultancies AquaBios and Teleos. A list of institutions involved in sampling and contributing data is provided in the acknowledgements.

In most lakes, littoral habitats were mapped and lake fish surveyed with two different gillnetting protocols, electrofishing and hydroacoustics (Figure 2, Appendix Table 15). In some lakes, a reduced set of survey methods were used, depending on the interests and funding of the local management authorities. Historic records of the fish community from published literature and local expert knowledge were consulted to begin to assess how the present-day species assemblages deviated from known historical conditions. Available environmental data (e.g. temperature, oxygen) was also compiled from various sources to help to understand patterns in the fish communities and their habitat associations.

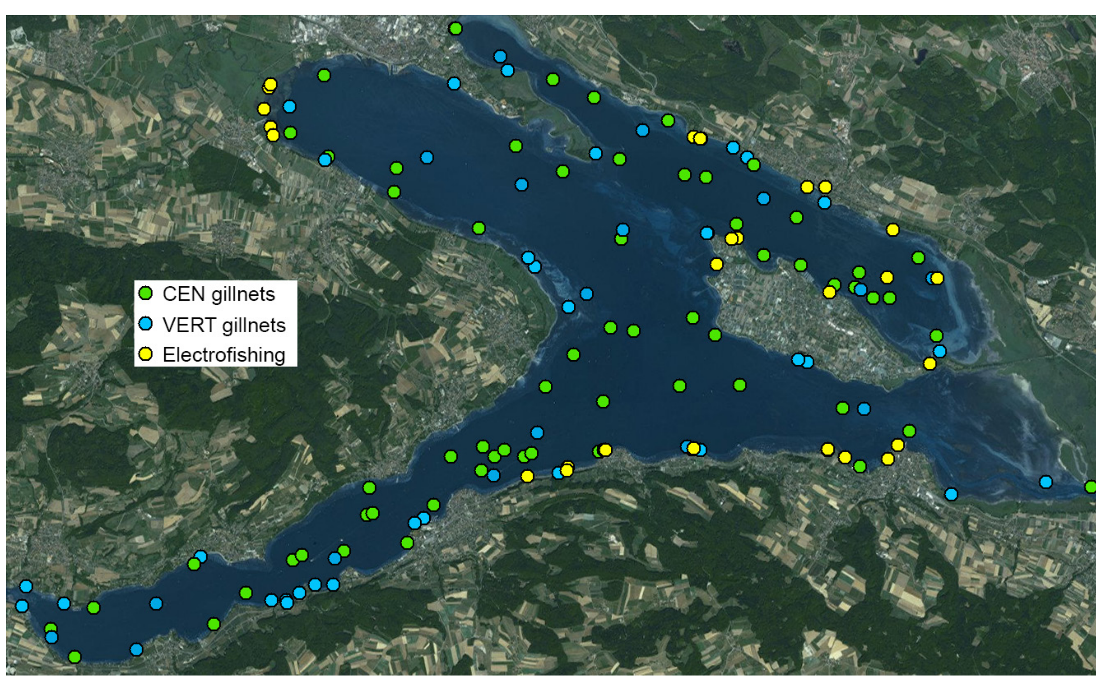

Figure 2: Example of the distribution of sampling actions throughout a lake (Constance Untersee).

[1] Full details of the sampling by Regione Lombardia are: Censimento della fauna ittica nei laghi alpini nel territorio della Regione Lombardia 2013 – 2015, con il contributo del Fondo Europeo Pesca 2007/2013 realizzato da GRAIA srl – Gestione e Ricerca Ambientale Ittica Acque Via Repubblica, 1 – 21020 Varano Borghi (VA) e da Consiglio Nazionale Ricerche – Istituto per lo Studio degli Ecosistemi – Largo Tonolli 50 – 28922-Verbania Pallanza (VB)

Species identification

Most fish were identified to species level in the field based on external features such as colour, shape and meristics. Kottelat and Freyhof [9] was used as the main guidebook and the standard for field identification. Similar-looking species were differentiated using diagnostic features such as position of fins, number of fin rays or scales on the lateral line, mostly following Kottelat and Freyhof [9]. Most fish were identified a second time later in the lab, independently of the first identification, through examination of standard and cuvette photos, as well as examination of preserved specimens in difficult cases.

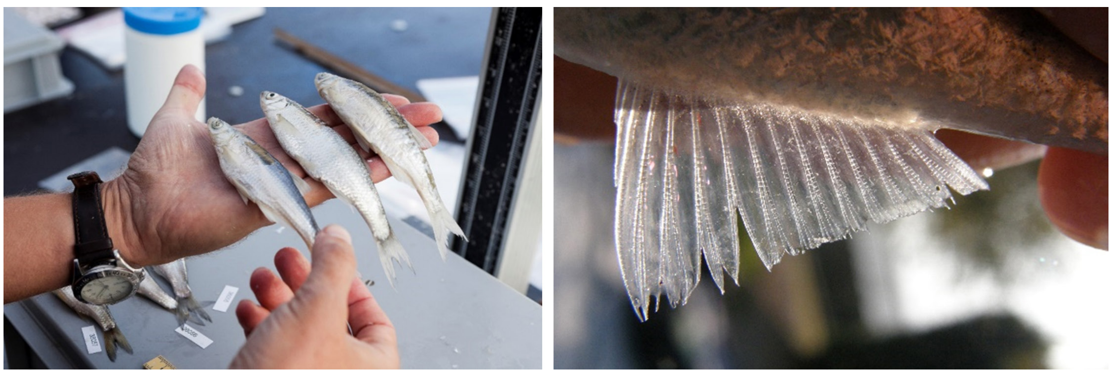

Figure 3: Identification in the field based on colour, meristics (e.g. fin ray counts) and morphology.

Several fish groups were particularly difficult to identify to species in the field. In these groups, identification to species level was often only possible for adult fish, where the diagnostic morphological or meristic differences between species are fully developed and visible. For such species, final identification was often made or confirmed in the Eawag laboratory after the fieldwork was completed. This was particularly the case for whitefish (*Coregonus* spp). In genera with several related species, it was often impossible to assign juveniles or intermediates (including putative hybrids) to species. For closely related, or otherwise difficult to identify species, it was sometimes not possible to identify all individuals clearly to one species or the other but it was often the case that the presence of a species in a lake could be unambiguously established by an adult phenotype clearly matching the species description or through genetic analyses. Identifying all or most individuals would then involve considerably more taxonomic work on larger sample sizes. Individuals for which species level identification was not possible, were labelled with the name of the genus and "sp.", for example, *Coregonus* sp. The label of genus and "spp" (e.g. *Coregonus* spp) was used when referring to a group of individuals that potentially included representatives of more than one species of the given genus. Finally, populations that are phenotypically, ecologically and/or genetically distinct from described species, but that have not yet been formally described as species, are referred to in this report by the name of the genus followed by 'sp.' and a vernacular name, for example *Salvelinus* sp. "Limnetic Thun/Brienz" (see Appendix A – Taxonomic profiles).

Formally describing and naming species

In order to have a new species officially recognized by taxonomists, a description of the species with its identifying features must be published in a peer-reviewed journal. A binomial scientific name is assigned to the species as part of this process (e.g. *Coregonus palaea*). The process of formally describing a species requires a considerable investment of time by a trained taxonomist, as the new species must be defined and differentially diagnosed against all similar, described species. The process is particularly complicated where the species is part of a group of many closely related species. The taxonomist must accurately measure many different features on many individuals of the new species, and on many individuals of all related, already-described species. This often requires travelling to museums that host the type-specimens of described species in their collections, or requesting the museums to ship the valuable type-specimens on loan. The features to be compared include meristic counts, such as number of gillrakers, fin rays and scales, morphometric distances, e.g. the relative size of anatomical features, such as head length, as well as live colouration, preserved colouration and genetic and ecological features when available. The traits of the new species are compared against those of its closest described relatives to identify the combination of features that distinguish the new from the existing species. A well-preserved set of 'voucher specimens' of the new species are deposited in a museum and one representative individual is designated as the 'holotype', which acts as the physical reference for the species. Future diagnosis of other new species need to consider and compare against this holotype.

DNA barcoding

The mitochondrial Cytochrome Oxydase I gene (COI) was sequenced from over 1,100 fish (usually three individuals of every species in each lake) to provide additional confidence in field identifications, to assess phylogeographic structure within widely distributed species and to reveal cryptic species diversity (i.e. species that appear similar in phenotype, but are genetically deeply divergent and may not have been recognised as distinct species). In this process, a sequence of 600 base pairs in the COI gene acts as the barcode. Variation in the base pairs in this sequence was compared among the sampled individuals and matched to barcode sequences of various species in online reference databases (mainly NCBI Genbank). One thousand Projet Lac fish have subsequently also been sequenced for the mitochondrial 12S rRNA gene as a reference database for environmental DNA (eDNA) investigations.

Barcoding has several, well-known limitations. It is generally unable to differentiate between species that diverged in the last few thousand years, such as the species in many important salmonid genera (*Coregonus*, *Salvelinus*, *Salmo*). This is because the divergence time was insufficient for the accumulation and fixation of mutational differences in this short DNA sequence. It is also potentially misleading in cases where much older species have hybridised (such as several cyprinids in the region, e.g. *Scardinius* spp). Since mitochondrial genes, such as COI, are passed exclusively from mother to offspring and do not recombine, hybrids cannot be distinguished from their maternal progenitor species based on barcoding. When hybrids interbreed with either of their parental species (known as "backcrossing"), the species assignments according to the barcoding sequence can differ from the phenotype (i.e. physical appearance of the fish) and from much of the remaining genome. In such cases, the phenotype-based identification was used in this report.

For some situations of particular interest, more in-depth genetic analyses were conducted to distinguish the species. Such studies used microsatellite DNA (for whitefish and *Phoxinus*) or Single-nucleotide polymorphism (SNP) data from Next Generation Sequencing of Restriction Site Associated DNA (RAD) tags (for sculpin, charr, trouts and roach). It was not a goal of Projet Lac to revise the taxonomy of fish across the region however, but rather to assess species distributions, taxonomic and ecological diversity and to point out important areas for future investigations, including taxonomy, and to provide data and samples for these. The available knowledge for difficult groups of fish, some of which are currently being investigated, is summarised in Appendix A – Taxonomic profiles. A more general introduction to what is a species can be found in Appendix B – Additional background information.

Terminology for diversity within species

Genetic, phenotypic and/or ecological differences within species, i.e. among populations, are also important components of biodiversity relevant for conservation and ecosystem services. The existing knowledge of genetic diversity among populations of perialpine fish species of Switzerland was last compiled in 2016 [11]. Two labels are used in this report to recognise diversity within species in cases where it is currently still unclear whether the taxa should be formally described as new species: 'divergent lineage' and 'sympatric form'.

In this report, the term 'divergent lineage' is used to refer to a population that is *genetically* distinct from other populations within the same taxonomic species, but where it is currently either unclear whether the divergence justifies to consider them different species, or where the boundaries of these species are unclear. Divergent lineages were identified mostly based on strong differences in the mitochondrial gene cytochrome oxidase I. They are often associated with different geographical regions, but they may be found together in parts of their range. This cryptic diversity is discussed in Appendix A – Taxonomic profiles.

The term 'sympatric form' is used in this report to refer to a group of individuals that are *phenotypically* very different from other individuals of a described species occurring in the same lake (e.g. geographical isolation cannot explain the differences), but where it is currently unclear whether the differences are associated with genetic differentiation or caused by phenotypic plasticity. In most instances where the term 'form' is used, no genetic data was available or interpretation of genetic data was inconclusive due to limitations associated with small sample sizes or the genetic markers used (see for instance the example of profundal and littoral sculpins in northern lakes).

Projet Lac catches, annual fisheries statistics and the "actual" fish community

One of the main differences between the picture of the fish community provided by Projet Lac and catch statistics from professional fisheries is that Projet Lac data represent the fish community in the lake at one point in the year, while fisheries catch statistics represent data over the entire year (Table 1). The minimum size of fish caught by professional fishers is determined by the legal minimum mesh size and the number of fish entering the catchable size range in a year depends on the size of the fish population and the growth rate of the individual fish. Almost all fish of catchable size may be caught in lakes with intense fishing pressure and/or slow individual growth rates.

Another important distinction is that Projet Lac provides information on all sizes of fish in the lake, while fishers focus only on the large fish. The distribution of fish throughout the lake is a further important consideration: fish concentrated in a small part of the lake, particularly close to the surface, will be more efficient for fishers to harvest. Changes in the distribution of fish throughout a lake therefore affect comparisons of fisheries catch rates through time or among lakes. Fishers generally focus on particularly productive and accessible regions of the lake, while Projet Lac surveyed the entire lake, including the deep profundal zones, the fishing of which requires large effort. Projet Lac data can however be subset to show the number of large fish in fishery-important habitats (e.g. surface waters) at the time of sampling. Both Projet Lac gillnet catches and fisheries catch statistics differ from the actual fish community through effects of the different 'catchability' of different fish (see section 'Gillnetting').

Table 1: Comparison of the objectives and information provided by Projet Lac and the catch statistics resulting from professional fisheries.

	Projet Lac	**Professional fisheries**
Objective	Precise, comparable estimates of abundance and biomass for all species (i.e. community composition) in all major habitats	Maximise catches (biomass) of particular species and size classes
Methods	Combination of sampling methods: gillnets, electrofishing, hydroacoustics	Gillnets
Habitats	Whole lake, all habitats	Particular parts of the lake, especially shallow
Distribution of effort	Random (CEN net protocol) and habitat-targeted (vertical net protocol and electrofishing)	Species-targeted. Targets locations where exploitable individuals of particular species are thought to be in high abundance
Size of fish	Wide range of fish sizes. Gillnet mesh sizes ranging from 5 mm to 70 mm. Electrofishing somewhat biased towards smaller fish	Size-targeted: larger fish only. Large gillnet mesh sizes only e.g. > 24 mm
Shape of fish	Gillnets over-represent deep-bodied and spiny fish. Electrofishing less biased for shape	Gillnets over-represent deep-bodied and spiny fish among the targeted species
Correction for effort	Catches are corrected for number and area of nets and soak time	Catches are generally only corrected for lake surface area for comparisons between lakes. Catches could also be corrected by the number of licenses, permitted number/area of nets (number of net-nights not yet regularly recorded)
Effects of time	"Snapshot" in time of fish community i.e. sampling generally conducted over one or two weeks in late summer – early autumn. (generating estimates of "relative standing biomass"). No information on other seasons. No time series available as yet	Annual statistics usually discussed. Catches throughout the year influenced by fish growth and seasonal differences in rates of movement (e.g. relating to food availability). Long time series available in many lakes

4. Fish biodiversity in the perialpine lakes

Taxonomic diversity

A total of 106 fish taxa were recorded in Projet Lac. Four additional species were recorded in the lakes in related Eawag studies, but were not recorded in Projet Lac sampling (Table 16, Table 5). These are included in the discussion here to provide a more complete picture of the lake fish diversity of the region. This diversity included 82 formally described species and 28 taxa that have not yet been formally described, although many of these had been previously distinguished in genetic and/or phenotypic investigations (Table 2). The undescribed taxa included nine genetically confirmed species, six deeply divergent evolutionary lineages (putative allopatric species that are undescribed) and thirteen phenotypically distinct sympatric forms. The taxa in the latter two categories are putative species, for which the available data is not yet sufficient to confirm with confidence. Lists of the taxa in these different categories as discussed in this section are provided in Table 2. For textual simplicity, species, undescribed species, sympatric forms and divergent lineages are all referred to in the following text as 'species'. See Appendix A – Taxonomic profiles for more details on the species status of groups with taxonomic uncertainty. Only in Appendix A we also report several fish that could not be assigned to any species but were caught in single individuals or very small numbers. These fish are not included in any tables or statistics.

Ninety-five species were recorded in Projet Lac as native. Fourty-one of the native species (including eleven forms) were endemic, occurring only in one lake or in several neighbouring lakes of shared geological origin. This is a remarkably high level of endemism. Sixteen species were native to some parts of the perialpine region, but were also recorded in lakes outside their native range, i.e. species that had been translocated between their native lakes and other lakes within the perialpine region. Many of these were species that have been translocated across the Alps in either direction (trans-Alpine translocations; Table 3). Four species were native to other parts of Europe, and had arrived in Switzerland and the sampled lakes only within the past 200 years (Table 3). *Gymnocephalus cernua* is native to the Rhine below the Rhinefall and is native to Switzerland according to Swiss law (VBGF), yet was not native to any of the lakes surveyed by Projet Lac. Two species had the unusual status of existing only in one lake (i.e. endemic to the lake), yet were partially non-native in the lakes (see *Coregonus* spp section of 'Common non-native and exotic species' for more information; Table 3). Six species had been introduced from North America and two from Asia. These are refered to in this report as exotic species (Table 3).

Seven native species of the region (including two endemics), were not recorded in Switzerland, and were only recorded in lakes of neighbouring countries (Table 4). Three of these have however been recorded in Swiss waterways in other Eawag projects, and one of them (*Salmo carpio*) never occurred in Switzerland. Three exotic species were recorded by Projet Lac only in lakes outside of Switzerland, although again, two of these are also known to occur within Switzerland.

Finally, 15 species are known to occur as native in Switzerland or nearby waters, but were not recorded in Projet Lac. Eight of these are considered extinct in Switzerland [12]: *Misgurnus fossilis, Alosa alosa, Hucho hucho, Salmo salar, Acipenser sturio, Acipenser naccarii, Lampetra fluviatilis, Petromyzon marinus*. The other seven are rare to very rare and do not typically occur in lakes (*Leucaspius delineatus, Barbus caninus, Parachondrostoma toxostoma, Romanogobius benacensis, Zingel asper, Thymallus aeliani, Lampetra zanandreai*).

Table 2: Lists of undescribed fish taxa by taxonomic category. See taxonomic profiles of each group for more detail.

Undescribed species, confirmed by molecular genetic data

Salvelinus sp. "Limnetic Thun"	Thun
Salvelinus sp. "Profundal-dwarf Thun"	Thun
Cottus sp. "Profundal Walen"	Walen

Deeply divergent evolutionary lineages (likely cryptic species, distinct from described species)

Barbatula sp. "Lineage I" (divergent from *Barbatula barbatula* and *Barbatula* sp. "Lineage II")	Lakes of Aare catchment
Barbatula barbatula "Lineage II" (divergent from *Barbatula barbatula* and *Barbatula* sp. "Lineage I")	Streams of Aare catchment, lakes Geneva and Constance
Cottus sp. "Po lineage" (divergent from *Cottus gobio* "Rhine lineage" + "Rhone lineage")	Southern lakes
Cottus sp. "Rhone lineage" (divergent from *Cottus gobio* "Rhine lineage" + "Po lineage")	Annecy, Chalain
Cottus gobio "Aare lineage littoral" (divergent from *Cottus gobio* "Rhine lineage")	Lakes of the Aare catchment
Salaria fluviatilis "French lineage" (divergent from *Salaria fluviatilis* "Italian lineage")	Annecy, Geneva

Phenotypically distinct sympatric forms (likely ecological species)

Cottus gobio "Profundal Thun" (sympatric with *Cottus gobio* "Aare lineage littoral"	Thun
Cottus gobio "Profundal Lucerne" (sympatric with *Cottus gobio* "Aare lineage littoral"	Lucerne
Cottus sp. "Po profundal" (sympatric with *Cottus* sp. "Po lineage")	Garda, Maggiore
Perca fluviatilis "Yellow-orange form" (sympatric with the red fin form of *P. fluviatilis*, in Lake Constance shown to be genetically distinct)	Large prealpine lakes
Salmo sp. "Blackspot", lake-spawning trout (sympatric with *S. trutta, S. marmorata* and *S. cenerinus* in Poschiavo)	Poschiavo
Salvelinus sp. "Limnetic Lucerne" (sympatric with *S. umbla* and other forms of *Salvelinus*)	Lucerne

Salvelinus sp. "Profundal-dwarf Lucerne" (sympatric with *S. umbla* and other forms of *Salvelinus*)	Lucerne
Salvelinus sp. "Giant Lucerne" (sympatric with *S. umbla* and other forms of *Salvelinus*)	Lucerne
Salvelinus sp. "Profundal Walen I" (sympatric with *S. umbla* and *Salvelinus* sp. "Profundal Walen II")	Walen
Salvelinus sp. "Profundal Walen II" (sympatric with *S. umbla* and *Salvelinus* sp. "Profundal Walen I")	Walen
Salvelinus sp. "Benthic Thun/Brienz" (sympatric with *S. umbla* and other species/forms of *Salvelinus*)	Thun, Brienz
Salvelinus sp. "Giant Thun" (sympatric with *S. umbla* and other species/forms of *Salvelinus*)	Thun
Salvelinus sp. "Profundal extreme Thun" (sympatric with *S. umbla* and other species/forms of *Salvelinus*)	Thun

Table 3: Lists of species recorded in Projet Lac that occur outside their native range.

Translocated from northern perialpine lakes to southern perialpine lakes

Coregonus sarnensis	Maggiore, Como
Coregonus helveticus	Maggiore, Lugano, Como
Coregonus sp.	Many lakes. Species unidentified
Esox lucius	Maggiore, Lugano
Phoxinus septimaniae	Poschiavo, Sils
Phoxinus csikii	Poschiavo
Rhodeus amarus	Garda, Idro, Iseo, Maggiore, Mezzola
Rutilus rutilus	Maggiore, Lugano, Varese, Como, Mezzola
Salmo trutta	Recorded in all southern lakes, except Varese (where water temperatures are too warm)
Salvelinus umbla	Iseo, Lugano, Como, Mezzola, Poschiavo, Sils
Gymnocephalus cernua	Maggiore. Also non-native in many northern peri-alpine lakes
Sander lucioperca	Maggiore, Lugano, Varese, Como, Mezzola. Also non-native in some northern peri-alpine lakes

Translocated from southern perialpine lakes to northern perialpine lakes

Cobitis bilineata	Many lakes. Original distribution is uncertain
Scardinius hesperidicus	Many lakes

Endemic species with non-native genetic contributions (hybrid species)

Coregonus acrinasus	Thun
Coregonus suspensus	Lucerne

Native to Europe, but arrived in Switzerland only in the past 200 years

Gasterosteus aculeatus	Many lakes
Carassius gibelio	Many lakes
Sander lucioperca	Many lakes
Salaria fluviatilis "French lineage"	Annecy, Geneva. Introduced from further south in the Rhone catchment

Exotic species from North America

Ameiurus melas	Bourget, Geneva, Garda, Maggiore, Varese, Como
Lepomis gibbosus	Many lakes
Micropterus salmoides	Garda, Idro, Iseo, Maggiore, Lugano, Varese
Gambusia holbrooki	Recorded only in Varese
Oncorhynchus mykiss	Upper Constance, Maggiore, Mezzola
Salvelinus namaycush	Poschiavo, Sils

Exotic species from Asia

Pseudorasbora parva	Recorded only in Garda, but known to occur in Switzerland
Carassius auratus	Recorded only in Garda, but known to occur in Switzerland

Table 4: Species recorded by Projet Lac only in lakes outside of Switzerland.

Native species recorded by Projet Lac only in lakes outside of Switzerland

Cottus gobio "Rhone lineage"	Chalain, Annecy. Assumed to be this lineage but needs genetic confirmation. Known to occur in Switzerland only in the Doubs river
Sabanejewia larvata	Mezzola. Recorded in a different Eawag project in Switzerland in an inflow to Lake Maggiore
Phoxinus lumaireul	Garda. Recorded by Progetto Fiumi as non-native in an inflow to Lake Geneva, but is the expected native *Phoxinus* in all southern perialpine lakes
Telestes souffia souffia	Chalain
Coregonus lavaretus	Endemic to Bourget
Chondrostoma soetta	Mezzola. Known in Switzerland from Lugano and Maggiore, but is extremely rare or extinct in these lakes
Salmo cf. *carpio*	Endemic to Garda

Non-native species recorded by Projet Lac only in lakes outside of Switzerland

Gambusia holbrooki	Varese. Native to North America
Carassius auratus	Garda. Known to occur throughout Switzerland. Native to Asia
Pseudorasbora parva	Garda. Known to occur in lakes Biel, Sempach and other parts of the Rhine catchment. Native to Asia

Native species

Native fish species diversity was distributed among 11 taxonomic orders and 19 families (Table 18). Native fish species were dominated by the carp family (cyprinids, family *Cyprinidae*; 27 species distributed among 16 genera), the whitefish family (coregonids, family Coregonidae; 23 species in the genus *Coregonus*) and the salmon family (salmonids, family *Salmonidae*; 19 species distributed among three genera).

Among the cyprinids, seven genera were represented by just one species (*Abramis, Alburnoides, Blicca, Cyprinus, Leuciscus, Rhodeus, Tinca;* although the taxonomic situation with *Rhodeus* is currently unclear). Three species were recorded in each of the genera *Rutilus* and *Phoxinus*, and two species were recorded from each of the remaining seven cyprinid genera. In many of these cases, different species were native to different river catchments, usually with one species native to lakes north of the Alps (Rhine/Rhone) and the second species native to the southern lakes (Po river catchment; Table 19). Exceptions to this are two sympatric species of *Rutilus* in some southern lakes (*R. aula, R. pigus*), two partly sympatric species of *Phoxinus* north of the Alps (with *P. septimaniae* of western provenance and *P. csikii* of Danubian provenance; see taxonomic profile for *Phoxinus* spp), and *Gobio, with G. obtusirostris* (native to the Danube catchment) sympatric with the Rhine/Rhone species *G. gobio* in Lake Constance. *Gobio obtusirostris* may be native to Lake Constance, which was part of the Danube drainage until the early Holocene (see taxonomic profile for *Gobio* spp). Within *Leuciscus leuciscus* and *Telestes souffia* we observed deep divergence between the genetic lineages of the Doubs/Rhone catchment and the Rhine catchment. For the latter species, this was consistent with a subspecific split into *T. souffia souffia* (Doubs/Rhone) and *T. souffia agassii.*

Among the other fish families (i.e. non-cyprinids), three recorded genera also had different native species in different river catchments: *Esox, Salmo* and *Cottus* (Table 19). The family *Nemacheilidae* contained one genus (*Barbatula*) with three species, the family *Cobitidae* contained two genera (*Cobitis* and *Sabanejewia*), each with a single species, the family *Percidae* included two species of perch, and the family *Clupeidae* contained one genus (*Alosa*) with two species. Only one native species was recorded from each of the seven remaining families of fish: *Anguillidae, Lotidae, Gasterosteidae, Blenniidae, Gobiidae, Petromyzontidae* (at least one other species known from the region was not recorded) and *Siluridae*.

Endemic species

The 41 endemic species were from the *Coregonus* family (*Coregonidae*; Table 18), salmon family (family *Salmonidae*) and sculpin/bullhead family (*Cottidae*). Most recorded endemic species were in the genus *Coregonus* (25 species), followed by *Salvelinus* (11 species), *Cottus* (3 species) and *Salmo* (2 species).

Non-native and exotic species

Non-native and exotic species were dominated by the same families that dominated among the native species: *cyprinids, coregonids* and *salmonids* (Table 18). Among the cyprinids, six recorded species had been translocated among catchments within the region. Two recorded exotic cyprinids were originally from Asia (Table 20). Six species of *Coregonus* had been translocated within the region by humans, along with two species of *Salmo* and *Salvelinus umbla*. The two exotic salmonids originally from North America included *Salvelinus namaycush,* common in the alpine lakes Sils and Poschiavo, and *Oncorhynchus mykiss*, recorded in lakes Upper Constance, Mezzola and Maggiore.

The remaining non-native species recorded in Projet Lac that had been translocated to Switzerland from elsewhere within Europe (including those that were also native to some of the surveyed lakes) included two species in the perch family, a blenny (*Blenniidae*), two species of stickleback (*Gasterosteidae*), a loach (*Cobitidae*) and a catfish (*Siluridae*; Table 20). Finally, the remaining recorded exotic species introduced from outside the region were all from North America and included two species of sunfish (*Centrarchidae*), another catfish (*Ictaluridae*) and a mosquitofish (*Poeciliidae*).

Table 5: Number of fish species recorded by Projet Lac in each lake. Cells are shaded to highlight differences among lakes. Note that the number of species can be influenced by sampling intensity: electrofishing was not conducted in Annecy and Bourget, and the vertical gillnet protocol was not conducted in Annecy, Bourget, Idro, Iseo, Varese, Como and Mezzola.

Catchment	Lake	Total number of species	Number of species		Number of native species		Number of non-native species	
			Native	Non-native	Endemic	Non-endemic	Within Europe	Exotic
Rhone	Annecy	14	11	3	0	11	3	0
	Bourget	18	12	6	1	11	4	2
	Bret	10	9	1	0	9	1	0
	Geneva	25	19	6	0	19	5	1
	Bonlieu	8	6	2	0	6	2	0
	Chalain	18	13	5	0	13	4	1
	Saint-Point	10	7	3	0	7	3	0
	Remoray	8	6	2	0	6	2	0
Rhine	Rousses	10	7	3	0	7	3	0
	Joux	11	10	1	0	10	1	0
	Brenet	12	10	2	0	10	2	0
	Neuchatel	26	22	4	2	20	3	1
	Morat	23	19	4	1	18	4	0
	Biel	28	22	6	2	20	5	1
	Thun	27	24	3	10	14	3	0
	Brienz	16	16	0	4	12	0	0
	Constance Obersee	31	25	6	4	21	4	2
	Constance Untersee	25	20	5	2	18	4	1
	Zug	19	17	2	1	16	1	1
	Lucerne	27	24	3	7	17	3	0
	Sarnen	22	19	3	2	17	3	0
	Hallwil	20	17	3	1	16	2	1
	Zurich Obersee	20	19	1	3	16	1	0
	Zurich Untersee	21	18	3	2	16	2	1
	Walen	20	20	0	6	14	0	0
Po	Garda	26	17	9	1	16	4	5
	Idro	14	9	5	0	9	3	2
	Iseo	22	15	7	0	15	5	2
	Maggiore	36	22	14	0	22	10	4
	Lugano	24	15	9	0	15	7	2
	Varese	15	7	8	0	7	4	4
	Como	26	17	9	0	17	7	2
	Mezzola	26	16	10	0	16	8	2
	Poschiavo	10	4	6	0	4	5	1
Danube	Sils	8	4	4	0	4	3	1

Newly discovered or rediscovered species

Projet Lac identified several fish taxa previously not known to science, seven taxa previously only known from outside the region and four taxa that were believed to be extinct or locally extirpated.

Table 6: Taxa newly discovered, newly recorded, reassessed or rediscovered in Projet Lac sampling.

New taxa

Coregonus acrinasus	Thun
Coregonus profundus	Thun
Coregonus alpinus	Thun, Brienz
Coregonus steinmanni	Thun
Coregonus brienzii	Brienz
Salvelinus sp. "Profundal Walen I"	Walen
Salvelinus sp. "Profundal Walen II"	Walen
Salvelinus sp. "Limnetic Thun"	Thun
Salvelinus sp. "Profundal-dwarf Thun"	Thun
Salvelinus sp. "Limnetic VWS"	Lucerne
Salaria sp. "Marble" *	Maggiore
Cottus gobio "Profundal Lake Thun sculpin"	Lake Thun
Cottus gobio "Profundal Lake Lucerne sculpin"	Lake Lucerne
Cottus gobio "Profundal Lake Walen sculpin"	Lake Walen
Cottus sp. "Po profundal form"	Maggiore, Garda

* Not included in other species lists as known only from three individuals. See taxonomic profile for *Salaria* spp.

New records of taxa previously only known from outside the region

Gobio obtusirostris	Constance Obersee	New record for Switzerland and Constance
Phoxinus csikii	Multiple lakes	New record for Switzerland
Phoxinus septimaniae	Chalain	New record for Chalain
Barbatula quignardi	Chalain, Geneva	New record for Switzerland and Chalain
Barbatula sp. "Lineage I"	Aare lakes	New record for Switzerland
Barbatula sp. "Lineage II"	Aare streams, Geneva, Constance	New record for Switzerland
Salaria fluviatilis "French lineage"	Geneva	New record for Geneva

Re-discovered taxa

Coregonus heglingus	Believed extirpated from Zurich
Coregonus litoralis	Believed extirpated from Sarnen
Salvelinus profundus	Constance Obersee
Salvelinus sp. "Profundal-dwarf VWS"	Lucerne

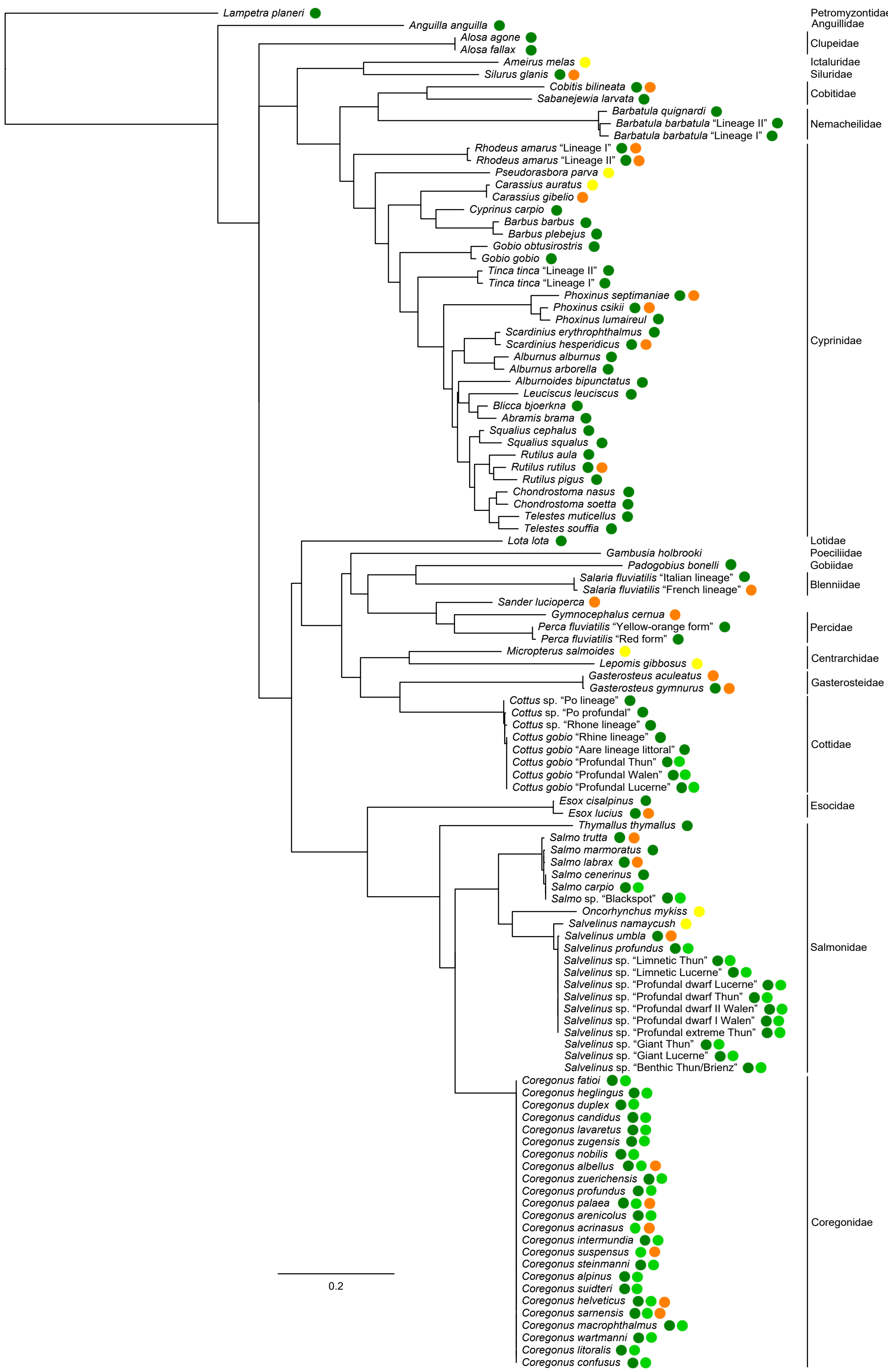

Figure 4: Estimate of phylogenetic relationships based on COI sequence variation between fish species caught in Projet Lac: ● endemic species, ● species native in at least some surveyed lakes, ● species non-native in some lakes, ● exotic species.

Extinctions

The human disturbances of the past centuries have driven multiple fish species in the region to extinction. Several unique species or populations are also known only from the writings of pioneering naturalists and were lost before the birth of Linnean taxonomy, and hence before they could be studied and described by modern taxonomists. Other fish species survive in neighbouring countries, but no longer occur in our study region or they disappeared from a given lake but can still be found elsewhere in the region (referred to as as extirpation or local extinction).

The endemic salmonids have fared the worst, with the loss of several species of *Coregonus, Salvelinus* and *Salmo*. The major cause of extinction for *Coregonus* spp and *Salvelinus* spp was changes in the lake ecosystems caused by eutrophication. Increasingly obstructed passage to the ocean led to the local extirpation of *Salmo salar* and the ocean-migrating ecotype of *Salmo trutta*. A species or form of *Salmo* that spawned (or at least became ripe for spawning) within the lake was also believed to occur in Lake Lucerne (and perhaps also other perialpine lakes). This species was known locally as "Schwebforelle", and is referred to in Kottelat and Freyhof [9] in the section on *Salmo schiefermuelleri*. This species was not recorded in Projet Lac, nor has it been recorded by local authorities in recent decades.

Other species considered to be locally extinct in the Swiss portion of their distribution area are *Acipenser naccarii, Huso huso* (from lakes Lugano and Maggiore), *Petromyzon marinus, Lampetra fluviatilis, Alosa alosa* and the weather loach, *Misgurnus fossilis* north of the Alps. The latter species lives in low-gradient, lowland streams and canals, including where these streams and canals enter lakes. Neither species were recorded in Projet Lac. Finally, there is a number of species that used to be recorded from many lakes and rivers in the region but were not recorded in Projet Lac from most of the lakes where they used to occur. Such species may be very rare in the lakes or may have become locally extirpated. Species in this category include *Chondrostoma nasus* (confirmed in Projet Lac in just one (Sarnen) of the nine Rhine lakes were it used to live), *Telestes souffia aggasizi* (missing in all four Swiss lakes where it was previously known) and *Alburnoides bipunctatus* (recorded in just two of the nine Swiss lakes where it was previously known to occur). At least some of these failures to record a lake population may reflect true extirpation. Several of these species were known to be in decline across the region.

Several species that were believed to be extinct or locally extinct, were recovered in the comprehensive sampling of Projet Lac (Table 6). These included *Salvelinus profundus* in Lake Constance, *Coregonus heglingus* in Lake Zurich (believed locally extinct in Zurich, but survived in Lake Walen), *Coregonus litoralis* in Lake Sarnen (believed locally extinct in Sarnen, but survived in Lake Lucerne) and *Salvelinus* sp. "Profundal-dwarf VWS" from Lake Lucerne. Confirming the extinction of a species is very difficult, particularly in the large and deep lakes.

Several other notable extinct species were not recovered in Projet Lac (Table 7). These include the Kilch *Coregonus gutturosus* from Lake Constance, the Féra *Coregonus fera* and the Gravenche *Coregonus hiemalis* from Lake Geneva, the Jaunet *Salvelinus neocomensis* from Lake Neuchatel, *Coregonus restrictus* from Lake Morat, *Coregonus* sp. "Zugeralbock" and *Coregonus* sp. "Zugeralbeli" from Lake Zug and several taxonomically undescribed species of *Salvelinus* in Lake Geneva [13] and Lake Zurich [13]. The absence of these species from Projet Lac catches provides further evidence to confirm the extinction of these species.

Finally, three fish species believed widely distributed in Switzerland were not recorded by Projet Lac (Table 7). It is possible, and in the cases of *Phoxinus phoxinus* and *Cobitis taenia* perhaps likely, that past records of these species from perialpine lakes are based on erroneous identification and confusion with phenotypically similar species of the same genera (see taxonomonic profiles for these genera). For *Carassius carassius* it can currently not be said if the species once was widespread in lakes (as the many previous records make believe) and has declined precipitatively or if the records of this species too were based on misidentifications.

All fish species recorded in Projet Lac

Plate 1. all fish species recorded in Projet Lac


Salmonidae
Salmo marmorata
Salmo cenerinus
Salmo trutta
Salmo labrax
Salmo sp.»blackspot»
Oncorhynchus mykiss
Salvelinus namaycush
Salmo carpio
Salvelinus sp.»giant Thun»
Salvelinus profundus
Salvelinus umbla
Salvelinus sp.»Limnetic Thun/Brienz»
Salvelinus sp.»Benthic Thun/Brienz»
Salvelinus sp.»profundal extreme Thun»
Salvelinus sp.»profundal dwarf Thun»
Salvelinus sp.»giant Lucerne»
Salvelinus sp.»Limnetic Lucerne»
Salvelinus sp.»profundal dwarf Lucerne»
Salvelinus sp.» Profundal Walen I»
Salvelinus sp.» Profundal Walen II»
Coregonus lavaretus
Coregonus palaea
Coregonus alpinus
Coregonus suidteri
Coregonus helveticus
Coregonus candidus
Coregonus steinmanni
Coregonus sarnensis
Coregonus confusus
Coregonus brienzii
Coregonus littoralis
Coregonus arenicolus
Coregonus duplex
Coregonus acrinasus
Coregonus intermundia
Coregonus macrophthalmus
Coregonus zürichensis
Coregonus profundus
Coregonus suspensus
Coregonus heglingus
Coregonus fatioi
Coregonus wartmanni
Coregonus nobilis
Coregonus albellus
Thymallus thymallus
Coregonus muelleri
Perciformes
Salaria fluviatilis Adria
Padogobius bonelli
Cottus gobio «Rhine»
Gambusia holbrooki
Cottus sp «Aare littoral lake sculpin»
Salaria fluviatilis Rhone
Perca fluviatilis
Micropterus salmoides
Cottus sp «Rhone lineage»
Cottus sp «profundal Thun»
Perca sp «Alpine lake perch»
Gymnocephalus cernua
Lepomis gibbosus
Cottus sp «Po littoral»
Cottus sp «profundal Lucerne»
Zander lucioperca
Gasterosteus aculeatus
Gasterosteus gymnurus
Cottus sp «Po profundal»
Cottus sp «profundal Walen»

Table 7: Notable taxa not recorded in Projet Lac.

Presumed extinct species

Coregonus fera	Geneva
Coregonus gutturosus	ConstanceObersee
Coregonus hiemalis	Geneva
Coregonus restrictus	Morat
Coregonus sp. “Zugeralbeli”	Zug
Coregonus sp. “Zugeralbock”	Zug
Salmo cf. schiefermuelleri	Lucerne
Salvelinus neocomensis	Neuchatel
Other undescribed *Salvelinus* spp	Documented in Geneva, Zurich

Presumed extirpated from region

Petromyzon marinus	
Lampetra fluviatilis	
Acipenser naccarii	
Acipenser sturio	
Alosa alosa	
Hucho hucho	Occured mostly in rivers
Misgurnus fossilis	Occured mostly in streams
Salmo salar	
Salmo trutta “Sea trout”	

Presumed taxonomic confusion

Carassius carassius Currently unclear if species was present in Switzerland north of the Alps and went extinct in the lakes or has always been misidentified.
Cobitis taenia Currently unclear if species was present in Switzerland north of the Alps and went extinct.
Phoxinus phoxinus All minnows of the northern perialpine lakes were previously considered to be *P. phoxinus*, however recent data revealed that the southern limit of this species is in central France and central Germany [14]. All records in Switzerland north of the Alps refer to two other species [15].
Barbatula barbatula All stone loaches of the northern perialpine lakes were previously considered to be *Barbatula barbatula*, however recent data revealed that the southern limit of this species is somewhere in northern France and Germany [151]. All records in Switzerland refer to three other species, *Barbatula quignardi* and two likely undescribed species (see Appendix A).

Commonness, rarity and distribution of fish species among lakes

Species-abundance distributions

The frequency distribution of species abundances in biological communities reflects the number of species recorded at each level of abundance. A fundamental characteristic of animal and plant community structure is that species abundances follow a lognormal distribution [16]. The distribution is almost invariably strongly right-skewed, with some species very rare (left side on the X axis), most species rare, fewer species abundant and just a few very abundant [17]. Because of its prevalence among a wide variety of taxa and ecosystems, the frequency distribution of abundances is referred to in ecology as the 'canonical distribution of commonness and rarity' [18]. It has been shown to be statistically robust and arise whenever a spatially structured community is sufficiently well sampled to recover also its rare species [19]. Variation in the shape of this distribution, especially the extent of skewness and the completeness of the left tail, contains information about the effectiveness of sampling and the extent of spatial abundance autocorrelation and species turnover between sites or samples. Specifically, larger turnover and larger spatial autocorrelation create greater right-skew, and effective sampling that includes the rare species, is expected to recover both tails of the species-abundance distribution. Conventionally, abundance distributions are log-transformed towards normality for better visualization.

The sampling data of Projet Lac was used to generate species abundance distributions for the CEN netting protocol, the VERT netting protocol and electrofishing for each lake (link methods). The data from all three methods was then combined in order to calculate an overall species abundance distribution for each lake. The occurrence of species in each lake was also used to generate a distribution of commonness and rarity in incidences of species across lakes. The distribution of the number of incidences (lakes) per species is related to the distribution of species range sizes. This distribution is not expected to converge on the canonical distribution of species abundances.

The 106 species of fish recorded in the lakes of the perialpine region range from very rare (occurring in a single lake and being rare there) to extremely common (nearly every lake and abundant in each). Based on incidences of species across lakes in the region (Figure 5), the distribution of commonness and rarity at this meta-ecosystem scale has its mode is on the smallest range class (occurrence in just one lake), and reflects a high degree of lake endemism in the perialpine lakes.

The species-abundance distributions for each lake revealed interesting variation between lakes and among catchments (Figure 6). As expected when sampling of a community does not recover all its rare species, the log-transformed distributions arising from any one sampling method alone often failed to recover the expected normal distribution. These distributions often peaked on very small, or even on the smallest abundance class (species recorded as a single individual; Figure 69). Combining the records from the three sampling methods moves the distributions for many lakes much closer towards the expected shape (Figure 6). This suggests that any one sampling method alone tends to fail to recover the complete species composition of the community, but that combining them can allow its recovery. However, interestingly, we find that the same combination of sampling methods and similar sampling effort that allowed the recovery of the expected species-abundance distribution for most lakes in the Rhine drainage still failed to recover the expected distributions in most Po and many Rhone drainage lakes. Especially in the Po lakes, including the intensively sampled Lakes Lugano and Maggiore, the most frequent abundance class were the species represented by a single individual. This suggests that additional rare species likely reside in these lakes that we failed to observe, more so than in most of the lakes of the Rhine catchment except Lake Morat. The reason for missing more rare species in these lakes, despite effort just as high as applied in the Rhine lakes, could lie in a stronger spatial turnover and/or stronger spatial autocorrelation in the southern lakes than in the Rhine lakes (e.g. rare species may be more strongly confined to specific small habitat patches), or that the southern lakes have a larger fraction of very rare species.

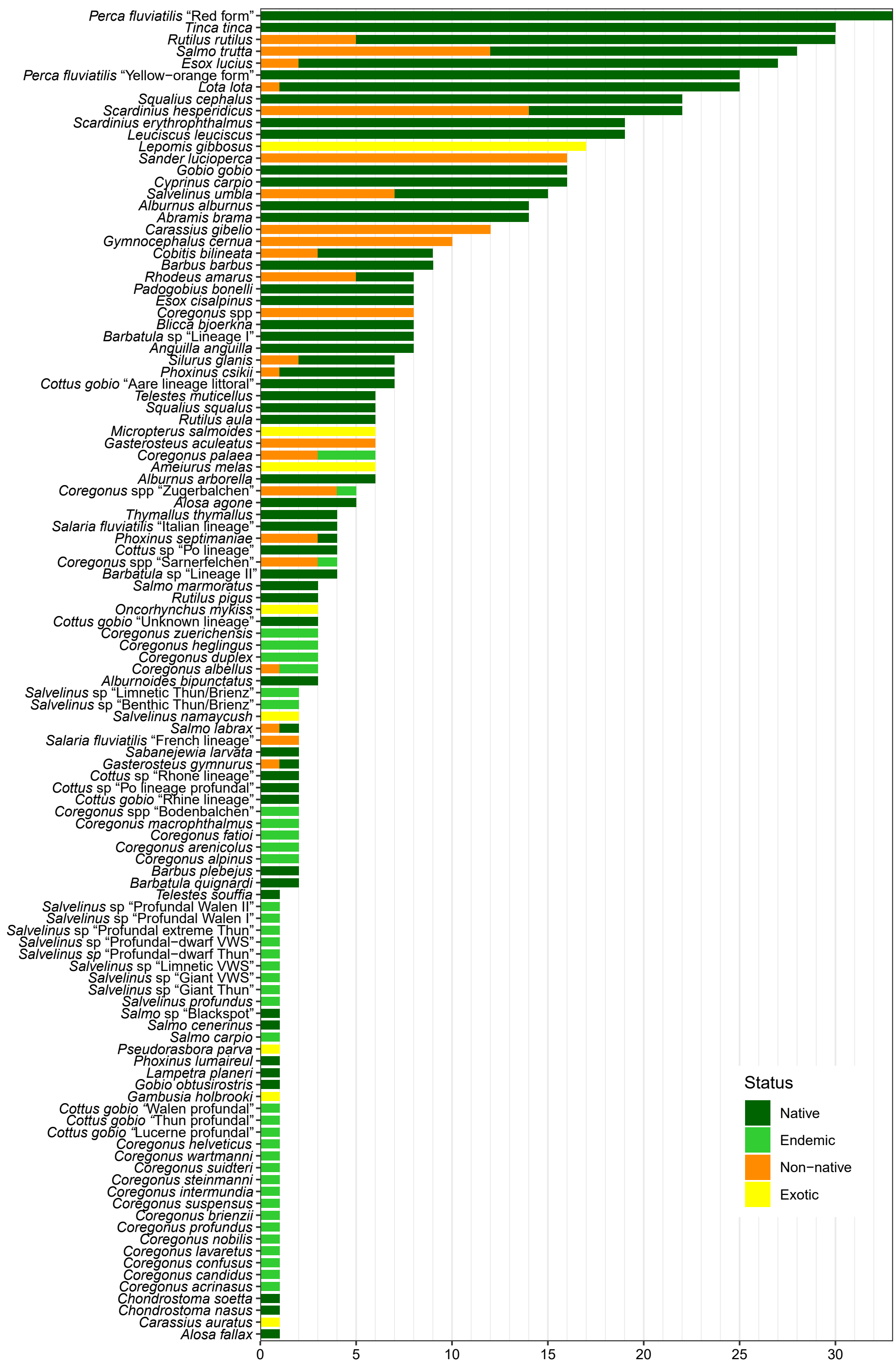

Figure 5: Number of lakes where each fish species was recorded in Projet Lac as native, endemic, non-native or exotic. Thirty-five lakes were surveyed as part of Projet Lac.

Widespread native species

The fish taxa most common among lakes, i.e. caught in the largest number of lakes, were *Perca fluviatilis* (both forms), *Esox lucius, Rutilus rutilus, Tinca tinca* and *Lota lota* (Figure 5). European perch (*Perca fluviatilis*) were recorded in all except the two alpine lakes, Sils and Poschiavo (33 lakes). All lakes contained the red fin form of the perch, whereas only the large northern perialpine lakes and three southern lakes contained additionally the yellow fin form. The yellow fin form dominated in many of the large northern perialpine lakes, whereas the red fin form dominated, or was the only perch form, in some of the large southern perialpine lakes and in all small and shallow lakes on either side of the Alps. Pike (*Esox* spp) were also recorded in all except the two alpine lakes: *Esox lucius* in northern perialpine lakes and *Esox cisalpinus* in the southern lakes (see taxonomic profile for *Esox* spp). Common roach (*Rutilus rutilus*) was present in all lakes north of the Alps and was recorded as introduced and invasive in Lugano, Maggiore and Varese (see taxonomic profile for *Rutilus* spp). *Tinca tinca* were recorded in all northern perialpine lakes, except Brienz and Walen, and in all southern perialpine lakes, except Garda. Finally, *Lota lota* was also common, particularly in the Rhine and Po catchments, recorded in 25 lakes. This species was notably absent from the catches in Lake Morat, although it was recorded in Neuchatel and Biel. It was also naturally absent from several French and Jura lakes (Bonlieu, Chalain, Remoray, Saint-Point), as well as the alpine lakes Sils and Poschiavo.

Some taxa were widespread at genus level, whereas their species were endemic. Different species of whitefish (*Coregonus* spp) were recorded in all northern perialpine lakes except Bret, were absent from the alpine lakes and were recorded as introduced species in most southern lakes (not recorded in Idro and Varese). Many of the endemic *Coregonus* species were locally abundant.

Common and abundant non-native and exotic species

Important non-native species across the surveyed region were *Lepomis gibbosus* (widespread and sometimes abundant) and *Gymnocephalus cernua* (relatively widespread and often abundant). Other non-native and exotic species contributed high numbers and/or biomass in certain lakes or sub-regions. For example, northern *Rutilus rutilus* dominated the fish community in southern lakes Lugano and Maggiore, and non-native salmonids *Salvelinus umbla* and *Salmo trutta,* and exotic *Salvelinus namaycush* dominated the alpine lakes Sils and Poschiavo. The non-native species caught in the largest number of lakes were *Lepomis gibbosus, Sander lucioperca, Scardinius hesperidicus* (non-native north of the Alps), *Carassius gibelio, Gymnocephalus cernua* in lakes across the region, and *Coregonus* spp, particularly in southern lakes.

Community composition by abundance/biomass among lakes and habitats

Abundance and biomass distribution

All lake assemblages had very large variation in the abundance of the recorded species. Most of the lakes in the Rhine catchment had abundance distributed over species in ways predicted by the lognormal "canonical" distribution of commonness and rarity [17], with few species abundant, most species rare and some very rare (Figure 6), whereas most lakes in the Po catchment and many in the Rhone catchment had the largest number of species very rare. Equitability of abundances varied considerably among lakes. The dominance by few abundant species was dramatic in Lakes Geneva and Zug that had more than 90% of their fish belong to two forms or incipient species, thed red and yellow fin types of perch (Figure 7). The distributions of biomass were slightly more even. Small lakes with few species tended to be less strongly dominated by single taxa, but tended to also have fewer rare species. Such lakes hence had numbers more equitably distributed over species (Figure 7)). Measuring abundance of species in natural communities is challenging and never free of methodological and observer biases. The necessity to combine several different methods for assessing abundance of fish across all the different lake habitats, each of which has its own biases, makes this especially difficult for whole-lake fish assemblages. Because of the associated caveats we refrain from more formal comparative analyses of biodiversity indices, variation within which resulst from variation in species richness and abundance equitability.

Whole-lake community composition

Characterising the lakes by the abundance of the most frequently caught species resulted in several groups of lakes with similar composition that we loosely refer to as lake fish community "types", albeit with some lakes intermediate between types (Figure 7). Catches in the alpine lakes Sils and Poschiavo were dominated by non-native *Salvelinus* (non-native *S. umbla* in Poschiavo and exotic *S. namaycush* in Sils). *Coregonus* spp dominated the catches in the lakes directly on the northern edge of the Alps (Lucerne, Walen, Brienz, Thun), as well as several Jura lakes as a non-native taxon (Saint-Point, Chalain). *Perca fluviatilis* dominated the whole-lake fish abundance in lakes Zug, Geneva, Neuchatel, Lower Zurich, Joux, Lower Constance and Upper Zurich. On the other hand, *Perca fluviatilis* dominated fish biomass only in Zug and Geneva, with *Coregonus* the dominant fish by biomass in the other lakes. *Rutilus rutilus* dominated the abundance in Lugano (non-native), Hallwil, Morat, Brenet, Remoray and Maggiore (non-native). Cyprinids, including *Rutilus rutilus, Scardinius* spp, *Abramis brama* and *Tinca tinca,* dominated the biomass in most of these lakes, however *Coregonus* spp were the dominant fish by biomass in Remoray and Maggiore (both non-native). Unique lakes were Lake Garda, dominated by the native pelagic species *Alosa agone*, and Upper Lake Constance, dominated in abundance by non-native *Gasterosteus aculeatus* (although whole-lake biomass was dominated by *Coregonus* spp).

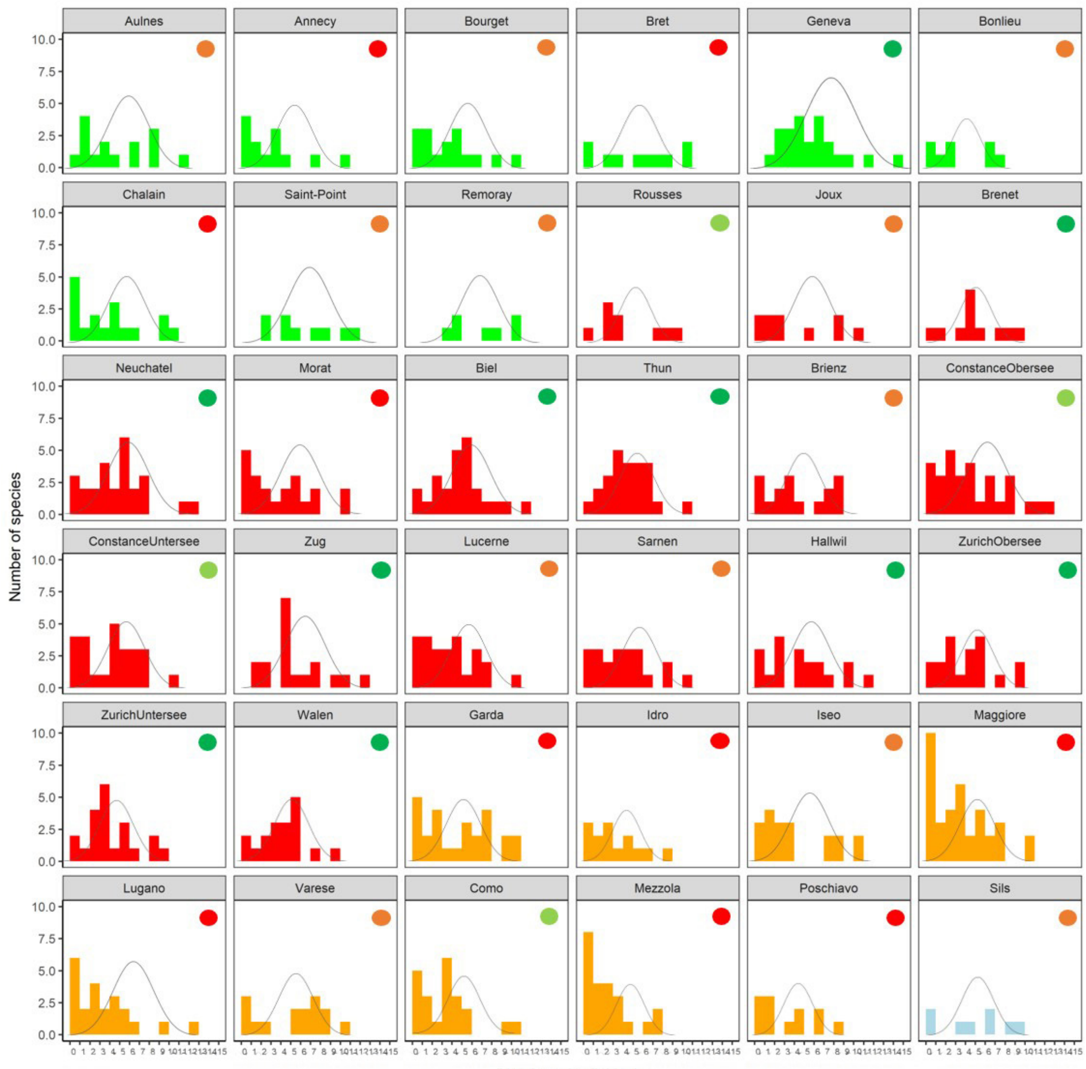

Figure 6: Species-abundance distributions (SADs) for each of 35 perialpine lakes and 1 lowland lake. These SADs result from combining partial SADs obtained by sampling with the CEN netting protocol, the VERT netting protocol and the electrofishing protocol (for all partial SADs see Appendix B Figure 69). Abundances are log2-transformed. Normal distributions are indicated by a thin line in each plot. The qualitative fit to the expected distribution is indicated by coloured circles: dark green = good fit, light green = modest fit, orange = poor fit, red = very poor fit. Colour of bars indicates drainage systems: green = Rhone, red = Rhine, orange = Po, blue = Danube. Note the systematic difference between Rhine lakes (9 good, 3 modest, 4 poor, 1 very poor) and Po lakes (0 good, 1 modest, 2 poor, 6 very poor). This difference cannot be due to differences in sampling effort because Maggiore and Lugano were among the best sampled lakes, but both have very poor fits to the expected distributions. Lake Aulnes is a lowland lake in the southern Rhone drainage that we sampled but did not otherwise consider in this report.

Community composition in major habitats

Fish community composition in the major habitats differed among lakes (Figure 70 to Figure 74), as reflected by the catches of the main sampling methods. The general pattern was for *Perca fluviatilis* to dominate the littoral and benthic zone to around 20 m deep (particularly in terms of abundance), while *Coregonus* spp dominated the pelagic, open water habitat (particularly in terms of biomass), and were especially numerous between 10 and 40 meters deep. There were however many interesting deviations from this pattern. For example, the fish communities of the alpine lakes, Sils and Poschiavo, were dominated by *Salmo* spp and *Salvelinus* spp, with *Phoxinus csikii* and *P. septimaniae* very abundant in the littoral zone of these lakes.

Littoral zone

This zone had a large number of species and the most even distribution of abundance and biomass among the resident species (Figure 70, Figure 71), however it contained the lowest number of endemic species. *Perca fluviatilis* was the most abundant fish in the littoral zone of many lakes, particularly in gillnet catches (Figure 70, Figure 71). *Rutilus rutilus* and *Scardinius* spp were also very common in this habitat. Biomass in the littoral zone was dominated by either *P. fluviatilis, Squalius* spp or *Esox lucius* in the electrofishing catches, while *Scardinius* spp, *Squalius* spp and/or *Rutilus* spp dominated biomass in the littoral of most lakes in the gillnet catches.

Benthic zone

This zone tended to have the largest number of species, and abundance was generally dominated by *Perca fluviatilis* (except in Sils and Poschiavo), often followed by *Rutilus* and sometimes by *Gymnocephalus, Scardinius* or *Coregonus* (only in ultra-oligotrophic Brienz, Thun and Walen) according to CEN gillnets (Figure 72). The benthic biomass was dominated by *Perca fluviatilis* and *Rutilus* spp in almost all lakes according to this sampling method, with *Scardinius* spp also making strong contributions in many lakes. *Coregonus* spp was abundant and contributed a substantial amount of biomass in the benthic zone of Thun, Brienz and Walen. Several endemic species of *Coregonus* occurred in this zone.

Pelagic zone

This zone had relatively few species but contained the largest proportion of endemic species. *Coregonus* spp dominated the biomass in the pelagic habitat in most perialpine lakes, while abundance was mostly dominated by one of either *Coregonus* spp, *Rutilus rutilus* or *Perca fluviatilis* (Figure 73, Figure 74). The pelagic zone of Lake Garda was dominated by *Alosa agone.*

Comparison between fish sampling methods in major habitats

The composition of fishes caught in the littoral zone differed greatly between gillnets and electrofishing (Figure 70, Figure 71). Abundance and biomass were more evenly shared among species within a lake in data from electrofishing compared to data from gillnetting (Figure 70). Community composition in the littoral zone was also more variable among the lakes by electrofishing compared to gillnet catches. In the open water, pelagic habitat, deep-set vertical nets (set in water > 5 m deep) and pelagic CEN nets provided a similar picture of fish community composition (Figure 73, Figure 74). Finally, the calculation of whole-lake community composition was heavily dominated by the fish caught in the open water, since this habitat constitutes a very high proportion by volume in the large lakes. On the other hand, the contribution of littoral and benthic fishes to the whole-lake community increases in smaller lakes. More details of the patterns of catches among habitats and sampling methods among lakes are provided in Appendix B – Supporting information.

Length frequency distributions

The length frequency distribution of a fish population, i.e. the number of fish of each size, is influenced by birth rates, individual growth rates and mortality rates of the population. Birth rates reflect the density of reproductively mature fish, the number of eggs produced by each female (fecundity) and the fraction of eggs that successfully hatch. The number of eggs per female and individual growth rates are influenced by the amount of food available to each individual, which is in turn affected by availability of the food resources and the density of competitors (i.e. density of the population, as well as populations of other species feeding on the same resource). Mortality rates include natural and harvest (fishing) mortality, with the relative importance of these changing with fish size. Smaller fish are most vulnerable to predation by birds and other fish, while larger fish of fishery-targeted species are more vulnerable to being removed from the population through fishing. Comparing length frequency distributions of common fish species among lakes can reveal differences in the relative importance of natural and anthropogenic pressures on the populations. The density of fish larger than the size efficiently caught by the smallest permitted gillnet mesh can also provide an indication of the amount of fish available to a fishery. Length frequency distributions were generated for the two genera that are most widespread, abundant and important to fisheries: *Coregonus* and *Perca*. Since the species in these genera are not, or not consistently, distinguished in the fishery catches, we present this data at genus level.

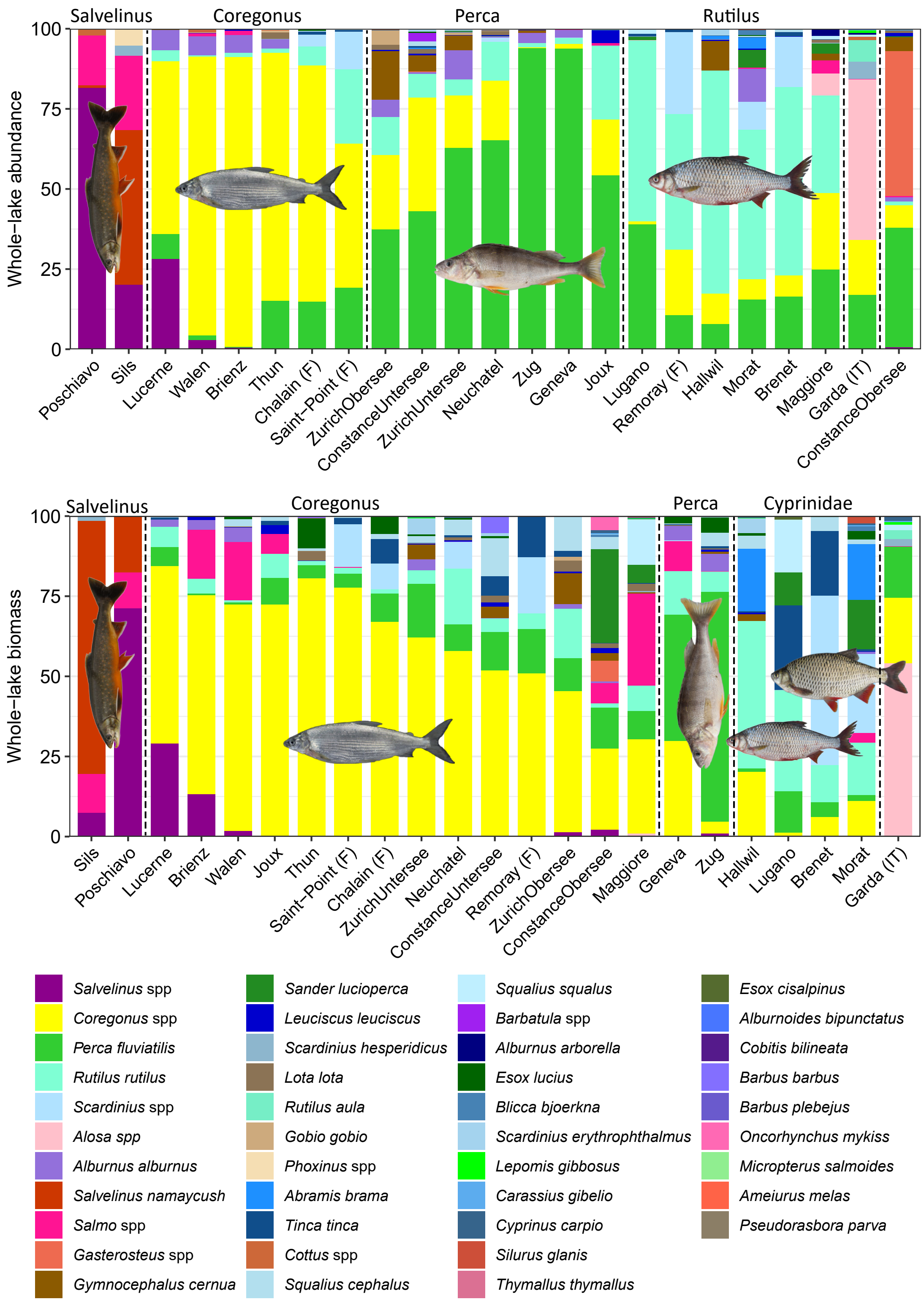

Figure 7: Whole-lake community composition based on CPUE in vertical nets. Upper panel shows volume-weighted average number of fish per 100 m² net area. Lower panel shows volume-weighted average biomass per 100 m² net area. Figure includes only lakes surveyed by the standard vertical net protocol. Lakes Sarnen and Biel were sampled with a modified protocol and are excluded here. The smallest lakes Bret and Bonlieu are also excluded. Note that sequence of lakes along the X axis differs between the panels.

Coregonus spp

The average minimum permitted mesh size for gillnets used by professional fishers to catch *Coregonus* spp at the time of Projet Lac sampling was 35 mm, however this varied from 23 mm in lakes Joux, Brenet and Morat, to 50 mm in Lake Annecy. Gillnet mesh of 35 mm efficiently catches Coregonus spp around 300 - 350 mm in length. Large lakes with very low nutrient concentrations (total phosphorus < 5 µg/L) tended to have very high numbers of small Coregonus spp (total length < 250 mm; e.g. Thun, Brienz, Lucerne, Walen). Very few Coregonus larger than the size efficiently caught in the minimum permitted mesh size by commercial fishers were caught by Projet Lac in lakes Lucerne, Walen, Brienz, Upper Zurich and Garda. The slower-growing species of Coregonus tend to dominate in lakes with low nutrient conditions, and other Coregonus species may also exhibit slower growth rates in these lakes. Under these circumstances, even light fishing pressure may remove most of the larger fish from the population. In general, few large Coregonus were caught in lakes with commercial fishing, with notable exceptions being Geneva and Joux, and to a lesser extent, Brenet, Neuchatel, Morat, Maggiore, Thun, Hallwil and Lower Zurich. Jura lakes, Chalain, Remoray and Saint-Point, had no commercial fishing and had the highest densities of Coregonus larger than 300 mm. These results suggest that the length frequency distribution of Coregonus in the sampled lakes was mostly shaped by a combination of lake productivity and fishing pressure.

Perca fluviatilis

The minimum permitted mesh size for gillnets used by professional fishers to catch *Perca fluviatilis* at the time of Projet Lac sampling was around 25 mm in most lakes, however this varied from no minimum size limits in Annecy and Bourget, to 37 mm in Lake Garda. Gillnet mesh of 25 mm most efficiently catches perch around 180-200 mm in length.

Lake Lugano had the highest numbers of *Perca fluviatilis* available to the fishery at the time of Projet Lac sampling, with high numbers also in Maggiore and Garda. This may reflect faster growth rates in the warmer water of the southern lakes [20] and/or a lower influence of fishing on the size structure of perch in these compared to other sampled lakes. Other lakes with large numbers of perch slightly larger than the size caught by the commercial fishers were Morat, Thun, Zug and Lower Zurich. Lakes without commercial fishing tended to have the highest numbers of perch in the largest size classes.

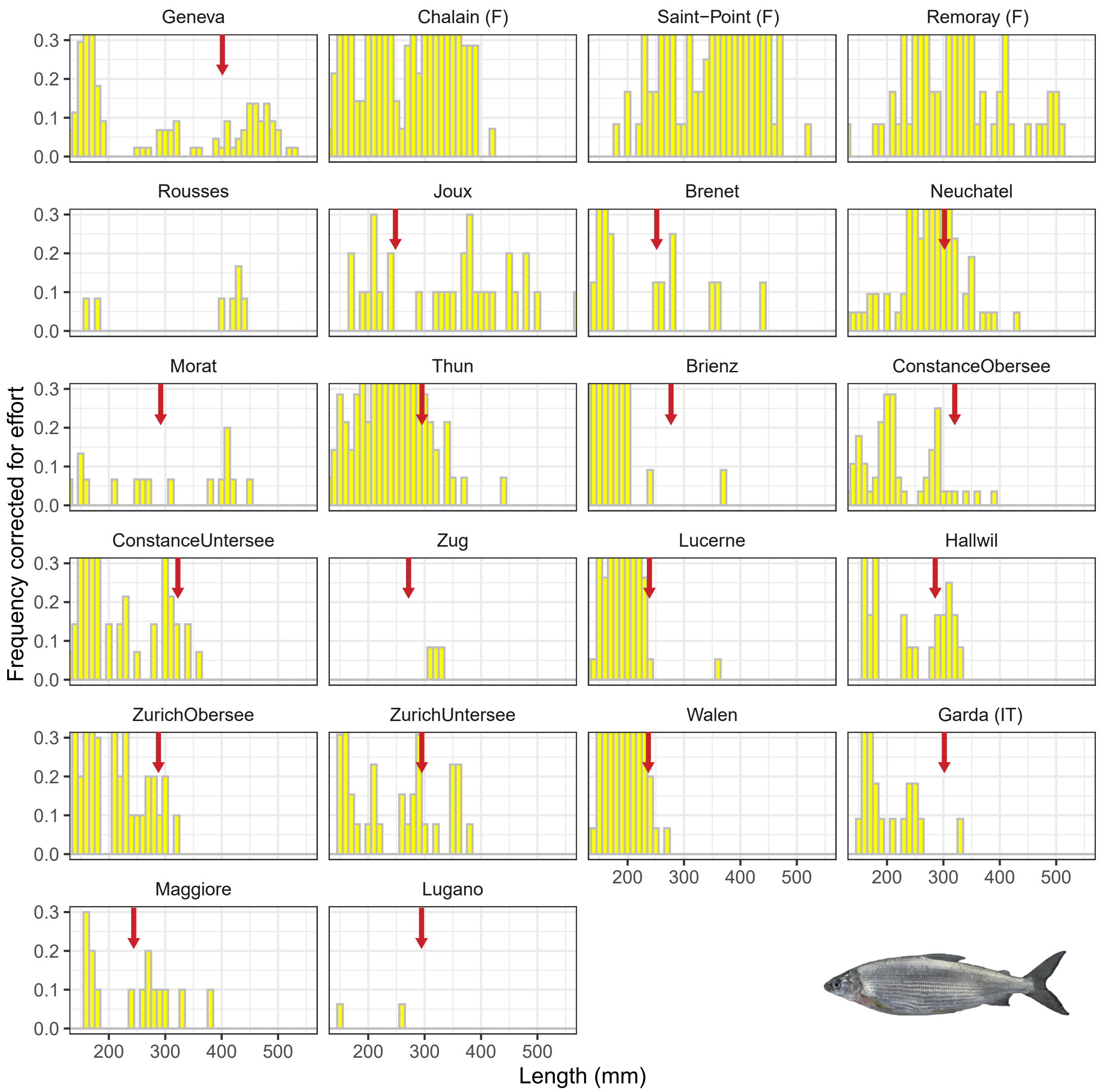

Figure 8: Length frequency distribution of Coregonus spp among lakes. Data from deep-set vertical nets (set deeper than 5 m). The number of fish is adjusted for the number of vertical net batteries deployed in the lake. Vertical axis is truncated at 0.3 fish per vertical net battery to focus on the occurrence of the larger fish. Arrows indicate the approximate length of fish at which permitted nets for commercial fisheries become efficient. There was no commercial fishing in lakes Chalain, Saint-Point, Remoray and Rousses at the time of Projet Lac sampling. Lakes Biel and Sarnen are excluded as the different mesh sizes used in the Projet Lac sampling of these lakes influences the fish length frequency distribution, meaning that it is not possible to directly compare them to the other lakes.

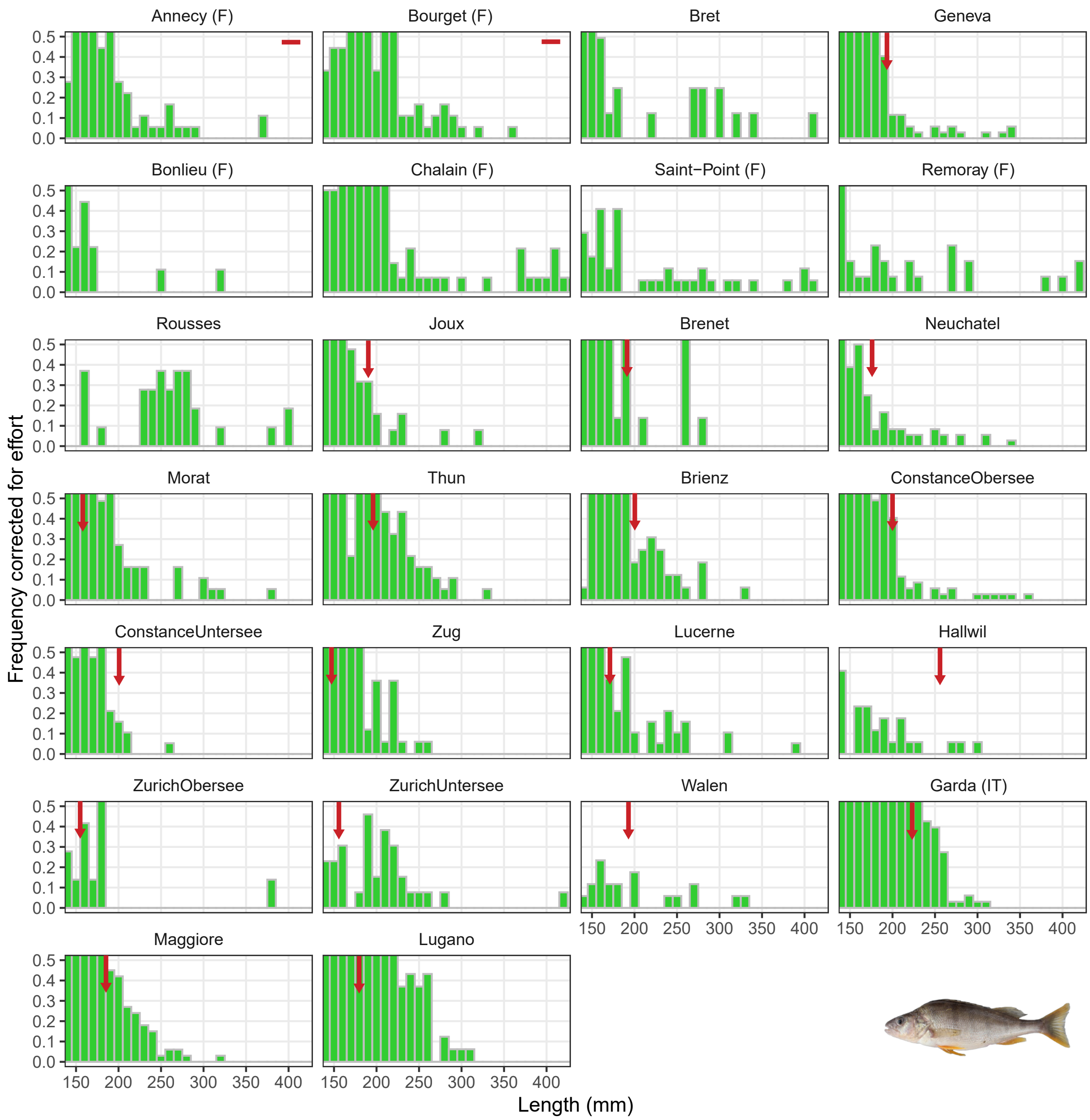

Figure 9: Length frequency distribution of large perch among lakes. Data from benthic CEN nets to 20 meters deep. The number of fish is adjusted for the corresponding gillnetting effort in the lake. Vertical axis is truncated at 0.5 fish per 100 m^2 of net to focus on the occurrence of the larger fish. Arrows indicate the approximate length of fish at which permitted nets for commercial fisheries become efficient. There was no commercial fishing in lakes Bret, Bonlieu, Chalain, Saint-Point, Remoray and Rousses at the time of Projet Lac sampling. No minimum size limit for perch in Annecy and Bourget. Lakes Biel and Sarnen are excluded as the different mesh sizes used in the Projet Lac sampling of these lakes influences the fish length frequency distribution, meaning that it is not possible to directly compare them to other lakes.

5. Natural and anthropogenic factors influencing lake fish communities

The following discussion addresses the major natural and anthropogenic factors influencing lake fish communities among and within lakes in the perialpine region, and highlights the insights gained from analyses of Projet Lac data. In cases where this first round of Projet Lac surveys are limited in the information they can provide on a particular topic, results from other relevant research are consulted in order to cover all of the most important factors.

Natural factors

Historical biogeography

Historical biogeography shaped native species composition
Geological histories of the lakes and evolutionary histories of the resident fishes shape the present-day distributions of species and the similarities and differences between assemblages. This is the subject of the field of 'historical biogeography' [21]. The particular set of fish species observed in each lake was strongly related to biogeography, primarily in terms of the three major river basins, Po, Rhone and Rhine. These patterns reflected the higher connectivity among lakes within the major basins, and the basin's current and past connections to glacial refugia [22] (Appendix B – Additional background information). Additionally, the position of the lake relative to the Alps (within, peripheral or away from the Alps) had detectable effects within major river basins. Clustering lakes by the set of recorded fish species revealed four major groups, which generally corresponded with the Rhone, Rhine, Po river catchments, as well as the truly alpine lakes (Figure 11). These groups of lakes differed in the number of native species, partly due to the uneven distribution of different-sized lakes among the catchments (see section 'Species area relationships and island biogeography'), and the composition of the native species, related to the lake's connection to different glacial refugia (Appendix B – Additional background information).

Despite the close match of the clusters of similar fish communities to the major river catchments, there were some exceptions (Figure 11). The set of native fish recorded in Lake Geneva (Rhone) was more similar to lakes in the Rhine, partially due to the higher number of species in this lake than in other Rhone lakes. It is also believed that Lake Geneva was mostly colonized by fish from the Aare/Rhine catchment. The lakes on the northern edge of the Rhone glacier (known as 'proglacial lakes'), just north of modern Lake Geneva, were connected to the Aare until very late in the Pleistocene or the beginning of the Holocene. At this time, the outlet of the southern proglacial lake became dominant and diverted the lake's outflow into the Rhone [23] (a process known as 'drainage capture'; Appendix B – Additional background information). Other exceptions in the groupings were three smaller lakes at the periphery of the Rhine catchment (Joux, Brenet, Rousses) that clustered with Rhone lakes. This similarity was driven by the absence of many common Rhine species from these lakes rather than having any Rhone-specific taxa.

The set of native fish species recorded in the alpine lakes, Sils and Poschiavo, were very different from those of the other lakes (Figure 11, Figure 7). The higher altitude and mountainous terrain around these lakes represent barriers to immigration, making the lakes difficult for most fish species to naturally colonise. As a result, these lakes contained a much lower number of native species and were missing many of the species that were common among other lakes e.g. *Perca fluviatilis, Rutilus* spp, *Esox* spp. Instead, the communities of the small, cold and isolated alpine lakes were dominated by several species of trout recorded by Projet Lac only there (but which were once more widely distributed; see taxonomic profile for *Salmo* spp), along with *Phoxinus* and *Cottus* (Poschiavo only), non-native *Salvelinus umbla* and exotic *Salvelinus namaycush.* On the other hand, the cool-water lakes on the immediate periphery of the Alps, as well as the Jura lakes, tended to be dominated by *Coregonus* (along with native *Salvelinus* spp in the case of Lake Lucerne and to a lesser extent Lake Brienz). Cyprinids tended to be most common in the warmer, lower-altitude midland lakes and the southern perialpine lakes (which also tended to have higher nutrient concentrations).

The lakes north and south of the alpine mountain chain had very different native fish communities, with most genera represented by different native species on either side of the Alps (Table 19) and with 21 species recorded exclusively in the southern lakes (Figure 11). In fact, *Anguilla anguilla* (European eel), *Cyprinus carpio* (common carp), *Tinca tinca* (tench), *Lota lota* (burbot) and the *Perca fluviatilis* (perch; yellow finned and red finned morphs) were the only species that naturally occur on both sides of the Alps. This said, carp was introduced in historical times, and it is actually unclear whether tench and yellow fin perch are truely native south of the Alps. The differences between the lacustrine fish assemblages north and south of the Alps were therefore primarily driven by biogeographic species turnover. Species recorded in all southern perialpine lakes were *Esox cisalpinus*, *Padogobius bonelli* and *Scardinius hesperidicus,* as well as the non-natives *Lepomis gibbosus* and *Carassius gibelio*. Species recorded only in the southern lakes were *Alburnus arborella, Rutilus aula, Squalius squalus, Telestes muticellus* and non-native Micropterus salmoides.

North of the Alps, differences in the lake fish communities between the Rhine and Rhone catchments were less pronounced (Figure 11), however a few genera have species or subspecies native to each basin. *Telestes souffia souffia* was recorded in Lake Chalain (Rhone), whereas *T. souffia agassii* occurs in the Aare-Rhine. The latter subspecies was however not recorded by Projet Lac. Deep divergence in mitochrondrial lineages of *Leuciscus leuciscus* was also detected between Lake Chalain and the Aare-Rhine lakes, however these lineages are not currently recognized as taxonomically distinct.

Rather than being driven by biogeographical species turnover, the differences between the Rhone and Rhine lakes were driven mostly by differences in environment and isolation that resulted in reduced species richness in Rhone lakes where most species were shared with Rhine lakes. A higher number of larger and deeper lakes in the Rhine group (including Lake Geneva) corresponded with a larger number of native and endemic species in these lakes (see section 'Species-area relationships and island biogeography'). Fourty-five native species were recorded as native only among the lakes of the Rhine group, including many species of endemic *Coregonus* and *Salvelinus*. The Rhone biogeographic group (i.e. Lakes Bourget and Annecy, and the small Rhone lakes, but also Joux, Brenet, Rousses that group with the Rhone lakes) were mostly smaller lakes, with low numbers of native species. The native species recorded in these lakes were largely a subset of the common species recorded in the lakes of the Rhine group. Only four native species were recorded as native only in the lakes of the Rhone group (none of them in the small Rhine lakes that cluster with the Rhone group).

Within the major river catchments, differences between lakes in altitude and distance along rivers explained variation in the similarity of fish community composition among lakes (Figure 82). In the Rhine catchment, the distance between the lakes along rivers, as well as differences in altitude, explained differences in the fish species composition between the lakes (Mantel tests: $p < 0.001$, $R^2 = 0.285$ for distance by river; $p < 0.001$, $R^2 = 0.290$ for altitude). Altitude also explained differences in the species composition among lakes in the Po catchment ($p = 0.014$, $R^2 = 0.842$; with strong explanatory power also when Lake Poschiavo was excluded). No clear driver of the composition of fish community emerged within the Rhone catchment. The altitude of a lake influences lake water temperature and the connectivity to the rest of the lake-river network. Higher altitude lakes are generally cooler and more isolated, as well as tending to be smaller than their lowland counterparts. The distance between lakes along the river network correlates with differences in altitude, but also reflects the higher similarity of communities within the different subcatchments, e.g. Aare, Limmat, Reuss, nested within the major river catchments.

Highest number of endemic species in Rhine lakes Thun and Lucerne

Spatial patterns of endemic species were also closely related to biogeography, with the highest number of endemic species in the lakes of the Rhine catchment (Table 5). The lakes directly on the edge of the Alps, particularly lakes Thun and Lucerne, had especially high numbers of endemic species. All of these endemics are cold-water-adapted fish (whitefish, charr, sculpins), with many adapted to living in the profundal habitat. Likely drivers of this pattern are the cooler water temperature and good oxygenation of the deep waters in these lakes. This is related to the comparatively lower influence of human activities (i.e. lower human population density, more natural land cover in the catchments and weaker anthropogenic eutrophication), such that few endemic, deep-water species went extinct in these lakes.

The highest recorded number of endemic species was in Lake Thun with ten species: six species of *Coregonus*, at least three species of *Salvelinus* and a profundal sculpin (*Cottus gobio* "Profundal Thun"; in addition to a littoral sculpin (see Appendix A)). Note however that the endemic *Coregonus acrinasus* (Albock) carries a strong signature of hybridisation between native and non-native *Coregonus* species, the latter of which were introduced from Lake Constance several decades ago [24]. This species is thus considered to be both endemic and (partly) non-native. At least two additional endemic, ecologically distinct forms of *Salvelinus* are known from Lake Thun [25], which were not recorded in Projet Lac (Appendix A – Family Salmonidae).

Five endemic species were recorded in Lake Lucerne, with three species of *Coregonus* and two distinct sympatric forms of *Salvelinus* (in addition to the sympatric generalist *S. umbla*). Two additional endemic *Coregonus* species and at least one additional distinct ecological form of *Salvelinus* are also known in Lake Lucerne, but were not recorded in Projet Lac [26, 27]. Similar to *Coregonus acrinasus* in Thun, one of the endemic species of whitefish of Lucerne (not recorded in Projet Lac), *Coregonus suspensus*, shows strong signatures of hybridization with Lake Constance species that were stocked into Lake Lucerne several decades ago [26].

Also in the Rhine catchment, six endemic species were recorded in Lake Brienz (four *Coregonus* species; plus at least two endemic species of *Salvelinus* known from other Eawag work but not encountered during Projet Lac), and four in each of lakes Walen (two *Coregonus* species and two *Salvelinus* species [forms]) and Upper Constance (three *Coregonus* species, *Salvelinus profundus*). The smallest lakes, Rousses, Joux, Brenet, as well as Hallwil, were the only lakes of the Rhine catchment where no endemic species were recorded. Importantly, these lakes do not harbour endemic phenotypically distinct morphs either.

Only a single lake-endemic species was recorded in each of the Rhone and Po catchments. The endemic profundal trout *Salmo carpio* was recorded in the largest lake of the Po catchment, Lake Garda (it is possible that the profundal *Cottus* species in Lakes Garda and Maggiore are endemic, but this is currently unknown). *Coregonus lavaretus* was the only recorded endemic species in the Rhone catchment in Lake Bourget (a second endemic species, *C. bezola*, is extinct from this lake). The high number of endemic species in the lakes of the Rhine catchment resulted in a high uniqueness of the fish assemblages in many of these lakes compared to those of the Po and Rhone catchments (Figure 10).

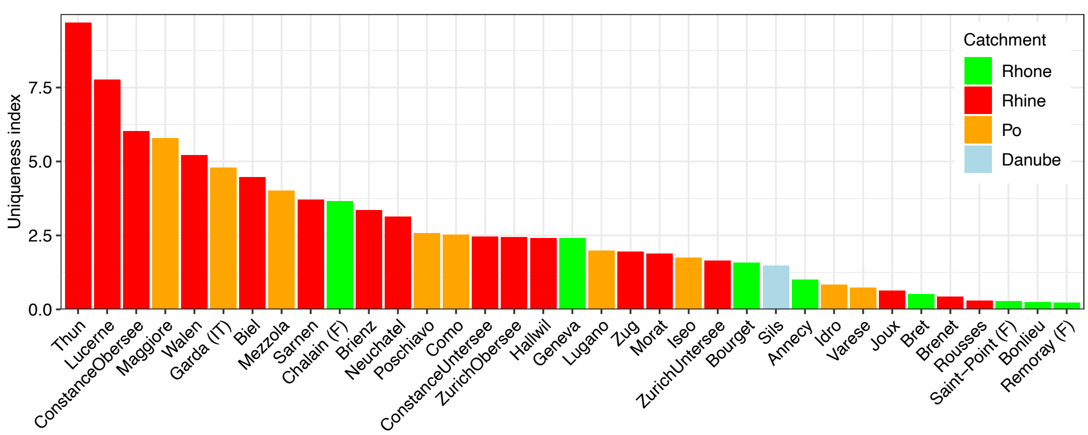

Figure 10: Uniqueness of the fish communities of all lakes and catchments. Uniqueness index for each lake was calculated as the sum of the inverse of the number of lakes where each species in the lake was recorded.

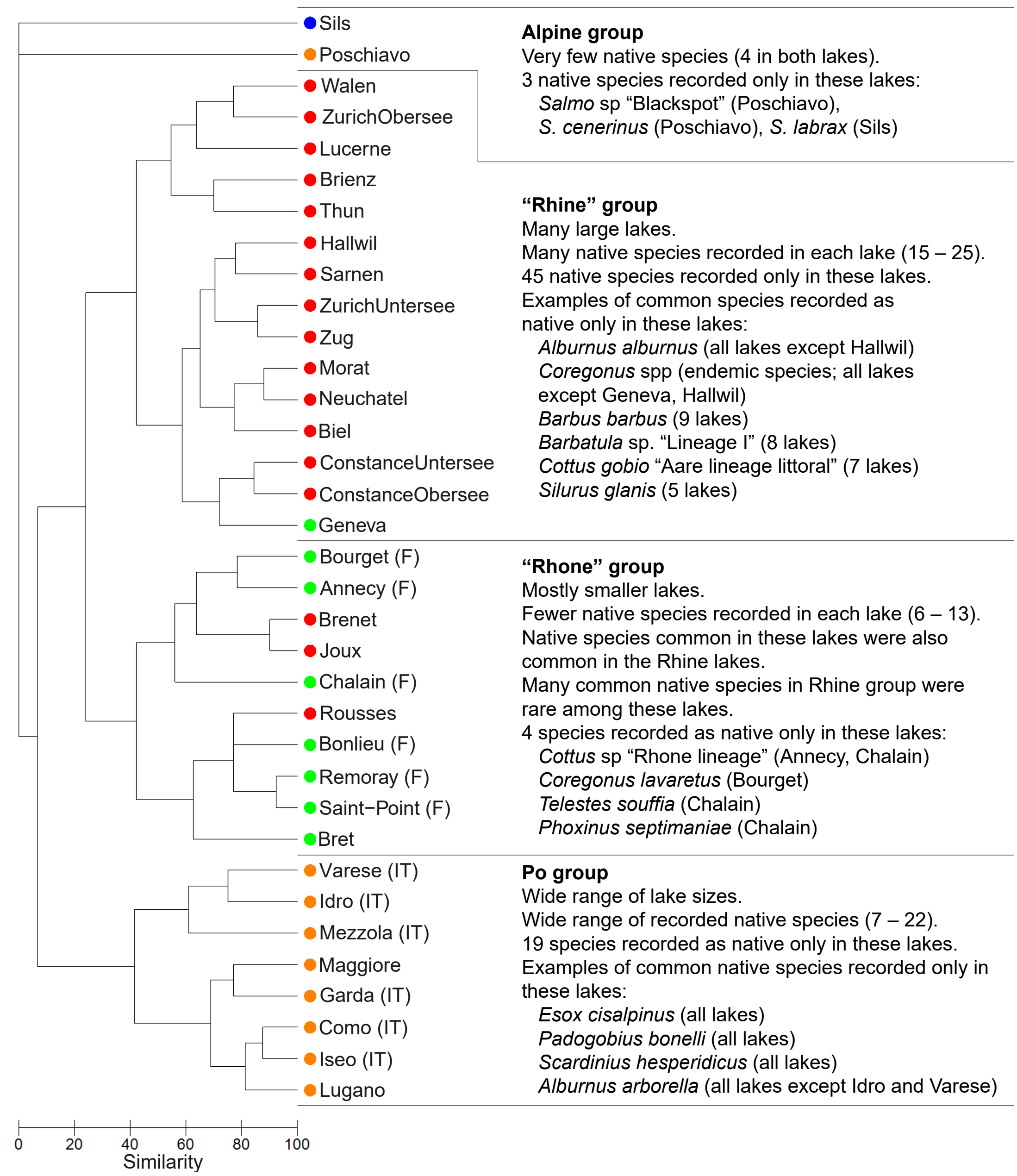

Figure 11: Similarity of the native fish species assemblages among lakes sampled by Projet Lac depicted by hierarchical cluster analysis (Sørensen index based on presence/absence of taxa; complete linkage). Lakes joined by shorter branches share a higher proportion of their fish species. Colours indicate river catchments: red = Rhine, green = Rhone, orange = Po, blue = Danube. See Figure 82 for an exploration of factors driving differences in the fish communities among lakes within catchments.

Species-area relationships and island biogeography

Whereas historical biogeography seeks to explain geographic patterns in biodiversity by historical influences, such as past and present connections between drainage systems or distances to different glacial refugia, island biogeography explains patterns based on general ecological and evolutionary principles. These two domains of biogeography are complementary in their explanatory approach. Island biogeography is powerful for explaining variation in species richness in space and time, but it ignores the identity of species and their characteristics. Historical biogeography on the other side wants to explain how specific regional biota came to be. It is explicit about the identity of species and their characteristics, but is less powerful for explaining larger scale variation in richness. Understanding both is essential for applied biodiversity management and conservation because it is the starting point for understanding variation between lakes in species richness.

The general ecological principles that island biogeography builds on include the relationships between area size, population size and population persistence or probability of extinction and the relationships between spatial isolation, dispersal and colonization rate ("insularity"). Its development is rooted in classical work by Arrhenius [28], Gleason [29] and Preston [17] and was influentially formalized by MacArthur & Wilson [30] in the Equilibrial Theory of Island Biogeography and later by Whittaker [31] and others in nonequilibrial theories. Although initially developed based on terrestrial islands in the ocean [30], lakes have played importantly in island biogeography, sometimes referred to as "inverted islands". Even though many lakes are ultimately connected by rivers, dispersal between them is usually limited. For species adapted to specific lacustrine niches, such as the profundal zone, rivers often constitute hostile habitat (e.g. a profundal char will rarely swim down the Rhine out of Lake Constance). Island biogeography predicts that species richness is positively correlated with habitat area and negatively correlated with isolation from the source, and that biotic uniqueness increases with increasing distance and increasing area. These predictions have been confirmed for fish in lakes [32], but had not previously been tested for the fish communities of the perialpine lakes of Europe.

Area is by far the strongest predictor of species richness across a wide range of habitats and taxa [33]. Lake surface area has been shown to be a strong predictor of fish species richness among sets of lakes in lowland Europe [34, 35], North America [35] and Africa [36], among others. Lake surface area has also been shown to predict the richness of fish species in a broad-scale analysis of lakes across Europe surveyed with the CEN gillnet protocol [37]. Species-area relationships are statistically assessed by fitting linear models of the number of species in a community versus area size occupied by that community (e.g. lake size). Variation in slopes reflects variation in the extent of isolation: when communities are strongly isolated from the source pool (i.e. the next large lake), such that colonisation is a rare event, local extirpation of a species cannot quickly be compensated by renewed immigration of the same or another species into the community from outside. Because the rate of extinction is inversely related to area size (mediated by effects on population size, extinction is more common in smaller lakes), smaller lakes are the more depauperate in species relative to larger lakes the stronger they are isolated. Different intercepts of the species-area relationship for different regions reflect variation in the richness of regional species pools (the number of species available for colonisation). The slope and intercept of the relationship between the number of fish species and lake size in the perialpine lakes therefore provide important and management-relevant information on the forces that rule community composition, drive variation in species richness, and on the effects of local population extirpation on long term local species richness. For instance, steeper slopes that imply that communities in different lakes are strongly isolated from one another, lead to the expectation that lake populations of one species are genetically isolated between lakes and may hence represent unique units of biodiversity with implications for conservation.

All aspects of lake fish diversity increased with lake surface area

Differences in the number of fish species recorded by Projet Lac in each lake were indeed best explained by differences in the lake surface area. Larger lakes supported more species. The total number of recorded species increased with lake area, as did the number of species within each of three categories of species that differ in the intimicy of historical and evolutionary association with a lake and the rest of its community: endemic species that have arisen within a lake, native species that have been present in a lake for many centuries or millennia, and non-native species that have arrived in recent decades. Larger lakes also tended to be deeper, warmer and at lower altitude (Figure 86, Figure 87), but none of these variables explained richness variation as well as surface area.

The slopes of the species-area relationships varied between catchments and between the three categories of species (Table 8; Figure 12). Intercepts of the species-area relationship for native species did not differ much between catchments even though the species pool was much larger in Rhine and Po than in the Rhone (Table 9). This may suggest that in small lakes richness is determined primarily by the ecological carrying capacity for species which would be similar between catchments. If true, then richness of small lakes could be rather independent of the number of species that exist in the regional species pool. Slopes of the species-area relationships for native species are steeper in Rhine and Po than in the Rhone, indicating stronger biotic isolation and associated stronger dependency of species richness on lake area. This was true when for each lake we counted the number of taxa that had colonized it (i.e. counting each endemic species radiation just as a single taxon, i.e. derived from a single colonization event) and also when we counted each member species of an endemic species radiation. Slopes of these relationships were generally relatively shallow (z=0.11-0.165 for native species; Table 8, Table 1), suggestive of overall limited isolation, but they became steeper when all members of endemic species radiations were counted, as opposed to when radiations were counted as single taxa ($z$max 0.165 vs 0.148). This is consistent with the theoretical expectation that origination of species richness through local (*in-situ*) speciation is more strongly dependent on area size than accumulation of species richness by colonization (because between speciation, occasional colonization, and recurrent dispersal as processes for species addition, speciation is the slowest). In the Rhine catchment with its many endemic species radiations, the slope for endemic species alone is again much steeper: z=0.28. This value lies within the range known for island communities of terrestrial animals in oceanic island archipelagos (typical range z=0.25 - 0.55). It implies that the importance of speciation as a source for adding fish species to a lake in the region increases steeply with lake size [36]. That in-situ speciation increases the slope of the species-area relationship for fish in lakes had previously been demonstrated for cichlid fish in African lakes [36]. Our data suggest that it applies to the fish communities of the pre-alpine lakes too, albeit detectably so only in the lakes of the Rhine catchment.

When non-native and exotic species were included, the species-area relationships for lakes in the Rhine and Po catchments became shallower while that among lakes in the Rhone catchment became steeper. The species-area-relationship for non-native and exotic species alone were also positive in all catchments, but very shallow and non-significant in Rhine (z=0.095) and Po (z=0.077), while the relationship in the Rhone was significant and somewhat steeper (z=0.132; Table 8). This suggests that in the Rhone catchment but not necessarily in Rhine and Po, larger lakes either receive more introductions than smaller lakes, or non-native and exotic species establish populations more often in larger lakes.

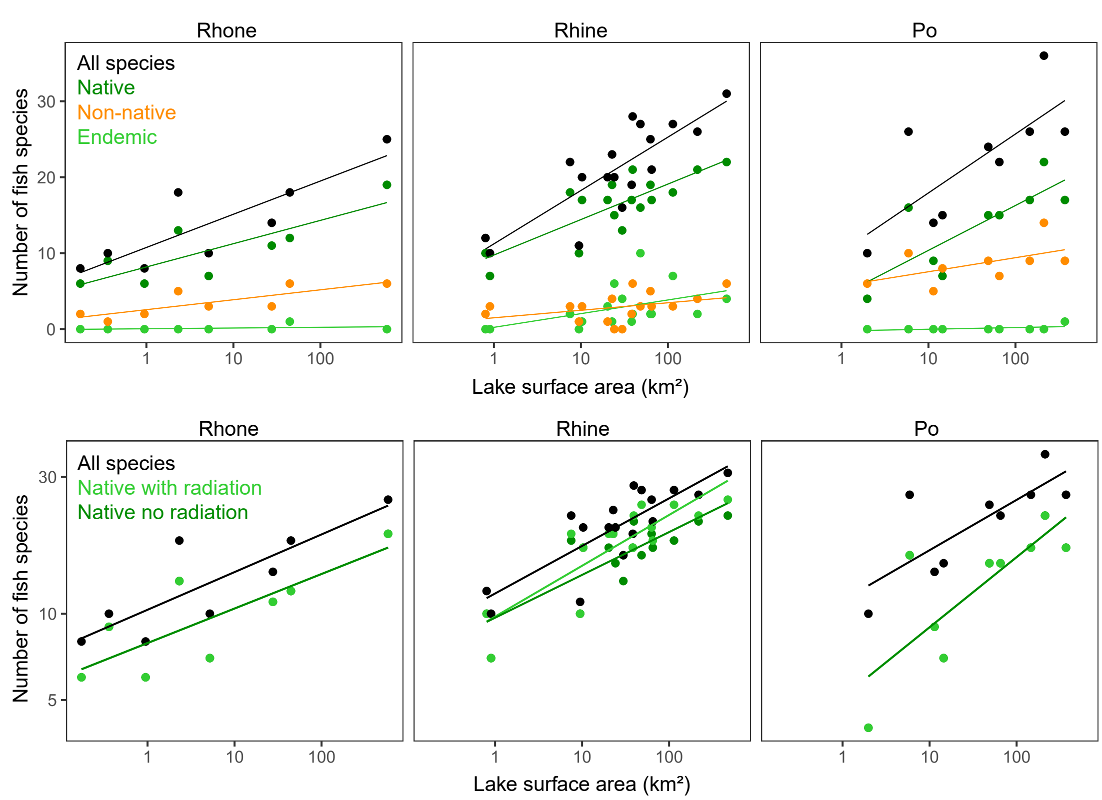

Figure 12: All components of fish species diversity increase with lake surface area: total number of species, number of native species (counting each endemic radiation as a single taxon), number of endemic species (including each radiation species), and number of non-native and exotic species. Slopes and intercepts varied among river catchments. In the upper panel, only the horizontal axis is on log scale, in the lower panel both axes are on log scale. Regression statistics are provided in Table 8.

Table 8: Regression statistics for species-area relationships shown in Figure 12. Coloured cells indicate significant relationships. Models log(X)-log(Y+1).

	Catchment	p-value	Slope	Intercept	R-squared
All species	Po	0.102	0.123	2.687	0.383
	Rhine	0.00004	0.157	2.546	0.685
	Rhone	0.008	0.122	2.43	0.717
All native species	Po	0.088	0.148	2.134	0.409
	Rhine	0.00002	0.165	2.379	0.713
	Rhone	0.016	0.11	2.19	0.647
Native species but radiations counted as single taxon	Po	0.088	0.148	2.134	0.409
	Rhine	0.00008	0.138	2.37	0.655
	Rhone	0.016	0.11	2.19	0.647
Endemic species	Po	0.163	0.089	-0.262	0.297
	Rhine	0.004	0.283	0.182	0.44
	Rhone	0.441	0.029	0.039	0.102
Non-native and exotic	Po	0.275	0.077	1.959	0.194
	Rhine	0.289	0.095	0.917	0.075
	Rhone	0.019	0.132	1.202	0.63

The intercepts of species-area relationships for all native species and for all species combined were similar in all catchments but a little higher in the Rhine than in Po and Rhone. The intercept of the species-area-relationship for non-native and exotic species was much higher in the Po than in the Rhine catchment and was intermediate in the Rhone catchment. This suggests a larger pool of non-native and exotic species in the Po (Table 8, see also Table 5).

The above analyses were based only on species records from Projet Lac. However, we note that in the Projet Lac survey, several species that are generally distributed in rivers and lakes are missing from lakes where they were recorded in recent years by others ([38]; Table 16). Therefore, we performed a second analysis of species-area-relationships using Projet Lac data complemented by the additional published species records from Zaugg and Huguenin [38]. Some of these species may have been extirpated in some of the lakes in recent years, others may be so rare that we failed to find them. Including such species in the estimation of species-area relationships is important. Unfortunately no similar standardized and reliable data was available to us for the Rhone and Po catchments.

Additionally to these cases of species missing-in-action, a significant number of fish species extinctions and extirpations is indeed known to have occurred in historical times. Therefore, we wanted to include also these species in order to estimate the species-area-relationships for communities prior to these recent extinctions. This again was constrained by heterogeneity in the quality and completeness of historical records and we could only assemble this data with modest confidence for the lakes in the Rhine catchment. The resulting relationships are presented in Figure 13 and Table 9 and are summarized as follows. Adding extinct and extant species that were not recorded in Projet Lac increased the slopes of species-area relationships for all categories of species, and all became statistically significant. The slope for the relationship for all native species increased the most, from z=0.165 to z=0.228. The steepest slope (z=0.288) was again observed for endemic species. The number of extinctions also showed a significant positive relationship with lake size, suggesting that recent extinctions happened primarily in the larger lakes. These analyses show us that with survey data alone, we strongly underestimate the combined effects that isolation and lake size play in the assembly of these lake fish species communities. Especially noteworthy is that adding to the survey data only those species that had been recorded in recent years and are presumably extant but were not recorded during the survey (not including the known extinct species), increased the slope from z=0.157 to 0.184. This means that lacustrine populations of these more widespread but locally rare species are or were largely confined to the larger lakes. Everything else being the same, larger lakes allow larger populations of each species, meaning that population fluctuations rarely make a population size drop to zero (e.g. go locally extinct). Because larger lakes can accommodate more individuals across all species combined, they can also support a larger number of species at population sizes that are long term viable. This of course only matters to populations that are selfstustaining in the lake. It would not matter to species thar live in rivers and only enter lakes sporadically. That lacustrine populations of species that occur in rivers and lakes are or were largely confined to the larger lakes is not expected if the lacustrine records of these taxa were just based on stray individuals from river populations because such should be at least as often seen in small as in large lakes (recall that all lakes in the Rhine system are connected by the rivers). Instead the data suggest that lake populations of many of the more widely distributed but locally rare species may be (or have been) isolated from and hence possible genetically differentiated from the populations in nearby rivers. This is an example of an insight of conservation relevance that only the analysis of our data in an explicit island biogeography context can provide.

Larger lakes also tend to provide a greater variety of ecological niches, allowing co-existence of larger numbers of species. The greater number of ecological niches is due to greater spatial variation in environmental conditions such as differences in temperature and light associated with larger depth gradients, more distinct inshore-offshore gradients, more diverse littoral habitats and more spatial variation in wave energy. Finally, the combination of larger populations and a greater variety of ecological niches facilitates ecological speciation in larger lakes. Given the geological youth of the lakes in the perialpine system, the latter, however requires the presence of lineages with an evolutionary propensity to quickly speciate within lakes, as is known from whitefish and char that dominate the Rhine catchment[36]. Lake surface area was correlated with maximum depth among the lakes surveyed in Projet Lac (Figure 86). Divergence and speciation of *Coregonus, Salvelinus* and *Cottus* into shallow and deep-water forms only occurs in deeper lakes [39, 40, 41]. Indeed, maximum lake depth correlates positively with the number of species of *Coregonus* occurring in any one lake among the northern perialpine lakes [42]. It is therefore likely that some of the area effect on endemic species richness is mediated by the positive correlation of lake area with lake depth and hence habitat diversity.

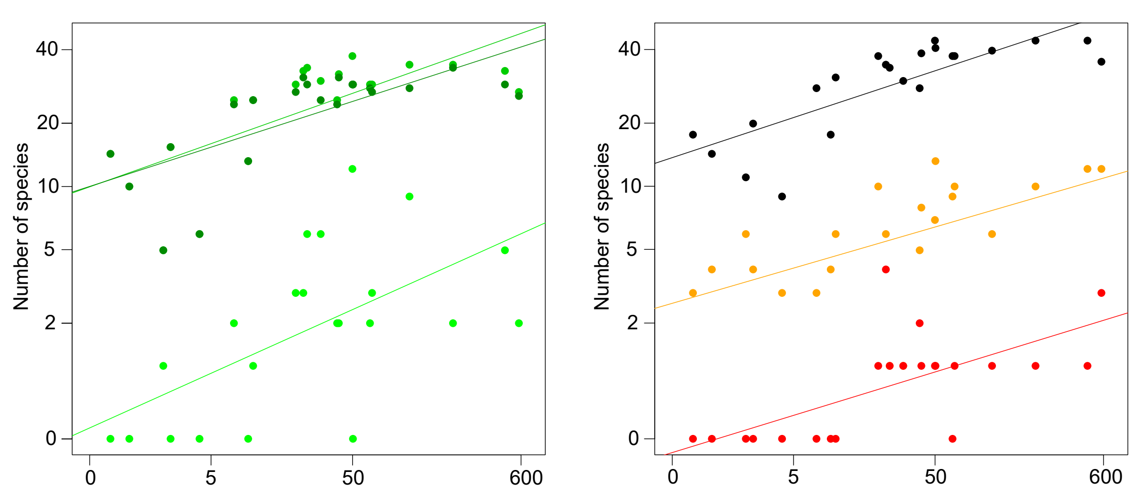

Figure 13: Species-area relationships for lakes in the Rhine catchment when, additionally to the species recorded in Projet Lac, all known recently extant, and all known extinct and locally extirpated species are included. Left panel: dark green = native species, but each species radiatation only counted as one taxon, medium green = all native species, i.e. counting each radiation species separately, light green = endemic species only. Right panel: *black* = total number of present-day fish species (species recorded in Projet Lac, plus other species recorded in the lake in other recent surveys), *orange* = non-native and exotic species (species recorded in Projet Lac, plus other species recorded in the lake in other recent surveys but excluding species that have failed to establish self-sustaining populations), *red* = extinct and extirpated native species. Regression statistics are provided in Table 9.

Table 9: Regression statistics for species-area relationships shown in Figure 13. All relationships are positive and all are significant. Models log(X)-log(Y+1).

	Catchment	p-value	Slope	Intercept	R-squared
All extant species	Rhine	0.00001	0.184	2.791	0.633
Endemic species	Rhine	0.00295	0.288	0.104	0.364
Extinctions	Rhine	0.00072	0.17	-0.018	0.443
Non-native and exotic	Rhine	0.00961	0.156	1.409	0.291
Native (no radiations)	Rhine	0.00021	0.207	2.399	0.505
Native (radiations included)	Rhine	0.00015	0.228	2.395	0.52

Effects of lake morphology

The shape of a lake basin influences almost all physical, chemical and biological processes in a lake [43], with corresponding dramatic effects on lake fish, their environment, habitats, predators and prey. Among the strongest effects of lake morphology on fish and the lake ecosystem are its influence on temperature dynamics, mixing regime, nutrient cycling, productivity and environmental heterogeneity.

Fish biomass per unit net area decreased with lake maximum depth

Biomass per unit net area, averaged throughout the entire volume of the lake (whole-lake BPUE), decreased with increasing lake depth (Figure 14). This is because the proportion of the lake volume that receives sunlight (the euphotic zone), where primary production takes place, decreases with increasing lake depth and area. The depth of the euphotic zone depends on water clarity, which in turn depends on productivity (nutrient supply) and other factors, such as the amount of dispersed and dissolved inorganic matter and fine sediment in the water. In clear, low-nutrient (oligotrophic) lakes, sunlight can penetrate to around 30 m depth. Thus, in shallower lakes, the entire water column may be receiving light. In deeper lakes however, a high proportion of the lake volume consists of dark, cold and less productive habitat. This results in a naturally lower whole-lake biomass for deeper lakes when biomass per unit net area is averaged throughout the entire volume of the lake.

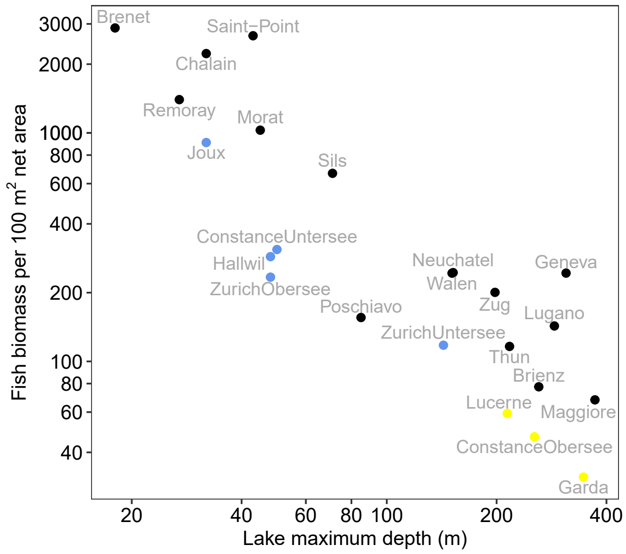

Figure 14: Whole-lake average fish biomass per unit net area in vertical nets was lower in deeper lakes due to their proportionally larger volume of less productive habitat. Note that vertical and horizontal axes are on a log scale. Lakes that have returned from a period of eutrophic conditions with hypoxia in the hypolimnion in at least part of the lake to meso- or oligotropic conditions are indicated in blue, while yellow points indicate re-oligotrophied lakes that have lost profundal fish species.

Deviations (residuals) from the relationship between lake depth and average biomass per unit net area may provide information on other aspects of ecosystem functioning. In near-natural deep lakes, ecologically versatile salmonids such as *Coregonus* and *Salvelinus*, as well as deep-water benthic species such as *Cottus* and *Lota lota*, occupy the entire depth range. In lakes that experienced oxygen deficiencies in deeper waters either in the past or in the presence, most of these species (*Lota lota* being the only exception) are absent from deep waters (Figure 26). The biomass of fish in the profundal zone are in these situations particularly low, causing the whole-lake BPUE to be lower than expected. A low BPUE in the profundal zone can however be masked by productive surface waters. Thus, eutrophic lakes such as Zug and Lugano have relatively high whole-lake BPUE for their depth, despite severe hypolimnetic oxygen deficiencies that extend from the lake floor to high into the water column. The lakes with lower whole-lake BPUE than expected for their depth were generally those that have both few fish living in the deeper parts of the lake, but are also less productive in their surface waters. These are lakes that returned from eutrophic to meso- or oligotrophic conditions, but either still experience hypoxia in the hypolimnion/profundal zone, at least in parts of the lake (Joux, Upper and lower Zurich, Hallwil, Lower Constance), or had already lost their profundal fish species (Garda, Upper Constance, Lucerne; Figure 14).

Temperature

Water temperature has a major influence on biological and chemical processes in aquatic ecosystems. In fishes, higher water temperature accelerates physiological processes, such as egg development, digestion, metabolism and growth. Differences in water temperature among lakes are associated with the height of the lake above sea level (Figure 87) and its position relative to the Alps, which corresponds with latitude and exposure to warmer Mediterranean and cooler northern weather systems (Figure 88). Lake water temperature can strongly influence which fish species and families dominate a lake (e.g. see section 'Non-native and exotic species'), as well as the length frequency distribution of lake fish communities, with a tendency towards more larger individuals in the colder lakes that are dominated under natural conditions by cool-stenothermic salmonids [44]. High fishing pressure and a slow individual growth rate in these populations can however result in truncated length frequency distributions containing few large individuals (section 'Length frequency distributions').

Within lakes, fish species generally distribute themselves by depth to occupy water that matches their thermal tolerances and/or bio-energetic requirements [45]. The vertical distribution of dietary resources (e.g. zooplankton, macroinvertebrates), presence of competitors and predators, light and dissolved oxygen concentrations also play important roles, and mismatches between temperature, oxygen and food requirements can become detrimental to the survival of fish populations. Seasonal changes in water temperature regulate the timing of spawning (directly or indirectly through availability of prey). Tracking preferred temperatures through the seasons is the cause for the shift of warmwater fish species into deeper water, and coldwater fish species into shallower water during the cooler months of the year [46].

Depth zonation of fish species in Projet Lac associated with temperature gradient

The highest abundance of fishes in Projet Lac catches in the benthic and pelagic zone was generally between 5 and 15 meters from the surface (Figure 15, Figure 16, Figure 80, Figure 81) usually corresponding with the upper edge of the thermocline. In low nutrient lakes (e.g. Thun and Walen), the peak abundance of fish in open water tended to be somewhat deeper (15 - 25 m), driven by the high proportion of *Coregonus* in the communities of these lakes. In the benthic zone, fish abundance dropped dramatically below around 20 m, usually corresponding with a temperature of around 10°C. Benthic fish biomass remained relatively high below 20 m however in lakes with large populations of *Coregonus* (Walen, Brienz, Thun) or *Salvelinus* (Lucerne, Sils, Poschiavo).

Species composition of fish in Projet Lac catches changed steeply with increasing depth (i.e. distance from the surface of the lake) in many lakes, likely reflecting different thermal niches of different fish species (as well as other factors). The warmest layer of water close to the lake surface during the Projet Lac sampling months, was generally dominated by cyprinids, mostly *Rutilus, Scardinius* and *Alburnus. Rutilus* remained abundant in many lakes down to 15 m (Figure 15, Figure 16). Perch abundance peaked just below the cyprinids in most lakes at around 5 – 15 m in the benthic zone (Figure 15), as well as in the open water zone in the lakes where they were abundant (Figure 16). Immediately below the perch was the zone of highest *Coregonus* abundance, beginning in most lakes around 10 meters and remaining high to around 35 meters in many lakes, and deeper in Lakes Brienz and Walen. In Lakes Walen, Geneva and Upper Constance, the lower edge of the peak whitefish zone was overlapped by a peak in the biomass of lake trout (*Salmo trutta*) (20 – 55 m, depending on the lake; Figure 81). In Lake Lucerne, a remarkably high abundance and biomass of *Salvelinus* below the peak of *Coregonus* (Figure 16, Figure 81) was unique among the perialpine lakes. These patterns suggest an important influence of water temperature on species depth distribiutions and species interactions such as competition and predation.

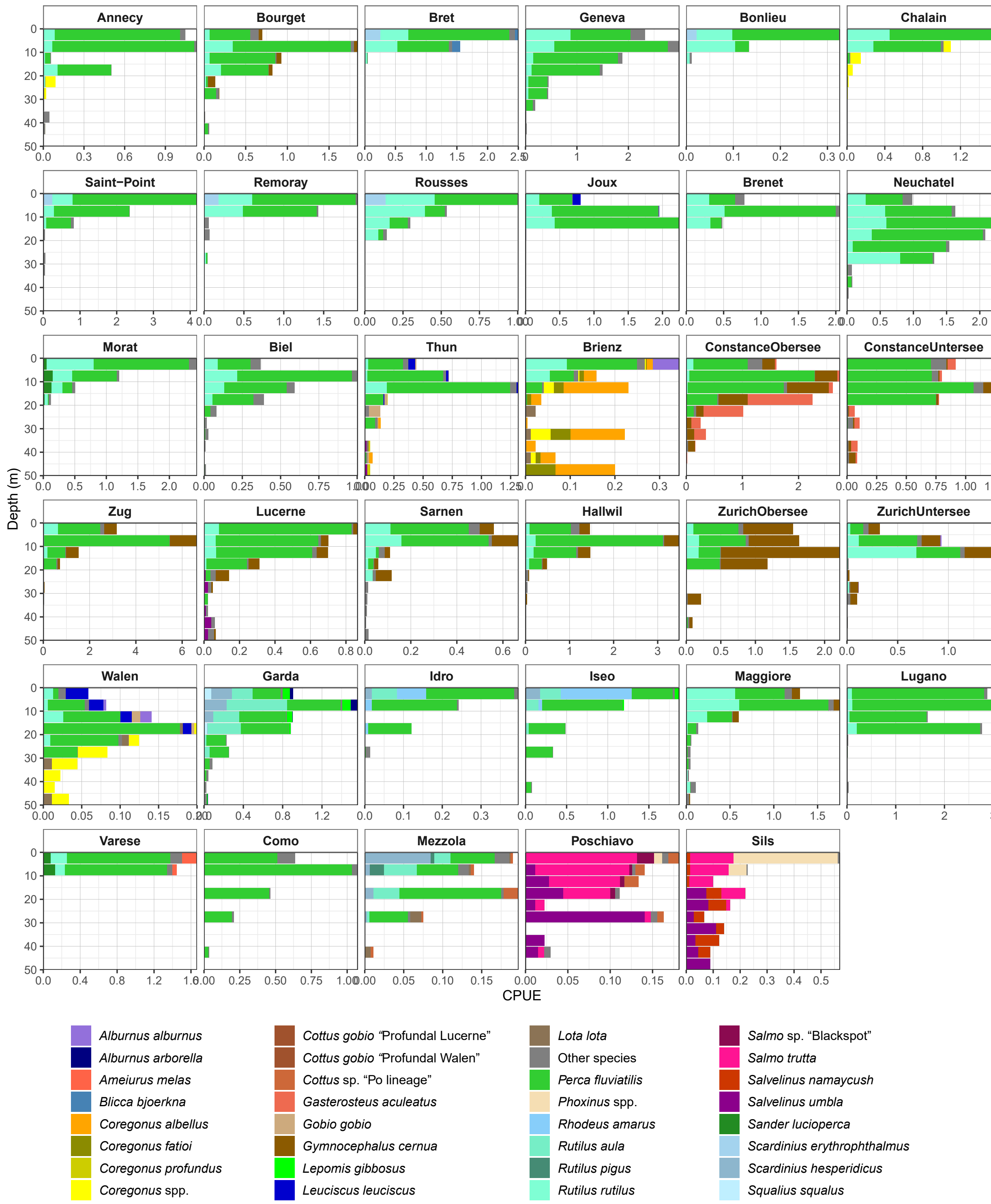

Figure 15: Depth distribution of fish abundance by species (individuals per unit effort) in benthic habitats to 50 m deep according to CEN benthic nets.

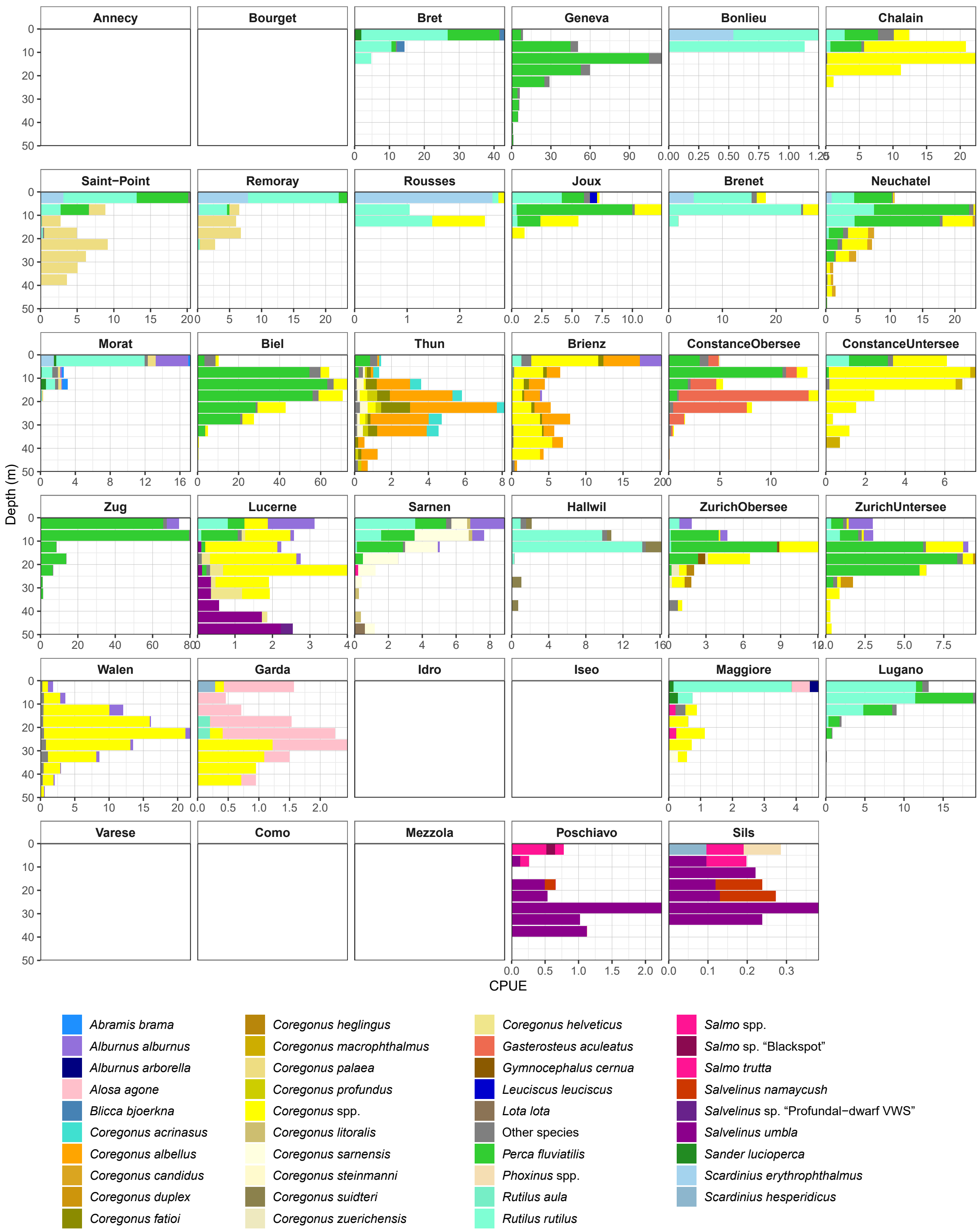

Figure 16: Depth distribution of fish abundance by species (individuals per unit effort) in pelagic habitats to 50 m deep according to deep-set vertical nets (fish in the 3 m of net close to the lake floor were excluded).

Littoral habitats

Littoral habitats influence the distribution of fish species within the shallow parts of lakes [47]. Several fish species deposit their eggs on submerged vegetation in the littoral zone (e.g. *Perca fluviatilis, Esox* spp, *Rutilus* spp, *Scardinius* spp and many other cyprinid species), while others make nests in shallow rocky habitats (e.g. *Cottus* spp and *Salaria fluviatilis*) [9]. Shallow areas are also important for the winter-spawning of endemic *Coregonus* species [42, 48]. Juveniles of many fish species use structurally complex littoral habitats and the shallower water depth as refuge from predators. Adult and juvenile fish feed on invertebrates, algae and other organisms living on the submerged and emergent vegetation and on rocky substrates. Similar importance can be attributed to specific habitat structures in deeper parts of the lakes but there this is much harder to study and mapping habitats in deeper waters requires the operation of divers, submarines or remote operated diving verhicles. In the absence of such in Projet Lac, we were confined for our analysis of fish-habitat associations to the littoral habitats.

Different species associate with different littoral habitats

Analyses of Projet Lac data showed that many littoral fish species exhibited strong associations to certain littoral habitats, and that these were often but not always consistent among lakes [47]. Many littoral fish species were most frequently caught in river deltas and inflowing streams (see section 'Interactions between lakes and rivers'). Within the lake itself, habitats that were particularly attractive to many fish species included boulders, woody structure and reeds (Table 10). While some habitats seemed particularly attractive to many fish species, almost all habitats had at least one species positively associated with them, reflecting the importance of maintaining a diverse array of natural littoral habitats in each lake.

Many species are known to change habitat-associations through their ontogeny. For the two most common and widespread littoral species *Perca fluviatilis* and *Rutilus rutilus* [47] we, therefore, investigated littoral habitat associations for juveniles and adults separately. These were the only species recorded frequently enough in the littoral zone to allow analyses for different size classes within and across multiple lakes, but they may stand representative for many other species. For both species, habitat associations changed throughout the life of the fish. Smaller fish tended to associate with more structurally complex habitats such as reeds or macrophytes, while larger fish were more commonly caught in open habitats such as over bare sediment. This highlights the importance of different habitats not only to different species but to different life-stages and age classes of the same species too.

Table 10: Number of species of each conservation status according to the Swiss Red List with positive, weighted-mean associations (in late summer/autumn) to each littoral habitat type. 'Proportion' represents the number of positive species associations to the habitat type as a proportion of the number of species occurring in lakes where the habitat was sampled. Numbers in the table differ from associations shown in Figure 17 as the latter was restricted to species recorded in the littoral zone in at least three lakes. Note that species that do not occur in the littoral zone are not included in this analysis.

Status	Number species	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Sediment	Reeds	Macrophytes	Floating plants	Woody debris
Crit. Endangered (CR)	6	3			3	2	1	1		1	2	1		1
Endangered (EN)	4	3	1		2	1				2	1	1		
Vulnerable (VU)	5	4			1	1			1	2		1		1
Near Threatened (NT)	19	11	6	6	5	8	4	2	1	3	4	5	3	5
Least Concern (LC)	13	8	8	4	5	4	7	6	4	7	3	8	4	6
Data deficient (DD)	10	4		2	6	6	2	1	2	1	1	2		1
Non-native	8	5	4	3	3	3	2	2		4	5	3	2	5
Total number of recorded littoral species	65	38	19	15	25	25	16	12	8	20	16	21	9	19
Proportion		58	29	23	38	38	25	18	12	31	25	32	14	29

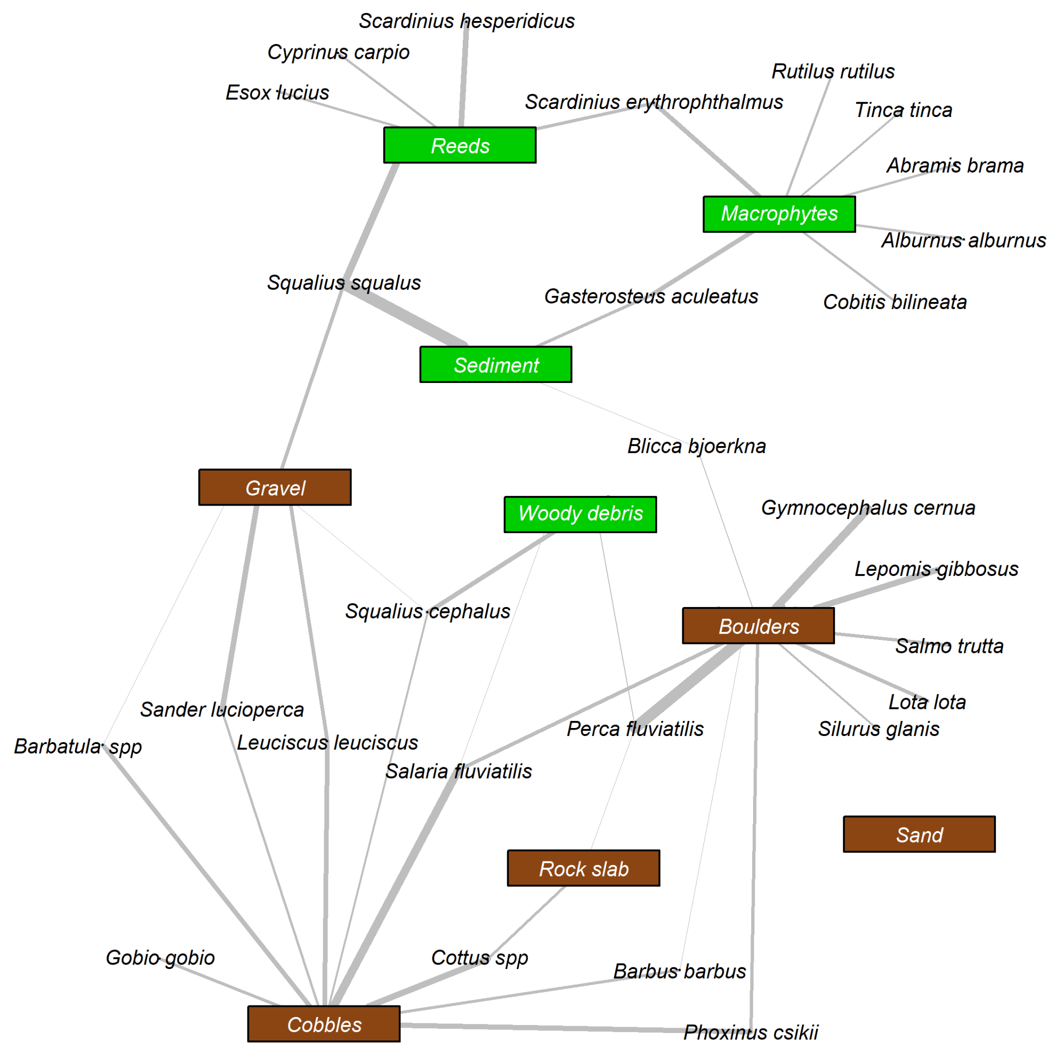

Figure 17: Habitat associations of fishes in the littoral zone in late summer/autumn based on sampling in 28 perialpine lakes. Grey lines indicate that the species was recorded (electrofishing and shallow-set vertical nets) more often in this littoral habitat than in other habitats. The thickness of the line reflects how much more frequently than random the species was recorded in the habitat. Associations were averaged among lakes and shown only where the association was positive in more than half of the lakes in which a species was recorded. Only fish species recorded in the littoral zone of at least three lakes are shown. Three species were recorded in at least three lakes, but had no clear habitat association (*Carassius gibelio, Rhodeus amarus, Telestes muticellus*). Lineages of *Barbatula* spp and forms of *Perca fluviatilis* could unfortunately not be differentiated in the analysis. Inflows and outflows are excluded to focus on the lacustrine habitats. Note that some of these species may have their strongest associations with other habitats outside the littoral (e.g. the sublittoral, profundal or pelagic), but such habitat occurrences could not be included in this analysis. See [47] for more information on the calculation of habitat association.

Anthropogenic factors

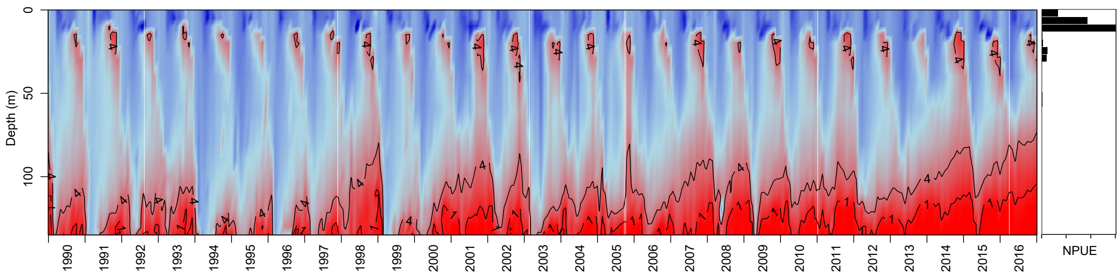

Figure 18: Zone of low oxygen in Lower Lake Zurich has been increasing in severity and vertical extent since around 1990, offsetting gains of oxygenated deepwater habitat that would otherwise be associated with the reduction of eutrophication. Severe hypoxia also occurred between 1940 and 1960 and is believed to be caused by a combination of elevated nutrients and inverse stratification in winter during this period [50]. Isobars for dissolved oxygen concentrations of 1 and 4 mg/L are indicated. Data source: Canton Zurich, Amt für Abfall, Wasser, Energie und Luft (AWEL) and Wasserversorgung Zurich. Black bars on the right side: depth distribution of Projet Lac fish catches by abundance (net per unit effort catch).

Climate change

The water of most lakes in the perialpine region has been rapidly warming over the past decades, particularly in the surface layers. In Lake Geneva, the annual average temperature of the water 5 m below the surface has increased by around two degrees since 1970 [49]. The surface waters of Lake Zurich have also increased by an average of around 1.5 degrees in some months of the year since the beginning of the routine monitoring in 1937 [50]. Water temperature in many lakes showed a particularly abrupt increase around the end of the 1980s [51], corresponding with similar shifts in other long-term time series across the northern hemisphere [52].

The warming of the lake waters has direct impacts on lake fish communities, including changes to growth rates, age structure, the distribution of species throughout a lake, and community composition [53]. Warmer water means faster larval growth rates, with potentially higher survival and stronger recruitment of some species as fish move more quickly through the smaller size classes, which are most vulnerable to predation [54]. Generally however, the salmonids such as *Coregonus, Salvelinus, Salmo* and *Thymallus* are adapted to cooler, oxygen rich water and therefore are more likely to be among the species that are disadvantaged by the changes [55]. Indeed, these species are already being forced to live deeper in some lakes [56] in order to take refuge from the warmer surface waters in summer. In shallower lakes and in deep lakes with oxygen deficiencies, the thermal refuge of the cooler, deeper water may not be sufficient to maintain thermally sensitive species through warmer periods, leaving them vulnerable to thermal stress and associated parasites and disease.

Unlike ocean fish [57] and many terrestrial species that respond to climate warming with latitudinal or elevational range expansion or shifts (e.g. [58, 59, 60, 61]), most perialpine lake fish will not be able to shift their ranges to higher altitude lakes. Instead, shrinking and eventual loss of species' thermal niche will in most cases imply population extinction unless the thermal niche can be adjusted through rapid evolution. The effects of climate change are generally likely to be strongest in the cooler lakes on the northern edge of the Alps (Thun, Brienz, Walen, Lucerne) and the higher-altitude Jura lakes (Rousses, Joux, Brenet, Remoray, St-Point). Likely changes to the communities of these lakes include loss of coldwater fishes and establishment of new non-native and exotic warmwater fish species, increases in the relative abundance of some non-native species already present [62], as well as increased relative abundance of generalist, eurythermic native species such as perch, roach and other cyprinids [53].

Warming lake water also has indirect effects on lake fishes through changes to other aspects of the physical environment. Higher summer temperatures result in longer and more stable stratification [53] and milder winters mean reduced mixing and circulation (see Appendix B – Additional background information). This means that nutrients released from decomposition of organic material in the profundal zone are less strongly transported upwards. Weaker upward transport of nutrients may mean comparatively lower spring growth of phytoplankton and other primary producers at the base of the food chain. Oxygen consumed by decomposing material and respiration of organisms below the thermocline is also less completely replenished through mixing with surface waters [63]. Changes in these processes are already increasing the intensity and vertical extent of the hypoxic, "dead" zone in deep water in some lakes. For example, no fish were recorded in Projet Lac in Lower Lake Zurich below 80 m from the surface, which approximately corresponded to where oxygen concentrations reached 4 mg/L [50] (Figure 18).

A further negative side-effect of weaker mixing is the proliferation of harmful cyanobacteria, such as *Planktothrix rubescens,* in some lakes [64]. Since this toxic alga is unpalatable to most zooplankton, its biomass is only reduced when it is forced into deeper water during vertical mixing. Gas vesicles within the cells collapse in depths below 100 m due to hydrostatic pressure, preventing the return of cells to surface waters. Weaker vertical mixing therefore likely contributes to increasingly high biomass of this species year after year, because fewer cells get lost to the profundal. The negative effect of the proliferation of cyanobacteria is that nutrients used by the toxic species are not available for the growth of other more palatable phytoplankton species. The result is that this organic material is not transferred to zooplankton nor further up the food chain. This reduction of trophic transfer efficiency causes reduced productivity in higher trophic levels such as fish. Instead, much of the biomass of the cyanobacteria goes directly to the lake floor as detritus, further contributing to oxygen deficiencies as it decomposes.

Effects of climate change on the lakes directly on the edge of the Alps (Thun, Brienz, Walen, Lucerne) could be accelerated with the anticipated loss through melting of all small glaciers and most of the large glaciers by 2100 [65]. Higher volumes of cooler meltwater from glaciers during warmer weather may partially buffer the effects of climate warming in smaller perialpine lakes immediately downstream of glaciers, but this effect is transient and will cease when the glaciers are gone. The reduced volume and eventual absence of glaciers across the Alps will have significant effects on stream [59], river [66] and lake [67] ecosystems through accelerated warming of water, reduced water levels in summer, reduced sedimentation and decreased turbidity [67]. The cooling effect of rivers is believed to be negligible in larger lakes, such as Lake Constance however, where the changes to the heat budget are instead dominated by increasing solar radiation and the warming atmosphere [68].

In summary, climate change will be one of the greatest threats to lake fish communities in the coming decades. The unique endemic salmonids, *Salvelinus* spp and *Coregonus* spp, are likely to be most affected through warming surface temperatures, altered food webs and deteriorating environmental conditions. The fish of medium depth lakes are most likely to be most strongly affected due to the loss of a thermal refuge in deeper and cooler water (fish communities of shallow lakes may be less affected because these do already now no longer host sensitive coldwater fish except at higher elevations). Lakes with characteristics that reduce their propensity for vertical mixing (Appendix B – Additional background information) are also more likely to suffer from climate warming through hypolimnetic oxygen deficiencies and reduced upward nutrient transport.

Nutrients

Elevated nutrient concentrations

The key nutrient in freshwater ecosystems is phosphorus, with nitrogen and other trace nutrients also important under certain conditions. Perialpine lakes are naturally low in these nutrients, however human activities increased the quantities of these substances entering the lakes. Nutrient concentrations in many perialpine lakes had been increasing since the beginning of industrialisation and perhaps even earlier, however phosphorus loads increased substantially between 1945 - 1980 due to a rapid increase in the human population density of the catchments and the connection of the majority of the population to sewer systems that discharged insufficiently treated wastewater into the natural waterways. Nutrient loads from agriculture, primarily fertilisers, had also been progressively increasing over this period. Consequently, the growth of planktonic algae increased in nearly all lakes visibly starting in the 1960s, with massive blooms in the more strongly affected lakes. This led to intensive research, which revealed that phosphorous was the limiting nutrient in lake ecosystems and that its massive enrichment was to be blamed for the eutrophication of lakes [69]. Staring in the late 1970s, the governments responded by upgrading wastewater treatment facilities to include phosphorus precipitation, and by the removal of phosphorus from detergents. Agricultural practices were also adapted to reduce nutrients in runoff. This resulted in lake phosphorus concentrations in most lakes beginning to decline by the mid-1980s. Today, the phosphorus concentrations in many lakes in the region approach or are close to pre-eutrophication levels.

The direct effect of increasing concentrations of nutrients is to increase growth rates of primary producers, i.e. plants and algae. Increasing productivity generally corresponds with a shift among major functional groups of primary producers and associated shift in primary production between habitats from benthic periphyton, epiphytes and macrophytes to phytoplankton. Shifts also occur within these major groups, such as increasing dominance of the phytoplankton community by cyanobacteria in lakes with elevated nutrients [64, 70]. In highly eutrophic lakes, primary production occurs mostly through phytoplankton in a relatively thin layer of water close to the lake surface, while the deeper layers and benthic zone are shaded, associated with the loss of benthic macrophytes. Increasing nutrient levels also alters the seasonality of phytoplankton dynamics, advancing the period of peak phytoplankton biomass [43] and delaying the depletion of phosphorus in the epilimnion [71]. While the link between nutrients and algae growth is well established, the flow of this energy/biomass to higher trophic levels is less predictable. The response of a particular trophic level to increased primary productivity depends on the palatability of the lower trophic levels and on how abiotic changes associated with increased nutrients affect the target trophic level, as well as trophic levels above (predators) and below (prey) through trophic cascades [72]. The increased primary production under eutrophication indirectly affects the physico-chemical conditions of aquatic ecosystems. High rates of primary production resulting from elevated nutrients can result in super-saturation of oxygen in the epilimnion during daylight hours of summer months. Respiration by the high density of organisms in surface waters of eutrophic systems also consumes large amounts of oxygen during night hours, resulting in large daily fluctuations. High concentrations of organic particles also affect the ambient light environment. Increased biogenic turbidity results in lower light penetration and a shallower photic zone. Organic particles absorb and scatter sunlight of certain wavelengths, resulting in changes in the spectrum of visible colours [e.g. 73]. Increased density of organic particles also changes water transparency and visibility, affecting the visual range for detecting prey by fish [74]. When growth rates of primary producers and other trophic guilds exceed rates of consumption, large quantities of deceased organic material can also accumulate in the system. Decomposition of accumulated dead phytoplankton, macrophytes, zooplankton, and other organic material occurs in the water column and on the lake floor. Decomposition of these organic particles below the thermocline, and at the sediment-water interface, can result in oxygen depletion in the hypolimnion of lakes, making it unsuitable as habitat for most animals. Even when eutrophication is only relatively mild, decomposition of organic particles that accumulate on the sediment can lead to oxygen depletion at the sediment surface, precluding the development of fish eggs [75]. Eutrophication therefore changes the amount of biomass in a lake, its spatial distribution and allocation among trophic levels and taxa, the availability of habitat for fish and recruitment. Consequently, elevated nutrient concentrations influence the entire biological structure of a lake ecosystem, along with its physico-chemical conditions. The data gathered in Projet Lac together with data collected previously and concomittently allowed investigation of responses of fish communities to current and past nutrient enrichment in the perialpine lakes. These are discussed in the following sections with an emphasis on those fish taxa that are of particular interest to the fishery.

More Coregonus caught per net in lakes with low total phosphorus

Whole-lake average catch per vertical net battery for all fish species and sizes combined was not significantly correlated with any major environmental drivers. However, investigating the trends for the dominant fish groups among the larger lakes (average depth greater than 50 m) revealed opposing relationships with lake phosphorus for *Perca fluviatilis* and *Coregonus* spp [2]. Among the large lakes, abundance and biomass of *Coregonus* spp per vertical net battery was highest where the total phosphorus [3] was less than 5 µg/L (Figure 19, Figure 20). Biomass of *Coregonus* was highest in Lakes Walen and Thun, while abundance was by far the highest in Lakes Walen and Brienz. Lakes Geneva and Neuchatel also had particularly high biomass of *Coregonus*. On the other end of the spectrum, the lakes with the highest phosphorus concentrations, Zug and Lugano with total phosphorus of around 83 and 55 µg/L respectively, had by far the lowest abundance and biomass of *Coregonus*. This pattern is noteworthy since it seems to contradict patterns in fisheries catch statistics, which are low when total phosphorus is less than 5 – 10 µg/L (e.g. [76]). It is important to remember however that high catch rates during a "snapshot" in time does not necessarily mean high fisheries yields (see section 'Projet Lac catches, annual fisheries statistics and the "actual" fish community', but also see below).

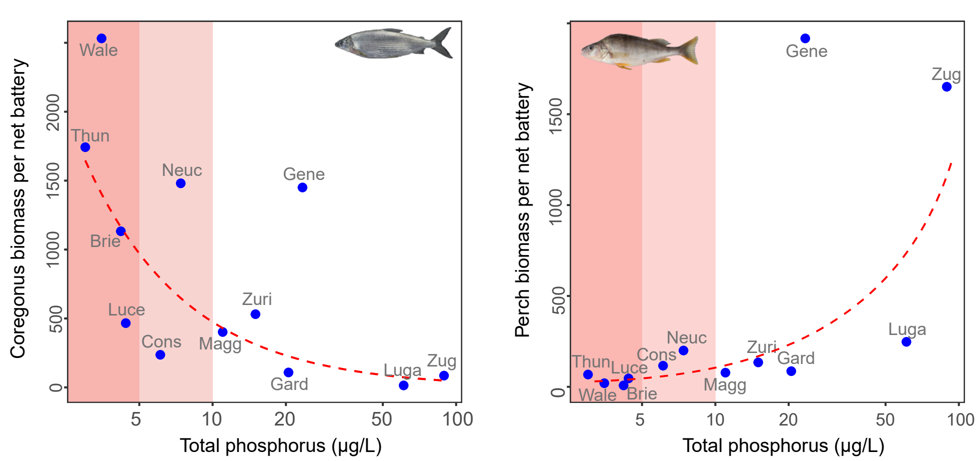

Figure 19: Opposing relationships with total phosphorus for the biomass of the two most common fish taxa among the large and deep lakes (average depth > 50 m). Data are whole-lake average biomass (in grams) of fish per vertical net battery. Note that the horizontal axis is on a log scale. Regression statistics for *Coregonus* are p-value = 0.005, R^2 = 0.57 and perch are p-value = 0.004, R^2 = 0.58. Shaded regions show thresholds for total phosphorus of 10 µg / L and 5 µg / L.

[2] Small and large lakes were analysed separately because small/shallow lakes have higher average fish biomass and fewer fish species compared to large/deep lakes (see above section 'Lake morphology'), with a threshold at around 50 m average depth. Phosphorus concentrations among larger lakes ranged also widely from <5 to 85 µg/L, allowing for an effective test of the effect of this variable on fish. On the other hand, phosphorus concentrations among smaller lakes covered only a narrow range (15 – 25 µg/L).

[3] Total phosphorus values used were the volume-weighted average measured at the deepest point of the lakes at winter-spring mixing. Data from the Federal Office of the Environment.

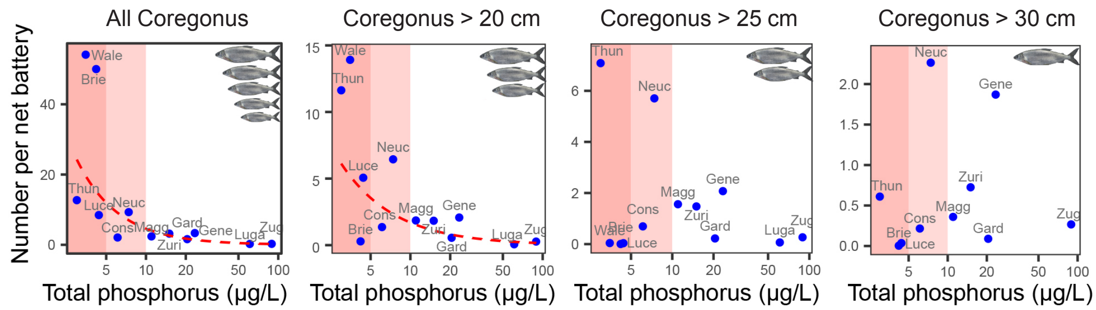

Figure 20: Whole-lake average number of fish of *Coregonus* spp per vertical net battery compared to total phosphorus concentration in large and deep lakes (average depth > 50 m). First panel shows the relationship for all *Coregonus* caught in the lake. The other panels shows the relationship when only fish larger than the size thresholds shown at the top of the panel are included (length measured from snout to the tip of the tail). Note that the horizontal axis is on a log scale. Dashed red lines indicate statistically significant relationships (from left to right: p-value = 0.0001, R^2 = 0.79; p-value = 0.008, R^2 = 0.52; p-value = 0.87, R^2 = 0.003; p-value = 0.412, R^2 = 0.09). Shaded regions show thresholds for total phosphorus of 10 µg / L and 5 µg / L.

Further investigation of the *Coregonus*-phosphorus relationship revealed that the high biomass of *Coregonus* in the low nutrient lakes was strongly influenced by many small fish. The negative relationship between *Coregonus* biomass and total phosphorus was significant and strongest when fish of all sizes were included in the analysis. Focussing on only larger fish revealed a different pattern (Figure 20). The negative relationship was weaker (although still significant) when considering only the number of *Coregonus* larger than 20 cm in length. Lake Brienz had one of the highest overall densities of *Coregonus*, however this lake had very low densities of fish larger than 20 cm. Increasing the threshold to consider only the number of *Coregonus* larger than 25 cm, revealed a very low density of larger *Coregonus* in Walen, Brienz and Lucerne compared to other lakes. Finally, considering exclusively *Coregonus* larger than 30 cm revealed that Neuchatel and Geneva had the highest density of very large *Coregonus*, followed by Thun and Lower Zurich. There was no significant relationship between the biomass of large *Coregonus* and total phosphorus.

The higher biomass of *Coregonus* caught by Projet Lac in the most oligotrophic lakes thus represents a picture that is different from fisheries catches. This difference is mostly due to the fact that the majority of fish caught by Projet Lac in the low-nutrient lakes were smaller than would be caught in the nets of professional fishers. Indeed, variation in the biomass of larger *Coregonus* and larger perch caught by Projet Lac significantly correlated with variation in fisheries yields among lakes (Figure 21).

The lower numbers of *Coregonus* spp in lakes with higher total phosphorus may be driven by a combination of factors. Natural reproduction of *Coregonus* clearly suffers during eutrophication [75]. The hypoxic profundal zone of eutrophic lakes means that eggs have insufficient dissolved oxygen to develop. Even in mesotrophic lakes, where dissolved oxygen in the water column should be sufficient for adult fish to inhabit, consumption of oxygen by decomposing organic matter can create a steep oxygen gradient at the sediment-water interface [77]. Under these conditions, part of the developing *Coregonus* egg is exposed to oxygen-deficient conditions. Decomposition of organic matter may also result in the diffusion of toxic metabolic compounds (H_2S, CH_4) from the sediment into the egg [75]. The higher rate of organic sedimentation also alters the composition of the substrate in the benthic habitat in terms of organic content and particle size composition. This changes the suitability of the habitat for benthic invertebrates [78], which are important prey for many species of *Coregonus, Salvelinus* and for profundal *Cottus*.

Lakes with low phosphorus concentration, especially those that have not experienced high nutrient loads in the past, have higher rates of successful development of *Coregonus* eggs [75], resulting in more juvenile fish. The lakes with low phosphorous concentration and high *Coregonus* densities are dominated by slow growing species of *Coregonus* that reach maturity at small sizes, possibly in adaptation to oligotrophic conditions. Slow individual growth means fewer fish enter the size range at which they can be caught by fisher's nets each year. It also means that even moderate fishing intensity (e.g. a moderately-high number of net-nights per hectare per year) can remove most large individuals of the larger growing *Coregonus* species (Figure 8).

The perialpine lakes, which have been inhabited by whitefish for the past 10,000 or more years, are naturally low in nutrients. This is a result of their small and mostly mountainous catchments, which have also limited the historical density of human settlements and area of agricultural land. The low productivity of these lakes means that native fish populations, especially those of endemic species, have experienced many generations of natural selection for performance in low nutrient environments. Salmonids such as species in the genera *Coregonus,*

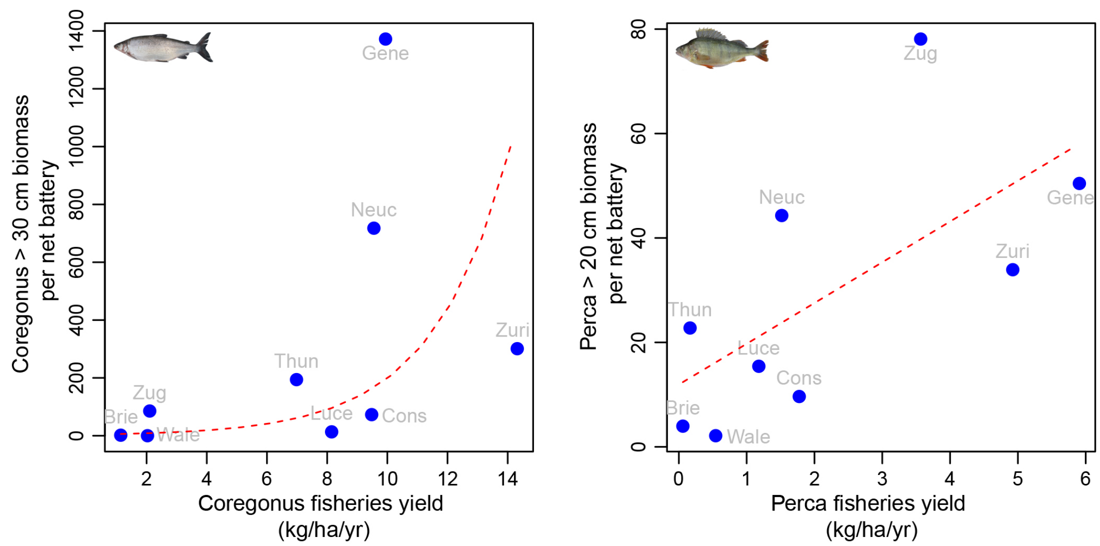

Figure 21: Significant correlations between whole-lake average biomass of large fish caught in Projet Lac vertical nets and corresponding yields of (the sum of) commercial and recreational fisheries in kilograms per hectare per year in large and deep lakes (average depth > 50 m) for *Coregonus* spp (left; p-value = 0.03, R^2 = 0.51) and *Perca fluviatilis* (right; p-value = 0.053, R^2 = 0.43). Maggiore, Lugano and Garda are not included, as reliable data on recreational fishing catches were only partially available.

Salvelinus and *Salmo* are particularly renowned for their ability to adapt to such conditions [79] and to rapidly (on evolutionary timescales of several thousand years) differentiate into distinct species adapted to different niches within the same lake [24, 80]. The low nutrient conditions and corresponding structure of the food web may therefore provide an advantage to the endemic salmonids over common generalist fish species such as *Perca fluviatilis* and *Rutilus rutilus*. In addition, the cold water of the perialpine lakes, resulting from their great depth, higher elevation and inputs of glacial meltwater may similarly favour *Coregonus* and other salmonid species adapted to these conditions, and constrain the warmwater fish of the families Percidae and Cyprinidae that recolonized the area from warmwater refugia after the end of the Pleistocene.

More perch caught in lakes with higher total phosphorus

While the biomass of *Coregonus* was higher in low-nutrient lakes, the biomass of the other most common taxon, European perch (*Perca fluviatilis*), showed the opposite trend. Perch had higher biomass in those of the large and deep lakes with high phosphorus concentrations, such as Lake Zug (Figure 19). This relationship became even clearer when considering only the number of large perch, with total length greater than 20 cm (Figure 22). Interesting was also the very high number of small perch in Lake Geneva, the majority of which were less than 20 cm.

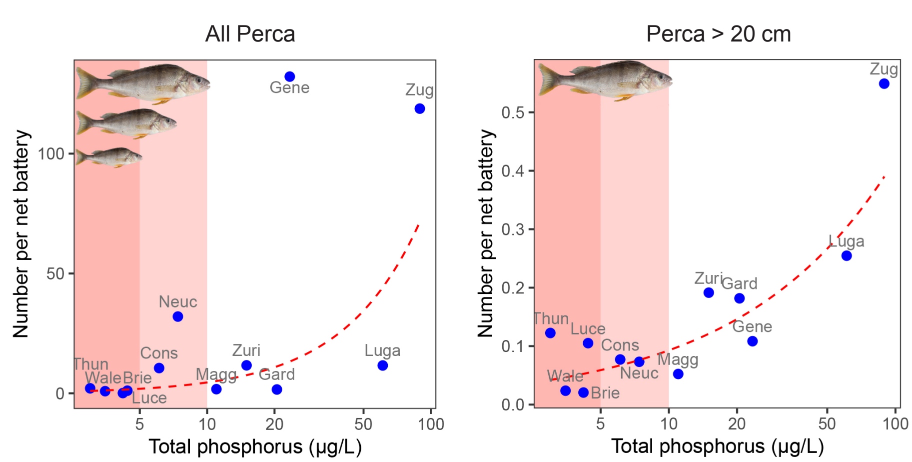

Figure 22: Whole-lake average number of European perch (*Perca fluviatilis*) per vertical net battery compared to total phosphorus concentration in large and deep lakes (average depth > 50 m). The left panel shows the relationship for all perch caught in the lake (p-value = 0.022, R^2 = 0.42). The right panel shows the relationship for only perch larger than 20 cm (length from snout to the tip of the tail; p-value = 0.003, R^2 = 0.6). Note that the horizontal axis is on a log scale. Dashed red lines indicate statistically significant relationships.

Other research in lakes across Europe has shown similar shifts in community composition with increasing phosphorus from salmonids (*Coregonus* and *Salvelinus*) in oligotrophic lakes, to domination by percids and/or cyprinids in mesotrophic lakes [81, 82]. Cyprinids, especially *Rutilus rutilus*, tend to dominate with increasing nutrients in smaller lakes, while percids, such as *Perca fluviatilis*, are generally most common in deeper lakes at mesotrophy [83]. Within lakes through time, a decline of *Coregonus* spp and *Salvelinus* spp and increasing dominance by *Perca fluviatilis* in fisheries catches with increasing phosphorus concentrations was reported in Lake Constance [84]. An analysis of long-term fisheries catch statistics among Swiss and French lakes showed a similar decrease in salmonids and increase in percids and cyprinids with increasing concentrations of nutrients [76].

Among the deep lakes investigated by Projet Lac, the increase in whole-lake abundance and biomass of *Perca fluviatilis* with increasing concentrations of phosphorous was driven mostly by the expansion of this species to the offshore, pelagic habitat. *Perca fluviatilis* were particularly abundant in the open water of lakes Zug, Neuchatel and Geneva (also Joux and Bourget), with almost all pelagic-caught perch less than 20 cm in length. This habitat expansion in perch may be a result of stronger recruitment associated with elevated nutrients. The removal of large numbers of *Coregonus* from the open water by commercial fishing may also play a role [85], for example by relieving perch from interspecific competition for pelagic resources.

Responses to lake phosphorus varied among depth-habitats

The relationship between nutrients and benthic fish biomass varied between different depth zones within the lakes. In shallow waters, to around 12 m, the biomass of fish caught near the lake floor was higher in lakes with high phosphorus concentrations (Figure 23). This trend of lakes with higher phosphorus having more fish in the shallow, sunlit littoral waters, was mainly driven by *Perca, Rutilus* and other cyprinids (see analysis of factors influencing littoral fishes in [47]). Fish biomass, however, quickly declined with increasing water depth in these high-nutrient lakes. Lakes with lower nutrients had generally lower benthic fish biomass in the shallows, but biomass declined less quickly and remained higher into the deep. Comparing among lakes, benthic fish biomass in the profundal zone was highest in lakes with low phosphorus (Figure 23). Lakes such as Zug with very high phosphorus have almost no fish living in benthic or pelagic habitats of the profundal zone. The high productivity of the surface waters generates a high volume of organic particles, which sink to the lake floor. The decomposition of this material consumes the dissolved oxygen from the water and the sediment surface, making both an unsuitable habitat for fish, their eggs and their prey.

The relationship between productivity and fish biomass was strongest in the littoral zone where nutrients and sunlight stimulate primary production in both phytoplankton in the water column and algae and plants growing on the lake floor. The proximity to the lake surface means that there is usually sufficient oxygen. Importantly however, littoral fish biomass was higher in high-nutrient lakes for the catches in the two gillnet methods, but not for electrofishing [47]. This partly reflects the importance of *Perca fluviatilis* and *Rutilis rutilus* in driving the overall trend, since these species respond positively to increased lake productivity and dominate the gillnet catches, but are less frequently caught by electrofishing.

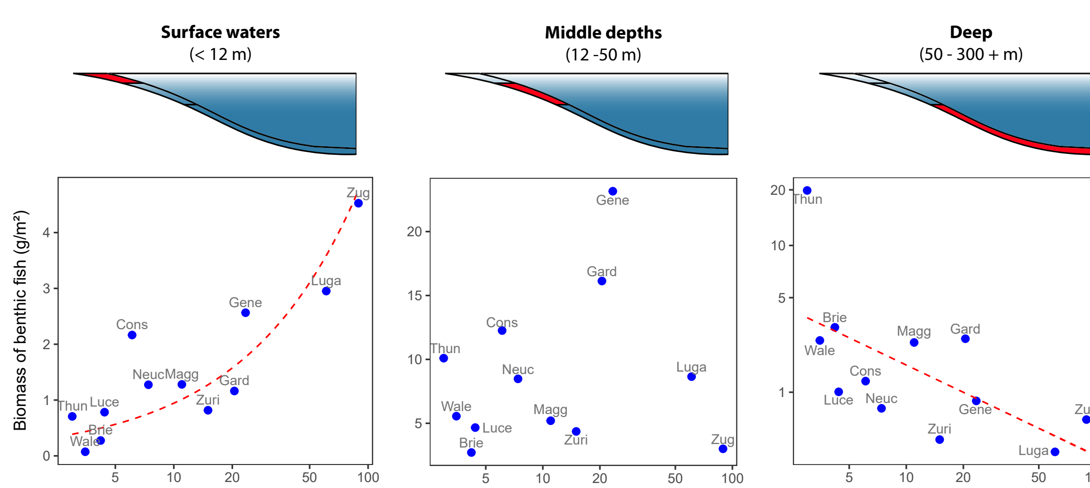

Figure 23: Fish biomass (CEN gillnets) in the shallow sunlit zone near the lake floor to around 12 m was higher in lakes with more phosphorus. In the deeper parts of the lakes (below 50 m), benthic fish biomass was highest in the lakes with very low phosphorus. Dashed lines are shown for statistically significant relationships (surface: p-value = 0.003, R2 = 0.74; middle: p-value = 0.63, R2 = 0.02, deep: p-value = 0.014, R2 = 0.467). Horizontal axis is displayed on a log scale.

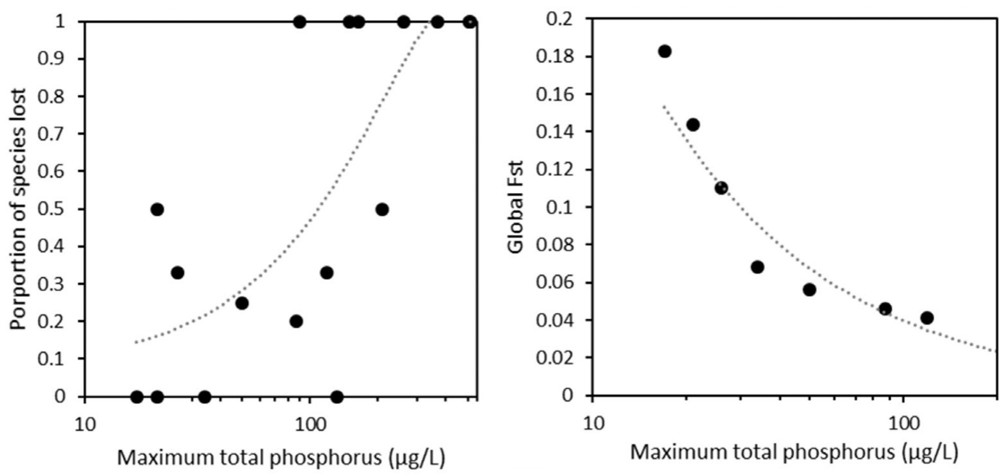

Figure 24: Relationship of the maximum total phosphorus concentration experienced by each lake versus the proportion of *Coregonus* species lost in each lake (left) and the genetic differentiation (global Fst) among the post-eutrophication *Coregonus* species within those lakes that retain native *Coregonus* species (right). Modified from [42].

A legacy of past eutrophication

Several lakes that had turned mesotrophic or eutrophic between the 1960s and the 1980s are now back to oligotrophic. However, the legacy of past eutrophication still influences the fish communities in most of these lakes. Eutrophication caused major changes to the lake environment, which led to the extinction of *Coregonus* and *Salvelinus* species in multiple lakes [42] (Figure 24), and probably also to the loss of deepwater sculpins. These extinctions occurred through a combination of demographic population decline in species adapted to the profundal habitat, an increased rate of hybridisation as deeper breeding species lost their habitat and could successfully reproduce only in the shallower habitats of related species, and relaxed divergent natural selection between formerly distinct niches as the environment becomes more homogeneous [42]. The process of species extinction through the loss of reproductive isolation and genetic differentiation among sympatric species is referred to as speciation reversal [86]. The extent to which this has affected communities of whitefish species in perialpine lakes depends on the eutrophication history of lakes (Figure 24). Loss of species differentiation in *Coregonus* caused a loss of functional diversity, e.g. in terms of the diversity in the numbers of gill rakers and their spacing. Variation in this trait influences the variety of types and sizes of prey that can be effectively consumed by the assemblage of *Coregonus* species in a lake [87, 88, 89]. Since *Coregonus* are such an important component of the fish community in the large perialpine lakes in terms of biomass (Figure 7), this likely has lasting effects on the food webs, as well as on the capacity of a local whitefish assemblage to take advantage of the available food resources [90].

Past eutrophication is also likely to have caused the extinction or near-extinction of several endemic *Salvelinus* species, including the extinct *S. neocomensis,* the recently rediscovered *S. profundus* and several historically recorded but only informally described species. It is likely to have further caused the extinction of deepwater forms of sculpins (*Cottus* spp) that were recorded in Projet Lac only in lakes that had never been eutrophic [41]. Ecosystem changes during past eutrophication may have also promoted the establishment of invasive fish and invertebrates, usually arriving from more productive habitats, by giving them an ecological advantage over native species [91]. For example, the invasion of northern *Rutilus rutilus* in several southern perialpine lakes, may have been facilitated by recently elevated nutrient levels in these lakes [92]. That said, anthropogenically increased nutrient loads are driven by human activities around the lake and the catchment, which is correlated with increased rates of immigration of non-native species. It is therefore often difficult to separate the role of eutrophication from other disturbances and increased translocation of animals by humans over the past century. When newly arrived species become invasive in habitats that supported native populations of related species, the resulting comparatively larger population sizes of invasive species in the altered environment in turn increases the likelihood of hybridisation and invasion through the genome of related native species [93]. Once established, the non-native species and/or the hybrids typically remain in the system even after the return of the lake to near-natural nutrient conditions. For example, the invasion of northern *Rutilus rutilus* in southern perialpine lakes is associated with genetic introgression into the native *R. pigus* and *R. aula* such that the latter species, even if they will survive, may remain strongly altered.

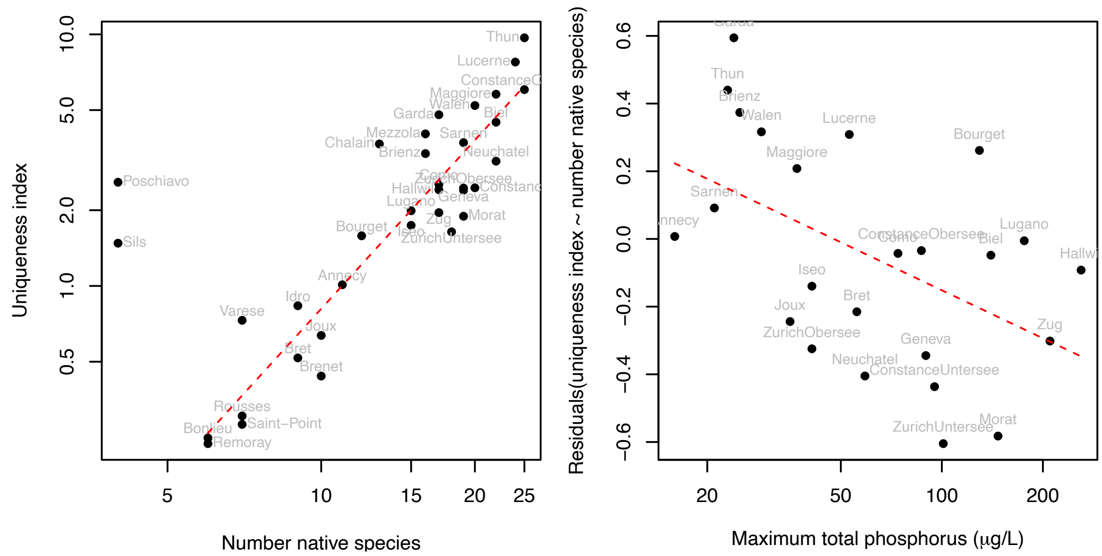

Figure 25: Left panel compares the "uniqueness" of the fish community to the number of native species to reveal outlier lakes with particularly "unique" fish assemblages for their size (lakes above the dashed line). Sils and Poschiavo were severe outliers and were excluded from estimation of the fitline and calculation of residuals. Sils was the only lake surveyed in the Danube catchment and Poschiavo was the only high-altitude lake surveyed in the Po catchment. Hence they shared few of their species with other lakes. Right panel shows that the uniqueness of the lake fish community relative to the number of recorded native fish species (i.e. residuals from the relationship in the left panel) decreased with the maximum total phosphorus that had been measured in the lake in the past (R^2 = 0.248, p = 0.013). Relationships of the residuals with other lake characteristics (lake surface area, lake maximum depth, present-day phosphorus) were not significant (Figure 83).

Fish communities are less unique in lakes that were previously more eutrophied

Clear indications of the history of past nutrient pollution were visible in the results of Projet Lac. Lakes that had never experienced strong eutrophication tended to support a higher proportion of range-restricted species, i.e. endemic species recorded only in few lakes. This is revealed by a negative relationship between the residuals from a regression of uniqueness index against number of native species (Figure 25, left panel) and the maximum total phosphorus concentrations that had been measured in the lake in the past (Figure 25, right panel). The uniqueness index for each lake fish community was calculated as the sum of the inverse of the number of lakes where each native species in the lake was recorded. Thus, an endemic species that was only recorded in one lake will have a high value of 1, while common species such as *Perca fluviatilis*, will contribute little to the uniqueness index score for the lake (*Perca fluviatilis* "Red form" was recorded in 33 lakes, giving a value of 1/33 = 0.03). These values are summed for all recorded native species to provide the uniqueness index for a lake. Larger lakes tend to support more species (Figure 12), generally resulting in a higher uniqueness index (Figure 25, left panel). Lakes positively deviating from the expected relationship of uniquess vs number of species are those that were least affected by eutrophication (Figure 25, right panel).

Range-restricted species include endemic species and other rare species of high value to conservation. Loss of these species from lakes that had experienced strong eutrophication at some point in their history, likely contributed to the lower uniqueness of these lake communities, when corrected for the total number of native species. Lakes with strong eutrophication also often suffered from other forms of ecological degradation, such as removal of complex littoral habitats such as reeds and woody structures, invasion of non-native species and channelisation of rivers in the local catchment. These factors may have also contributed to comparatively lower numbers of native species being recorded in the lakes that were previously strongly eutrophied.

Coregonus absent from profundal zone of re-oligotrophied lakes

In addition to influencing community composition, past nutrient pollution also appeared to reduce the proportion of the lake occupied by key fish groups. Large lakes that had experienced strong eutrophication in the past, such as Constance and Geneva, had lost deepwater adapted species and ecological diversity of *Coregonus* through population decline and hybridisation between previously distinct species [42]. Projet Lac data revealed that, despite the return of these lakes to low nutrient conditions, the deep waters of these lakes remained void of whitefish until now. On the other hand, *Coregonus* and other fish species were caught across the full range of depths, to the deepest points, in lakes Thun, Brienz and Walen, which had never been strongly eutrophied (Figure 26). Similarly, deepwater populations of sculpins (*Cottus* spp) were found exclusively in lakes that had never been strongly eutrophied (Thun, Walen, Lucerne, Maggiore, Garda), but were absent from all lakes that had once been eutrophic. The same was true for profundal forms of *Salvelinus*. These were recorded in Projet Lac in Thun, Brienz, Walen and Lucerne, but nowhere else (with the notable exception of the rediscovery of *S. profundus* in Lake Constance). The only fish that was caught regularly in the profundal zone of many lakes, including those that had once been eutrophic, was *Lota lota*. This species occupies the entire depth gradient of lakes and has pelagic eggs and larvae, such that recruitment into the profundal zone is likely independent of the habitat where spawning takes place. In other words, the occurrence of this species in the profundal does not require reproduction in this habitat. The existence of *Lota lota* in profundal habitats, however, speaks to the current habitability of the deep-water zone for fish in these lakes. In contrast, we did not find any fish in the profundal of lakes that still have a hypoxic water column (e.g. Lake Zug and Lake Zurich) (Figure 26).

The failure to recolonize the profundal zone by shallow water species other than *Lota* after return to sufficient oxygen concentrations suggests that the now extinct deepwater fauna had specific genetic adaptations for living in this habitat that are not shared by the closely related shallow water species that survived eutrophication. This effect has been surprisingly often neglected in discussions around ecosystem restoration. The loss of functional diversity in the lakes that experienced strong eutrophication therefore reduced the capacity of the fish community to make use of the full spectrum of depth-habitats and food resources [42]. The effects of these losses are likely to become most pronounced, potentially influencing fisheries yields, as the lakes return to an oligotrophic state [90].

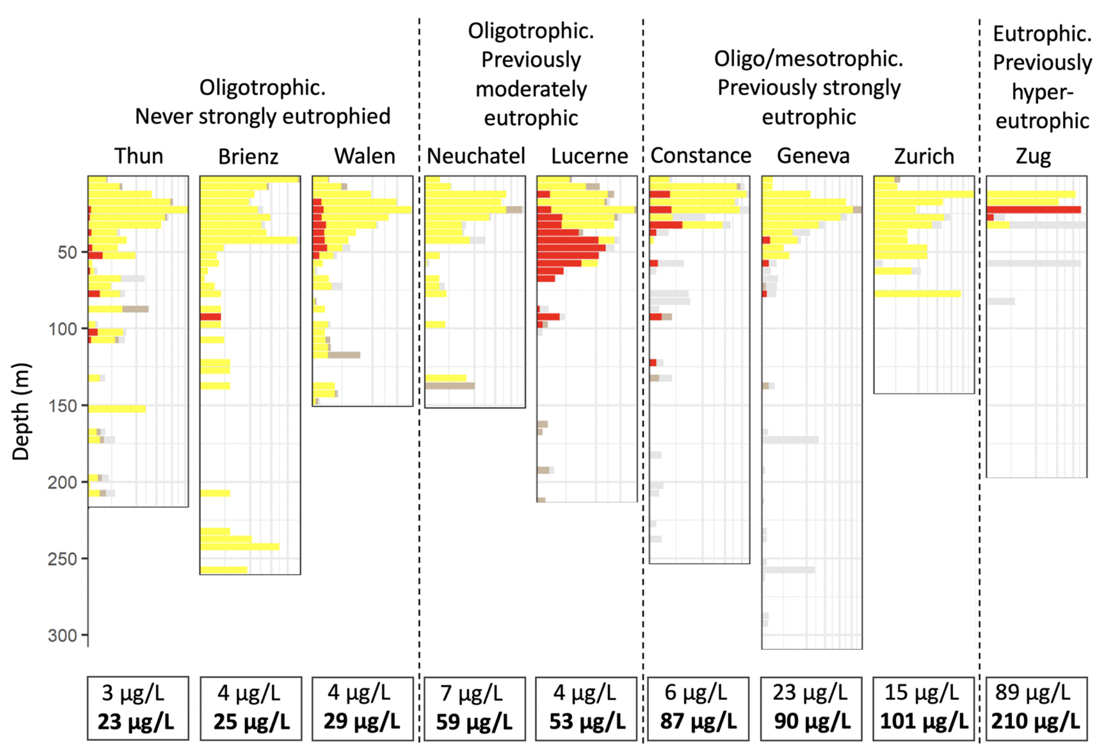

Figure 26: Depth distribution of catch per unit effort (CPUE; horizontal axis) for native fish species living in the deeper zones of the deep, northern perialpine lakes: *Coregonus* spp (yellow), *Salvelinus* spp (red), *Cottus* spp (grey/brown) and *Lota lota* (light grey). CPUE is the average of catches in deep-set vertical nets and benthic CEN nets. CPUE is square-root transformed to increase the visibility of the smaller values in the profundal zone. Note that the scale of the horizontal axis (CPUE) differs among the lakes. Whereas *Lota lota* has pelagic eggs and larvae and does hence not have to recruit locally, all other species recruit locally. Boxes at the bottom of the figure show the total phosphorus of the lake at the time of Projet Lac sampling (upper value) and the maximum measured total phosphorus value that had been experienced by the lake in the past (lower value in bold). The panels for Constance and Zurich show the data for the deeper lake in each of the pairs (i.e. Upper Constance and Lower Zurich).

Non-native and exotic species

Many non-native or exotic fish and invertebrate species have become established in perialpine lakes over the past centuries. Some of these new arrivals change the food web, some may even change the physical environment and most of them cause new species interactions with native species.

Non-native and exotic fishes

Newly arrived (non-native) fish species may deplete food resources through competition and predate upon native species. For example, *Gasterosteus aculeatus*, revealed by Projet Lac to be very abundant in the pelagic zone of Upper Lake Constance (Figure 27), feed on similar types of zooplankton as the commercially important native *Coregonus wartmanni* [94]. *G. aculeatus* have also been shown in aquarium experiments to be capable of feeding on the larvae of *Coregonus* spp [94]. Larval predation and food competition with *G. aculeatus* have been suggested as contributing factors in the recent declines in *Coregonus* fisheries catches in Upper Lake Constance [95], although much more work is needed to confirm the importance of these new species interactions. During the whitefish spawning season, the eggs of shallow spawning *Coregonus* spp also form the main prey of the abundant, non-native, benthic ruffe *Gymnocephalus cernua* in Lake Constance [96]. It is likely that *G. cernua* also predates on *Coregonus* eggs in other lakes. Piscivorous non-native species, such as *Sander lucioperca, Oncorhynchus mykiss* and *Micropterus salmoides* may influence the population age and size structure and within-lake distributions of some native fish populations. Resource competition with native species is probably often a significant effect especially where non-native species assume large abundance and may even outnumber ecologically similar native species. Examples are *Salmo trutta* that outnumbers native *Salmo* species in most of their habitats, and *Rutilus rutilus* that outnumbers native *Rutilus* and native *Alburnus* species in Lakes Lugano and Maggiore. The relative importance of the many new species interactions that are expected in the perialpine lakes are only beginning to be studied.

Finally, non-native fish species may interbreed with native species, eroding evolved differences between species with potential consequences for communities and ecosystems. Examples from Projet Lac include *Scardinius hesperidicus* invading the northern perialpine lakes and hybridizing with *S. erythrophthalmus, Rutilus rutilus* invading the southern perialpine lakes and hybridizing with *R. pigus* and *R. aula*, and *Salmo trutta* invading the southern lakes and hybridizing with *S. marmoratus, S. cenerinus, S. labrax* and *S. carpio* (see taxonomic profiles for these species for more information). In many of these cases, the native and the invasive species had distinct ecological adaptations that may be changed or lost through introgression.

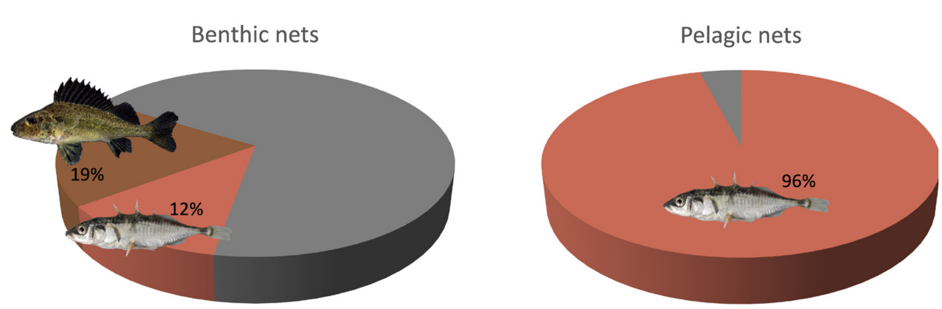

Figure 27: Contribution of two non-native fish species, *Gasterosteus aculeatus* (pink) and *Gymnocephalus cernua* (brown), to fish abundance in CEN gillnets set in the benthic (left) and pelagic (right) zones of Upper Lake Constance. The proportion of native species is represented in grey.

Highest number of non-native and exotic species in lakes south of the Alps

The number of non-native species was highest in the southern lakes of the Po catchment (Table 5). At least five non-native or exotic species were recorded in all southern perialpine lakes, with the highest number recorded in Lake Maggiore: ten species recently arrived from within Europe and four from other continents. Lake Garda had the highest number of all lakes of inter-continental translocations with a total of five exotic species, including *Carassius auratus* and *Pseudorasbora parva*, which Projet Lac recorded only in this lake, but which likely are more widely distributed. Non-native *Carassius gibelio* and exotic *Lepomis gibbosus* were recorded in all southern perialpine lakes, with *Micropterus salmoides* (exotic) and *Salmo trutta* (non-native) also frequently recorded in this region. Different attitudes and/or regulations towards species translocation and stocking of fishery-relevant species in the past may have contributed to the higher number of non-native fish species in this region [97]. Another contributing factor to the lower number of exotic species in the northern perialpine lakes may be that the cooler water temperature of these lakes (Figure 88) inhibits growth and/or reproduction of some warm-water exotic species (e.g. *Micropterus salmoides, Lepomis gibbosus, Ameiurus melas, Pseudorasbora parva* and *Gambusia holbrooki*) and has acted as a barrier to their widespread establishment. Consistent with this, the cooler, perialpine lakes Walen and Brienz were among the only lakes where no non-native species were recorded at all in Projet Lac. The recent and predicted future warming of lake waters due to climate change are likely to increase the vulnerability of the northern lakes to additional invasions.

Non-native and exotic invertebrates

In addition to non-native fish species, the food web in many lakes has also been changed by large numbers of non-native benthic invertebrate species. Non-native bivalves, the zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*) and Asian clam (*Corbicula fluminea*), are common in many lakes and can change sandy habitats into hard substrates through the accumulation of live and decaying shells [98, 99]. The increased substrate complexity can provide a refuge for other invertebrates against predation by fish [100]. It also provides new habitat for hard-bottom dwelling fish. One example is *Salaria fluviatilis* that recently became widespread and abundant in Lake Geneva, where (besides boulder fields) it inhabits reefs of invasive zebra and quagga mussels on otherwise open sandy lake floor.

Filter-feeding mussels also have the potential to remove large quantities of phytoplankton from the water column [101], transferring biomass from the pelagic food chain to the benthic food chain and away from fish. Other invertebrates, particularly the killer shrimp (*Dikerogammarus villosus*), can change the composition of native invertebrate communities [98, 102], changing the types of prey available to fish. Invasive crayfish can even displace juvenile benthic fish (*Lota lota*) from their preferred habitats [103]. It is possible that changes associated with non-native invertebrates favour generalist or ecologically flexible fish species (including many invasive species), further increasing pressure on ecologically specialized species (many of which are native species). Insufficient data on the prevalence of invasive macroinvertebrates among lakes, however, prevented investigations of their influence on lake fish communities across the region in Projet Lac. Such data should be collected systematically across all lakes in the future if the influences of invasive invertebrates on fish is to be better understood.

Status and diversity of littoral habitats

The existency of many specific habitat associations that differ between fish species means that changes in the type and amount of different habitats are expected to affect the species composition of lake fish communities. We could only study the status of habitats in the littoral zone but future research should investigate the status of habitats in deeper waters too, which will require the operation of divers, submarines or remote operated diving verhicles.

The littoral habitats are extensively modified in many lakes, with examples including harbours, retaining walls and artificial beaches (Figure 28). These modifications can have implications for littoral-spawning fish species, as well as for fish that use littoral habitats as feeding areas or nursery grounds. Comparisons of fish communities in natural and artificial habitats is difficult with Projet Lac data as the power to detect differences is limited by low replication i.e. low number of observations with a sampling method in a type of habitat of each state [natural/artificial] in each lake. Hence, we here limit ourselves to presenting the variation among lakes in the proportion of near-natural versus modified littoral habitat, and a discussion of the effects of modified water level dynamics.

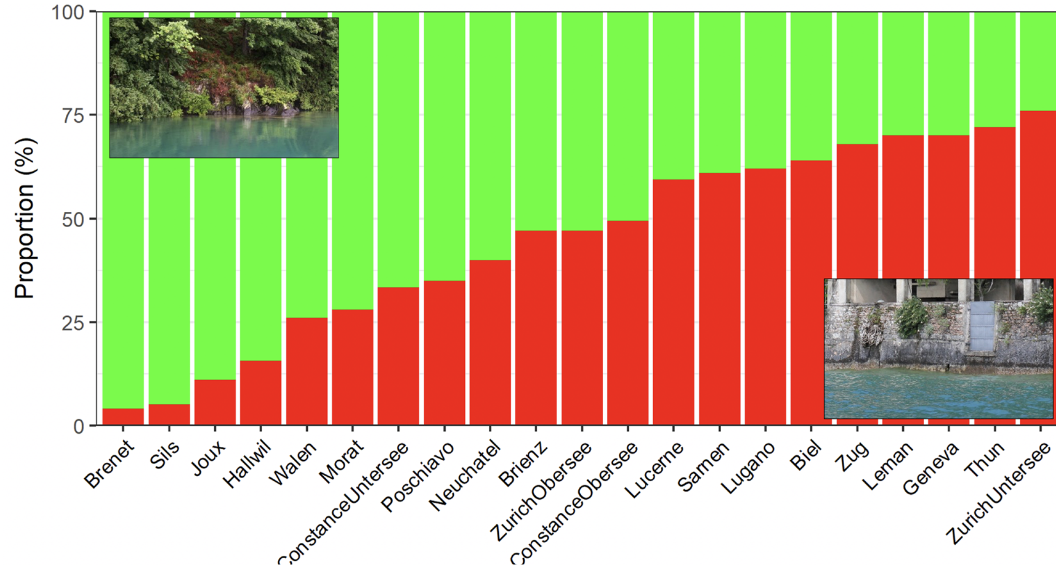

Figure 28: Proportion of the lake shoreline in a near-natural state (green) and un-natural, modified or artificial state (red) as determined during littoral habitat mapping in Projet Lac.

Regulation of lake water level

The water level of perialpine lakes and the extent to which it varies throughout a year have been changed dramatically over the past centuries for the purposes of flood mitigation and land reclamation. Present-day lake water levels are regulated primarily for flood mitigation or by upstream hydropower generation. Alteration of water level fluctuation regimes changes the physical environment of the littoral zone. This can have direct effects on fish such as through the loss of flooded areas for spawning and indirect effects by changing the composition of littoral habitats. Changes away from the natural water level fluctuation regimes may affect both the magnitude and seasonality of the fluctuations.

Research is required to understand the natural variation of water levels for different types of lakes, whether and how fish communities made use of this variation, how regulated lakes deviate from the natural variation and how fish communities, other organisms and habitats respond to these deviations. In general, lakes with reduced variation in water level tend to have a more stable littoral zone with accumulation of fine sediment and the expansion of reed habitats at the expense of gravel and cobble habitats, for example Lake Neuchatel [104]. Lakes with more variation tend to have less vegetation and more rocky or coarser mineral habitat, for example Lake Joux [105]. Fish species most likely to be affected by altered water level fluctuations are those that spawn exclusively in very shallow water, including several endemic winter spawning whitefish species such as *Coregonus alpinus* in Lakes Brienz and Thun, *C. litoralis* in Lake Lucerne, and perhaps *C. arenicolus* in Lake Constance. Also most likely affected are littoral spawning species with longer duration of egg development, species that build nests in shallow water such as the littoral forms of *Cottus* and species spawning at times of the year with greatest deviation from the natural regime. This again includes the above mentioned whitefish species, whose eggs would develop from spawning in December to hatching in February in the shallow littoral during the period of low water level in natural lakes, but could experience larger water level changes in the course of the incubation period in lakes with managed water levels (Fig 38). Variation in water level is most critical during months where many fish species or sensitive fish species are spawning in shallow habitats and the seasons when littoral vegetation is becoming established. Fish species spawning on flooded vegetation such as pike and carp are also likely to be affected.

Interactions between lakes and rivers

Many species caught in river deltas

A large number of fish species were caught most frequently in Projet Lac in the inflow of streams and rivers (Table 10) [47]. Among the lake littoral habitats, inflowing streams and rivers supported the highest number of endangered and threatened species. Although a proportion of these were species typically associated with rivers more than lakes, the fact that larger lakes had more of these river-associated taxa than smaller lakes, suggests that these are locally sustained populations rather than opportunistic visitors from the rivers (see section Species-area relationships and island biogeography). This diversity emphasises the importance of these ecotonal transition zones and the connectivity between lakes and rivers.

River redirection

Several rivers have been redirected to flow into lakes, where they previously bypassed the lake and met another river further downstream. Rivers were usually redirected for the purposes of flood protection and land reclamation. The redirections changed connectivity between lakes and dramatically altered the effects of rivers on the lakes. Prominent examples are the redirection of the Kander River to flow into Lake Thun (1714), diversion of the Aare River to flow into Lake Biel (1878) and diversion of the Linth into Lake Walen (1811), as opposed to all these rivers flowing into the outlets of the lakes. These redirections led to many changes in the lakes, including altered lake water levels, water retention times, sediment inputs and temperature regimes. The Kander Correction massively increased the amount of sediment entering Lake Thun [106], which changed the composition of the benthic habitat, smothered developing salmonid eggs and reduced fisheries catches to the extent that fishermen were reimbursed for the losses [107]. The Linth Correction had a similar effect on the ecosystem and fisheries of Lake Walen and is believed to have contributed to the decline of *Coregonus zuerichensis* in this lake [48]. Similarly, the diversion of the flood waters of the Adige River into Lake Garda has been suggested to be responsible for the collapse of endemic *Salmo carpio* as turbid waters of the river affected spawning grounds [108]. Finally, the diversion of the Aare River into Lake Biel as part of the Jura Correction resulted in the establishment in Lake Biel of *Coregonus albellus*, and perhaps most recently *Coregonus profundus,* both originally endemic to upstream Lakes Thun and Brienz [109].

Modification of river morphology and hydrology

Damming of rivers for flood protection, hydropower and/or drinking water, reduces connectivity among river reaches, between lakes and rivers and between lakes. The result is reduced movement of fish individuals between lakes and between lakes and rivers. The consequences are manyfold and include preventing the successful return of long-distance migrants such as *Salmo salar,* ocean-migrating *Salmo trutta* (sea trout), *Anguilla anguilla, Petromyzon marinus, Alosa* spp and *Acipenser* spp. Most of these species are extirpated from all lakes (and most streams) in the region. The only long distance migratory species that were still recorded in Projet Lac were *Alosa fallax* in Lake Maggiore (phenotypically determined) and *Anguilla anguilla* in Lake Constance and several lakes south of the Alps. Observations of *Anguilla anguilla* may however be the result of stocking as Germany and Italy both have stocking programs for eels.

Two other consequences of reduced movement between lakes and between lakes and rivers have received far less attention, but are equally important. Firstly, limitations to the movement of short distance migratory potamodromous species such as lake forms of *Salmo trutta* and *Salmo marmorata* and some cyprinid species such as *Chondrostoma* spp may make some lakes altogether unsuitable for these species that rely on stream habitat for recruitment. Second, increased isolation of lake populations of any species that used to occasionally disperse through rivers leads to increasing insularization of lake fish assemblages with the prediction of gradual decay of species richness through local extinctions that can no longer be compensated by renewed colonization. Such insularization might at least partly explain the unexpected absence of species such as *Alburnoides bipuncatus, Telestes souffia, Chrondrostoma nasus* and *Chondrostoma soetta* from most lakes in Projet Lac data. More historical data would be required to confirm this.

Dams and hydropower operation have further effects on rivers that subsequently influence lake ecosystems and fish populations migrating between lakes and rivers for feeding or spawning. Dams block the natural flow of sediment (including fine sediment, gravel and cobbles) along the rivers and into the lakes and this could have negative effects on endemic char and other species that spawn on sublittoral and profundal gravel beds that owe their existence to the inflow of mountain streams. Changing the flow of water through hydropower plants to match the demand for electricity also results in unnatural river flow regimes (hydropeaking) [110]. Sudden increases in water level can wash away developing eggs and larvae of river-spawning fish species, while sudden decreases in flow can leave them high and dry. Reduced discharge of water from dams and/or hydropower operation may also increase water temperature as the shallower, slower-flowing water is more readily warmed by the sun and heat exchange with the atmosphere. Dams may alternatively result in cooler water if water is released from the deeper parts of the reservoir. Through its influence on density, the temperature of river water arriving in a lake affects the depth into which nutrients, sediment and organic debris are transported. Cooler river water will flow into the deeper parts of the lake, while warmer water, and material that it brings with it, will remain closer to the surface.

Channelization of rivers and streams flowing into the lakes reduces habitat diversity in the rivers, and can impair populations of fish species that seasonally move between the lake and rivers for spawning or feeding. For example, *Salmo* spp spawn in streams, with part of the population migrating into the lakes to feed and mature [85]. Straightening and hardening the beds of inflowing streams and rivers dramatically reduces the diversity of water depths, flow rates and substrate types (e.g. fine sediment, gravel, tree roots) in these habitats. This consequently reduces the niche diversity and the amount of suitable spawning substrate, with expected negative effects on the diversity, carrying capacity and reproductive output of the potamodromous fish community that requires these habitats. Populations of lake fish species that utilise adjacent rivers for feeding, spawning and/or as nursery areas, will therefore be influenced by the ecological condition of the nearby rivers, as well as by impairments to connectivity between lake and rivers.

Chemical pollution

Perialpine lakes are influenced by a variety of chemical pollutants, with particularly high concentrations in some lakes. Industrial pollution has resulted in many perialpine lakes having high concentrations of Persistent Organic Pollutants (POPs), such as DDT and PCBs, as well as heavy metals, such as mercury. While concentrations in most lakes have declined since a peak mid-late last century [111], concentrations of POPs in agone of Lake Maggiore, and lake trout and char of lake Geneva still exceed environmental quality standards and thresholds for safe human consumption [112, 113]. These compounds accumulate in the tissue of fish, particularly those with high lipid content such as the three species mentioned above. Effects on fish can include disruption of the endocrine system of fish, and effects on reproduction and early development, such as through embryo mortality, reduced hatching success, malformation of larvae, and limited survival of juveniles [114]. Other potentially important forms of chemical pollution include pesticides, synthetic hormones, micropollutants and microplastics. Effects of most of these pollutants on lake ecosystems and fish populations are very poorly understood and very little can be said about their influence on fish and the fish community based on Projet Lac data. However, work in lakes elsewhere has recently implied potentially dramatic effects of neonicotinoids (globally the most widely used class of insecticides) on aquatic invertebrates that cascade to higher trophic levels by altering food web structure and dynamics. Using data on zooplankton, water quality, and annual fishery yields of eel and smelt, Yamamuro et al [115] showed that neonicotinoid application to watersheds since 1993 coincided with an 83% decrease in average zooplankton biomass in spring, causing fishery harvest of smelt in Lake Shinji (Japan) to collapse from 240 to 22 tons annually [115]. Neonicotinoids are very widely applied in Switzerland. Humann-Guilleminot et al [116] detected neonicotinoids in 93% of organic soils and crops in Switzerland, and in more than 80% of ecological focus area soils and plants – arable land supposedly free of insecticides. These authors showed that between 5.3%–8.6% of terrestrial above-ground invertebrate species may be exposed to lethal concentrations of clothianidin, and 31.6%–41.2% to sublethal concentrations, and that the use of neonicotinoids on crops may threaten biodiversity in terrestrial refuge areas. Investigations of effects of neonicotinoids on aquatic organisms and communities are yet to be conducted in Switzerland.

Fishing and fisheries management

Ecological and evolutionary effects of fishing

Fisheries can strongly influence populations of targeted fish species, with cascading effects on other aspects of the lake ecosystem. In lakes with intense commercial and/or recreational fishing pressure, especially where targeted species have slow individual growth, almost all large individuals of target species can be removed from the population (Figure 8). Projet Lac data recovered distinctly different size structure of commercially valuable species in lakes with and without commercial fishing. Several lakes with no commercial fishing (e.g. Chalain, Saint-Point, Remoray, Sarnen) had many large individuals of whitefish and perch, compared to populations of these taxa in lakes with commercial fishing (despite these populations being fished by recreational fishers). Intense fishing pressure also influences the structure of the food web through trophic cascades [117]. Removal of most large fish of targeted species releases organisms consumed by the target fish species from predation pressure and/or can promote population growth in competitors. For example, intense fishing pressure on *Coregonus* spp has been suggested as the reason for the dominance of *Perca fluviatilis* in the pelagic habitat of Lake Geneva [85]. Suppression of populations of pelagic *Coregonus wartmanni* and *C. macrophthalmus* through intense fishing may have also contributed to the establishment of *Gasterosteus aculeatus* in the open water of Lake Constance [94, 95]. Similar effects on the population dynamics of stickleback have also been invoked in the Baltic Sea. An important lesson learned from the Baltic system is that the population growth of the mesopretador (stickleback) once released from predation, can make recovery of the top predator very difficult through predation on its young. Such predator role reversal can have far reaching consequences for the foodweb, effectively generating alternative stable states of the ecosystem [118, 119]. The establishment of *Rutilus rutilus* in Lake Lugano has also been suggested to have been facilitated by suppression of populations of *Alburnus arborella* and *Alosa agone* through a combination of several factors, including through fishing and eutrophication-related oxygen deficiencies [120].

Fishing pressure in many lakes became particularly intense after commercial fishers began using highly efficient and size-selective nylon gillnets around the 1950s, such that it likely became not just an ecological but also an important evolutionary force on the targeted populations. By removing the largest, fastest growing fish within each age cohort, the smaller, slower-growing individuals that remain had a better chance to reproduce and contribute proportionally more offspring to the next generation, i.e. gained evolutionary fitness. Over multiple generations, this can result in the evolution of slower growth rates, younger age at maturation and increased fecundity as evolution favours genotypes that invest energy into early reproduction instead of growth [121]. Indications of fisheries-induced evolution have been observed in two whitefish species of Lake Constance [122, 123] and Lake Joux [124, 125]. In Lake Constance, the effect was estimated as a mean decrease in the size of 2-year-old fish by 6 mm every 10 years [122]. While the evolutionary effects of fishing may not seem immediately dramatic, they are cumulative and long-lasting if not managed appropriately. A related risk that is seldomly discussed is that in communities of several closely related species that differ in body size (e.g. whitefish), fisheries-induced evolution in the larger species in response to selection for slow growth and early maturation may interfere with ecological niche partitioning and reproductive isolation and may facilitate speciation reversal.

Stocking

Hatchery breeding and stocking of juvenile fish is a widespread practice intended to increase the number of juvenile fish entering an exploited population, with the ultimate aim of providing more fish for the fishery. There is much debate about the effectiveness of stocking and about its influence on the wild population and the species community. A discussion of the effectiveness of stocking as a management tool is beyond the scope of this publication, but its effects on species and communities deserve some attention here.

Stocking may have several negative, long-term impacts on fish populations that can be categorized as demographic, genetic and evolutionary impacts. Raising larvae under conditions optimal for growth alters the evolutionary selective forces acting on the developing fish. For example, larvae of Blaufelchen *Coregonus wartmanni* from Lake Constance naturally hatch very early in the season and must wait for the zooplankton population to start growing in early spring before they can start feeding [126]. This species consequently has one of the highest reported tolerances to starvation of all *Coregonus* species [127]. By growing larvae in a hatchery with abundant food, factors such as a fast growth rate or boldness become more important for survival than starvation tolerance. These traits may be favoured by selection in the hatchery, and where there are physiological tradeoffs, the increase in growth rate and boldness may come at the expense of starvation tolerance. This can result in a genetically programmed weakening of the tolerance to starvation in the population. If hatchery-raised fish subsequently breed in nature and interbreed with the wild population, the incidence of the hatchery-favoured traits can spread into the naturally breeding population in years of food abundance, potentially leading to reduced survival of wild born juveniles in subsequent years of food scarcity. The result would be increased dependence on stocking to support the population.

The use of wild fish from spawning fisheries as breeders (as opposed to maintaining broodstock over several generations) partly helps to reduce evolutionary effects of domestication. However, this is only true if the chance is negligible that breeders caught in spawning fisheries were themselves already born in the hatchery and stocked. With 83% of adult *C. wartmanni* in Lake Constance having been stocked as larvae, this condition is clearly not given, and evolutionary change through hatchery selection is a very real danger to the long term survival of the species.

A very different danger is that breeding in the hatchery with wild caught fish can involuntarily lead to genetic mixing of species that in nature are genetically isolated by the location of their spawning grounds, by spawning season or by behavioural mate choice. This can contribute to the erosion of the genetic, phenotypic and ecological distinctiveness among species within a lake. It is sometimes assumed that fish caught on a spawning ground in the same net at the same time and place are likely to belong to one and the same species. However, some species (such as *Coregonus* species in most lakes) overlap in spawning time and depth, yet remain genetically distinct e.g. [24], suggesting that individuals may actively choose mates of their own species.

Mixing of species through artificial breeding in hatcheries has been suggested to interact with the effects of eutrophication to accelerate loss of functional and species diversity [42, 128]. On the practical side of it, artificial hybridisation in hatcheries and/or hybridisation in nature due to eutrophication (and perhaps also fishery induced evolution in the larger more sought-after species) causes sympatric *Coregonus* species to loose their distinct appearance. This increases the difficulty for hatchery operators to keep the species separate which may result in a higher error rate and lead to further homogenisation of the species. The ultimate result is a complete meltdown of genetic and ecological species differentiation.

Finally, a negative demographic effect of stocking arises when hatchery-raised larvae released into a lake compete for food against naturally bred fish potentially resulting in slower individual growth of all fish in the population. Variation in the number or biomass of *Coregonus* competing for the same food resources within a large perialpine lake can have a significant influence on the growth rate, as has been shown for Lake Constance [129]. Particularly under oligotrophic conditions, adding millions of artificially raised fish means less food for each fish, likely resulting in slower growth rates for all members of the population.

Analysing effects of stocking on lake fish populations and communities is not possible with the current Projet Lac data. One possible option would be though to look for correlations between the intensity of stocking per unit lake area (if such data were available) and whole-lake catches of stocked species among lakes, but such a correlational analysis will always be confounded by differences between lakes and species.

Finally yet importantly, stocking has been a frequent cause of species introductions and stock transfer between lakes in the region. This effect is easily witnessed by the data from Projet Lac that reveal the high prevalence of non-native fish across the region, particularly in the southern perialpine and Jura lakes. Common non-native species previously stocked into southern lakes included *Coregonus* spp, *Salmo trutta, Esox lucius* and *Salvelinus umbla. Coregonus* is still being stocked in several southern perialpine lakes to support fisheries, with fish from the local populations now used as broodstock [97]. *Coregonus* spp was introduced through stocking also into the Jura lakes. However, invasions of lakes by species previously absent is just the most readily visible signature of stock transfer. The invisible problem, which is at least as significant, is the genetic homogenization of species and genera (i.e. multiple species) across the landscape by transferring populations and species that hybridize with each other. This process has led to replacement of native trout species by hybrid populations dominated by introduced Atlantic trout south of the Alps (Figure 51), to replacement of endemic whitefish species by hybrid stocks across many of the smaller midland lakes, and to partial homogenization of charr communities across lakes (Figure 56).

Multiple stressors

The fish populations of the perialpine lakes face a combination of many stressors, some demographic, some genetic and some evolutionary. It is likely that interactions between many of these will aggravate the problems for fish populations and species diversity. For example, weaker vertical mixing resulting from climate change can exacerbate oxygen problems in the profundal zone caused by elevated nutrient concentrations. Similarly, proliferating cyanobacteria can consume what little nutrients are being transported upwards against a backdrop of generally weaker upward transport due to lake warming [64, 130]. Warming water can reduce the habitat suitability, the volume of suitable habitat and/or delay and shorten the suitable spawning time for endemic salmonids, coregonids and other fish adapted to cold water. In turn it can facilitate the establishment of non-native warmwater species, which place further stress on the native species through competition or predation and the introduction of new parasites and disease. All of these stressors may impact a population that is already genetically depauperate because of habitat loss and fragmentation and because of overharvesting more severely than a genetically variable population. The result is further population decline and further loss of genetic variation. Loss of genetic variation may also make adaptation to new future conditions difficult. On the other hand, existing ecological adaptation of populations can be compromised by increased geneflow as a consequence of stock transfer from populations adapted to different conditions. Loss of ecological distinctiveness can also occur due to hybridization between distinct species as a consequence of stock transfer, identification errors in hatchery breeding, deterioration or loss of species-specific spawning habitat, phenotypic convergence due to fishery-induced evolution, or multiplicative interactions between several of these.

These many possible and even likely interactions are important to consider when trying to make predictions and when interpreting monitoring data and comparisons among lakes. Many of these stressors interact in ways that include negative feedback loops such that populations and entire species can get trapped between vortices of demographic, genetic and evolutionary decline [131], and multi-species communities can erode into single undiverse populations [132]. Indeed, we suspect that many communities, species and populations of fish in perialpine lakes are already stuck in such situations.

6. Recommendations for conservation of lake fish diversity

Recommended management actions for the conservation of lake fish diversity in the perialpine lakes can be grouped into three categories:

- **restoration** of key aspects of the lake ecosystems, lake-river ecotones and lake-river network to near-natural conditions in order to restore habitats, fish movement and metacommunity dynamics.
- improving **understanding** of the diversity of fishes in terms of their taxonomy, distribution, ecology, evolutionary relationships, and within-species genetic, phenotypic and ecological diversity. This includes the **identification** of unique and threatened species and intraspecific units, their biological and ecological needs and the definition of conservation targets.
- Identification of hot spots for unique and threatened species and intraspecific units for which specific conservations and protection measures should be defined.
- **regulating** the human activities that directly affect fish populations, such as fishing, stocking, translocation of fish within the range of a species and translocation of fish to outside a species' native range.

Restore near-natural conditions

The most effective way to protect and support the native fish diversity that remains in the lakes is usually by restoring the ecosystems that support these species to as near to natural conditions as possible. Several factors deserve specific mention because of their large influence:

Lake nutrients

The effects of nutrients on a lake ecosystem are pervasive and restoring near-natural nutrient conditions therefore is an important prerequisite for bringing a lake and its foodweb close to their original condition. This can go a long way towards restoring the physical and biological conditions that together shape the set of niches in which the native fish species assemblage, and especially the endemic species, evolved. Often when species were lost through hybridisation with other species caused by changes in environmental conditions and loss of their niche, some of the genetic variation of the lost species may still persist in the surviving species or in hybrid populations[132]. Restoration of the original ecosystem state provides the best chance that populations with similar adaptations may re-evolve through ecological sorting of and natural selection on this remaining genetic variation (see section Appendix B – 'Positive developments for lake fish communities'). This will not be instantaneous, but may well be relatively fast (e.g. within a few decades) and it remains the best option to recover what is left.

Sublittoral and profundal habitats

Most endemic species of the perialpine lakes require benthic habitats, some at great depths, to provide opportunities for spawning, development of eggs and larvae and feeding habitat. Such endemics include many species of whitefish and char in the northern lakes, fully lacustrine trouts in southern lakes and profundal sculpins on both sides of the Alps. Such species require good oxygen concentrations throughout the water column, as well as clean bottom substrate to prevent suffocation of fish eggs and to provide habitat for invertebrates that provide the food base for benthic and profundal fish. Chronic hypoxia at the sediment surface and in the deep waters of lakes are responsible for the largest number of species extinctions that have occurred in the perialpine lakes in the past 80 years [42]. Increased biomass production due to eutrophication, leading to increased oxidative activities in deep water and on the sediments is the most important cause. Another cause is loss of clean gravel as spawning habitat for salmonids due to changed sediment transport regimes from the rivers and possibly gravel harvesting. Also influential are changes in water turbidity and associated light regimes due to changes in the course of rivers and altered fine sediment transport in rivers, e.g. due to impact of upstream hydropower dams. Restoring nutrient conditions that are as natural as possible is usually the most important first step to restore deep water habitats, but the results of such restoration are not immediate because the accumulated load of oxygen-consuming biogenic materials in the sediments can delay the recovery of the sediment oxygenation beyond the recovery of oxygen in the water column [77]. Future restoration effort needs to pay more attention to the structure of the sublittoral and profundal habitats to understand how spatial variation in habitat conditions affects the different profundal fish species, and to be able to identify hotspots worth of dedicated conservation or restoration measures. Currently, the knowledge about benthic fish habitat in the profundal zone of perialpine lakes is extremely limited and does rarely permit spatially and ecologically informed conservation and restoration action.

Littoral habitats

Renaturalisation of littoral habitats can enhance the success of natural reproduction and improve juvenile survival and growth of many fish species with a littoral life stage. Different types of lakeshore habitats offer feeding grounds, breeding substrates and shelter from predators to different species of fish. Restoring the mosaic of natural habitats historically present in a lake and the connectivity between them is therefore expected to be instrumental for returning a fish community towards its original composition. In the absence of historic data or other information on the natural composition of the littoral habitats in a lake, establishing a diverse mosaic of littoral habitat types is thought to help to support a diverse littoral and whole-lake fish community.

Restoration or renaturalisation of large areas of Switzerland's lakeshore habitats is anticipated for the coming decades. While bringing the habitats closer to a natural state is a good start, restorations could be designed to particularly support rare, endemic and endangered fish species. A requirement for this is to learn whether relatively closely related yet genetically distinct littoral species (for instance different species of *Phoxinus* or *Barbatula*) have different habitat requirements. Such knowledge is currently lacking because congeneric species were rarely if ever distinguished until very recently. A better understanding of why different species use certain littoral habitats at certain times of the year and at certain life-stages would also allow predictions of how the fish community will respond, and thereby allow more effective planning and evaluation of the success of such restoration projects.

Appropriate management of lake water levels can facilitate restoration of littoral habitats and support littoral fish species. The seasonality and magnitude of fluctuations could be controlled to influence the establishment of littoral vegetation (and wetland areas) around the lake. Any such measure would need to be carefully designed on a case-by-case basis, with careful consideration of which species would benefit and which species (if any) might be disadvantaged.

Restore connectivity

Facilitation of upstream and downstream migration would benefit migratory fish species such as *Anguilla anguilla* and *Alosa fallax,* and is the only chance for the return of other long-distance lake migrants such as *Salmo salar* and the ocean-migratory form of *Salmo trutta* (sea trout). The most effective way to restore connectivity and increase the survival of migratory fishes is the removal of dams. However, this is unrealistic in many cases and alternatives must be considered. Fish ladders or passages are already installed on many dams within the region and facilitate upward migration at least for good swimmers or fish with leaping abilities. Downstream migration has the added challenge of needing to guide fish towards the fish ladder and preventing them from moving through the turbines with the main water current. Options such as vertical metal grills to divert fish into the fish passage and "fish-friendly turbines" are currently being tested. However, there still are several dams downstream of the perialpine lakes, especially in the Rhine downstream of Basel, that are impassable for upstream migration and making these dams passable is a precondition for the return of long-distance migrants.

Restoring the habitats of rivers and streams flowing into the lakes, and the ecotonal zones, to their near-natural state will also help short-distance and partially migratory species that move between the lakes and rivers for feeding and spawning. Species spawning in flowing water such as *Salmo* spp, *Thymallus* spp, *Leuciscus leuciscus* and *Barbus* spp will benefit from improved connectivity between lakes and the inflowing waterways, as well as renaturalisation of river habitat. The large number of fish species recorded in Projet Lac at the interface between streams and lakes, i.e. river deltas, emphasises the importance of this ecotone or transition habitat and the connection between these two ecosystems. Restoration of river connectivity should be done carefully however to prevent the further range expansion of invasive fish and invertebrates [133]. Information provided by survey data such as Projet Lac, Progetto Fiumi and monitoring databases, such as the Swiss Biodiversity Monitoring and the Swiss Fish Atlas [134], can be used to understand the distribution and prevalence of invasive species. They can also be used to understand changes in the distribution of native species but only if species are identified to species level within genera (as exemplified by the widespread but previously unnoticed invasion of *Scardinius hesperidicus* north of the Alps). Restoration of river sediment transport may also help lake fish species that spawn on gravel beds in the lake (such as *Salvelinus* spp).

Restoring connectivity between lakes and streams and between lakes (through intervening streams) will finally also be important to restore metapopulation and metacommunity dynamics including of weakly dispersing non-migratory species, to allow natural re-colonization of lakes to compensate for local population extirpations and restoration of genetic variation within increasingly isolated populations.

Improve understanding of lake fish and identify conservation priorities

Species descriptions and identification

Sustainable management and conservation of fish species diversity is not possible without excellent understanding of species level taxonomy. One of its applications is the early recognition of species showing up outside their native ranges. The cases of *Scardinius hesperidicus* (mistaken for *S. erythrophthalmus* in many northern lakes) and *Cobitis bilineata* (mistaken for *C. taenia* all across northern Switzerland likely for several decades) illustrate this problem well. Other genera where misidentificationof described species is widespread include *Carassius, Phoxinus, Coregonus* and *Salmo* but every genus with different species native to different drainage systems within the wider region (beyond Switzerland) need careful attention at all times. Excellent understanding of species level taxonomy also requires recognition of little known and yet undescribed species, or even unknown species that may exist, their delineation and their subsequent description. Genera that are in particular need of attention in this regard in Switzerland and the larger perialpine region are *Coregonus, Salvelinus, Cottus, Phoxinus, Barbatula* and perhaps *Salaria* and *Cobitis*. Formal description of species is a prerequisite for a legal basis for management and conservation action, as well as for public awareness of the existence of the species. Excellent species knowledge then is a prerequisite for effective implementation of the law, but also for effective monitoring, which in turn improves ecological understanding of the species, and will eventually allow tracking of trends in population sizes and distribution ranges. Improved species knowledge should be complemented by improved resources for the identification of fish species.

Increased use of genetic methods by managers could help to identify species, distinct populations and juveniles that are difficult to differentiate based solely on appearance. Genetic methods for broodstock identification can also be used to minimise the chance of accidental hybridisation of species during hatchery reproduction and stocking. The decreasing cost of genetic methods means that they could be used more routinely to identify species or management units in the future. The feasibility, in terms of practical and technical aspects, requires discussions between federal and cantonal management authorities, research institutions, ecological consultancies and fishers. Genetic identification methods are not error-proof and require good understanding of the limitations of different methods.

Understand ecological requirements

Coupled with the process of carefully documenting fish diversity, including the difficulty to identify poorly known species and distinct populations, should be the identification of the ecological qualities and requirements of these different species. Particularly important is an understanding of the key requirements for spawning grounds within profundal, sublittoral and littoral habitats, but also the required characteristics of refuge areas for juveniles and feeding grounds for all ontogenetic stages of the different species. Ecology of early life stages is for most lake fish hardly known. Improved understanding of the conditions that influence the amount and types of dietary resources available to the fishes is also valuable. While there is a considerable amount of general information available on ecological requirements of widespread fish species, some of this information may not apply to the populations of interest. Much published ecological information on perch for instance comes from Scandinavian shallow lakes and from shallow central European lakes and rivers. To what extent such information applies to perch populations in deep perialpine lakes is not obvious, and whereas such data from other regions may often be useful as a first approximation, it should not a-priori be assumed to capture specific requirements of target populations. This is particularly true in cases such as perch, where many perialpine lake populations are phenotypically distinct both from those in lowland lakes in Europe and the nearby river populations. Often times ecological information is available only in scientific publications and has to be collated to make it available to regional decision-makers. Such collation should then be combined with investigation of regional, population or lake-specific differences, which may include for the fished species utilising the knowledge of local fishers (e.g. [135]). It is important that ecological studies aiming to provide information for management acknowledge that the situation in the lakes today is very often not the natural state and may not reflect the condition to which the fish populations have adapted through their evolutionary history, nor may the current food web represent the natural state of and the ecosystem in question. Careful use of historical information can be useful in this regard, and increased use of palaeoecological and historical ecology approaches to reconstruct past conditions and past communities is already of great value and will become even more important in the future.

Regulate human activities

Avoid stock translocation

Further translocation of species and differentiated populations to outside their native range should be avoided. This is possible only if the fish species are recognised by the legislation. To achieve this, two work packages are important. The first consists of three elements:

1. clarifying taxonomy;
2. improving knowledge, resources and tools for identification of all species and divergent lineages;
3. establishing their past and current distributions.

The second consists of further educating hatchery managers, fishers, other lake users and the general public on the importance of maintaining endemic species, intra-specific diversity and the distinctiveness of populations of more widespread species. Finally, information on the dangers associated with the introduction and spread of non-native and exotic species needs to be made more easily accessible.

Fisheries management and stocking

Although rarely causing the total extinction of a stock, intense fishing pressure often has significant direct effects on the exploited fish populations, including fishing-induced evolution and eroding ecological differences between species. A putative example could be where a heavily exploited large whitefish species converges in size at maturity on a less exploited smaller species with which it coexists. If the species were ecologically segregated by size, and genetically isolated by size-assortative mating, and both are lost as species converge in size, the fishing-induced evolution in one species will have cascading evolutionary effects on the second species and diversity can be lost suddenly and unexpectedly. Intense fishing pressure also has indirect effects on other biological components and processes of the lake ecosystem, resulting in the removal of large amounts of biomass and almost all large individuals of target species. The main option for reducing the ecological effects of fishing is to reduce the amount of fish biomass being removed from the lake and to ensure that the populations of all species retain a proportion of older and larger fish. Diversifying fisheries to spread harvesting pressure across multiple fish species may also help to manage some effects.

The main options to slow or reverse evolutionary effects of fishing in lakes are protected areas and reduced fishing pressure [136]. The effectiveness of protected areas depends on dispersal distances of individuals and larvae relative to protected area size and is most effective for species with less mobile adults and widely dispersing larvae. The principle is that a proportion of the adult population are not exposed to selection caused by harvesting. The fish in the protected area do not experience fisheries-induced selection and contribute a high proportion of the lake-wide recruitment. For this to be an effective management tool in *Coregonus* or *Perca* populations in perialpine lakes, protected areas would probably have to be of significant size because fish in the reserve should spend all their reproductive life within the reserve in order to escape fisheries-induced selection. Reducing fishing pressure similarly reduces the evolutionary effects of fishing by allowing more fish to grow larger and contribute a significant proportion of offspring before eventually being harvested, i.e. reducing the strength of fisheries-induced selection against fast growing fish. The use of harvest windows, which involve setting a maximum limit on the permitted catchable fish length in addition to a minimum length, has been suggested as one option to slow the evolutionary effects of fishing on fish populations [137]. This approach may be effective for situations where line fishing (angling) is the major cause of mortality but is difficult to implement in net fisheries.
The potential negative effects of hatchery production and stocking of fish include evolutionary and ecological effects. The evolutionary effects include unwanted genetic blending of species with associated loss of species' ecological adaptations, and hatchery selection, i.e. selection of certain phenotypes and genotypes over others that perform best under the conditions in a hatchery but may not be adaptive in nature. Ecological effects include artificially elevated population densities resulting in slower individual growth of stocked and wild fish due to increased competition for food. Given these risks, it is likely best that hatchery production and stocking is only undertaken where there is no natural reproduction occurring in the target populations. In cases of uncertainty, cessation of stocking for several years, along with a corresponding monitoring program, may be an effective way to determine the relative contributions of natural reproduction and stocking to the fish population and fisheries catches (more details below in 'Key knowledge gaps'). The principle for sustainable stocking practices are defined in BAFU [138].

Ongoing monitoring, assessment and adaptive management

Projet Lac allowed a quantitative description and characterization of the composition of the fish communities of each of the large perialpine lakes of the western and central Alps and the Jura mountains for the first time. The project provides the starting point for a systematic, quantitative monitoring of trends and turnover in taxonomic, ecological, genetic and phenotypic composition of lake fish communities, species and populations in a large bioregion. Continuation of monitoring applying the same methods can identify recovery or decline of native species, whether already established non-native species are becoming invasive, can allow early recognition of the arrival and spread of any new non-native species or the return of a locally extirpated, or even a believed-extinct species. We have here demonstrated examples of each of these. Monitoring is particularly important for newly discovered, re-discovered or declining endemic and native species, as well as for invasive species and those that might become invasive. Such monitoring is most worthwhile when the data are evaluated and management responses are directly linked to the results of the assessment outcomes. Importantly, the detailed multifarious data assessment and documentation that characterized Projet Lac (photograph of every fish for taxonomy and trait measurements, tissue samples of many individuals of each population for genetic work, preservation of whole fish from each population of every species for morphological analyses) is a prerequisite for achieving any of these goals. It must not be compromised in future monitoring programs if these goals are are to me met. Without such documentation, mistakes can not be corrected, improved knowledge will never be applicable to older data and conclusions cannot be revised.

We see the combination of fish sampling methods of Projet Lac as a basis for a quantitative, objective, open and transparent framework for the assessment of the ecological state of lakes and other standing waters. Such assessments were required from European Union member countries under the Water Framework Directive and can be informative for decision-makers. An ideal assessment framework would reflect national and international legal obligations regarding biodiversity conservation, habitat protection and maintaining sustainable fisheries, as well as being sensitive to the concerns of local lake users. The assessment could highlight which lakes need management attention/investment across the region, identify key deficiencies in biodiversity conservation and ecosystem services and reveal options for remedying or minimising the deficiencies. The assessment would be most constructive where the assessed components directly link to tools available to conservationists, lake and fishery managers and/or national policy-makers and where these tools can influence the ecological state of a lake (e.g. restoration of littoral habitats, fisheries regulations, managing nutrient loads, protecting endangered species). At the same time, future assessments must not be constrained to components for which tools are already available. Instead, they but must be all-inclusive such that emerging problems and emerging needs for new management tools are being recognized as early as possible. Assessments should take advantage of the strengths of the fish sampling methods and robust aspects of the monitoring data, and supplement this with other sources of information wherever possible, especially in areas where the monitoring data are known to have weaknesses and to be associated with uncertainty (see 'Considerations for monitoring, assessment and adaptive management' below).

7. Considerations for monitoring and assessment of lake fish communities using Projet Lac methods

Gillnetting and electrofishing required to record lake fish diversity

All methods for sampling fish in lakes have their limitations and biases. The results of Projet Lac reinforce that a mix of sampling methods, particularly a combination of gillnetting and electrofishing, are indispensible for capturing the fish diversity in a lake. Unsurprisingly, there was a large number of instances where a fish species that is abundant in a lake was not recorded in electrofishing, but was abundantly recorded in the two types of gillnets. This includes all profundal specialists and many open water species. Around one third of these instances were *Coregonus* spp, critical for conservation and fisheries. However, it also includes many instances where typical littoral species were exclusively caught in gillnets (*Scardinius* spp, *Blicca bjoerkna, Abramis brama, Ameiurus melas, Sander lucioperca* where all caught in approximately 50% of their lake instances exclusively in gillnets). Less obvious, however, there were also many instances where a species was only recorded in a lake by electrofishing. This mostly applied to small, slender species that are rarely retained in gillnets, such as *Phoxinus*, *Barbatula* and *Cobitis*. The combination of a sufficient intensity of sampling with electrofishing in the littoral zone and gillnetting in all habitats, and especially in the deeper benthic, profundal and limnetic habitats, is important to record a high proportion of the fish species in a lake.

Among the gillneting methods, there were twice as many instances where species were absent only from the vertical nets, compared to species absent only from the CEN nets. The fish missing from vertical nets were mostly slender, benthic species, such as *Barbatula barbatula*, which were not well suited to being caught in gillnets. The higher intensity of netting effort in the benthic zone, as in the CEN gillnet protocol, therefore helped to record them in gillnets. This is less of an issue where vertical gillnetting is paired with electrofishing.

As shown in Figure 29, none of the three sampling methods was dispensible in any one lake. A total of 676 fish populations were recorded in Projet Lac. Of these 533 were recorded in lakes in which all three sampling methods were used. Between 40 and 60 populations (i.e. around 10%) were exclusively recorded with one of the three methods. This effect is also reflected in the species-abundance distributions (Figure 6, Figure 69): none of the three methods alone achieves the expected log-normal distribution of species abundances in a community even in the best sampled lakes. However, the same data also imply that several species are missing in Projet Lac records in most lakes even with the combination of the three methods. This is also born out of a comparison of Projet Lac records with species lists based on all records available from recent years for the Swiss lakes (see section below).

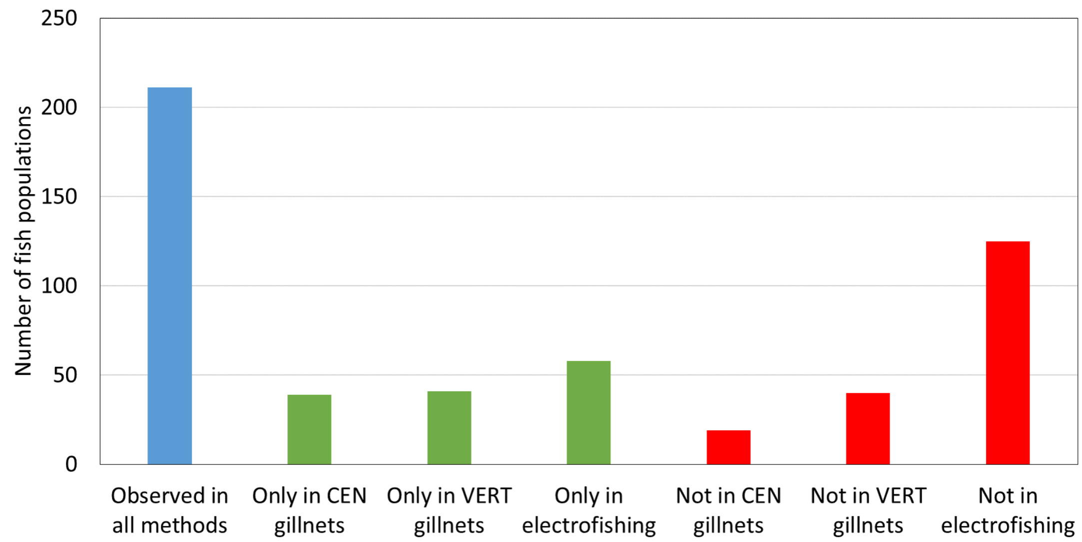

Figure 29: Comparison of the number of instances a species was recorded in a lake by the different methods. All lakes where the three sampling methods (CEN gillnets, VERT gillnets, electrofishing) were applied are considered. The blue column represents the number of instances a species was recorded in a lake by each of the three methods. Green columns show the number of instances a species was recorded in a lake by only one method. Red columns show the number of instances a species was not recorded by one of the methods (but recorded in the other two methods) in a lake. The total number of fish populations considered was 533.

Commonness and rarity

The sampling approach used in Projet Lac quantifies certain aspects of the fish community more reliably than others. These differences in reliability should be taken into account if quantitative assessments of the ecological state of lake fish communities, similar to those conducted by European Union countries under the Water Framework Directive, were to be based on monitoring using Projet Lac methods.

The sampling protocols used in Projet Lac are designed to provide reliable estimates of the composition of lake fish communities in terms of species, their abundance and biomass. In this manner, they are particularly effective in quantifying the abundance and biomass of abundant fish species. In doing so, they also identify which fish species are common, and which fish species are rare within lakes and across the region. Repeating the sampling in a lake with the same methods (i.e. same fishing, sampling, phenotypic documentation and taxonomic resolution) can reveal how the relative rarity and commonness of the species in a lake change through time.

By sampling in all major lake habitats with multiple methods, Projet Lac recovered individuals of the majority of fish species known to occur in each lake and of several that were not known to occur. The methods also revealed several widespread invasive species, the presence of which was not formerly known, discovered new diversity and rediscovered species that were thought to be extinct. For the purposes of monitoring and assessment however, it is important to note that the recording of rare or highly localised species is not guaranteed in the stratified random sampling design used in Projet Lac. Indeed, there were many cases where a species was not recorded by Projet Lac, yet had been documented in the lake by local authorities in recent years. A comparison of Projet Lac data with data in the latest edition of the Swiss Fish Atlas [38] reveals that in the lakes of the Rhine catchment alone more than 111 species populations recorded in recent years were not encountered in the Projet Lac survey (*Oncorhynchus mykiss* and *Salvelinus namaycush* were excluded as these can include records of farm escapees). This compares to 358 species populations recorded during Projet Lac in the same lakes. Some of these missing records probably represent cases of recent extirpation. Other data too suggest recent widespread extirpation in a few taxa such as *Chondrostoma nasus* and *Chondrostoma soetta*. It is perhaps unlikely however that most of these species have recently been extirpated in the respective lakes, but rather that they have become (or always were) very rare. These taxa, nearly one third of all species, then represent the fraction of species sufficiently rare in the respective lakes to have escaped capture in the Projet Lac survey. In community ecology the fraction of species diversity that escapes the eye of the surveyer is referred to as being hidden behind the veil line [17]. Larger sampling effort and perhaps other sampling methods, e.g. snorkelling and diving, would be required to record these species. Such work is indeed urgently needed to understand the status of rare taxa (for example *Telestes souffia, Alburnoides bipunctatus*). Our discovery exclusively by snorkelling of an unknown *Salaria* type (Figure 59) and photographic record of a very likely *Rutilus pigus* subadult (Figure 30) in Lake Maggiore, despite very large numbers of ordinary *Salaria* and *Rutilus rutilus* in electrofishing and net fishing respectively, bears witness that careful snorkelling/diving work can recover rare taxa missing in all fishing methods.

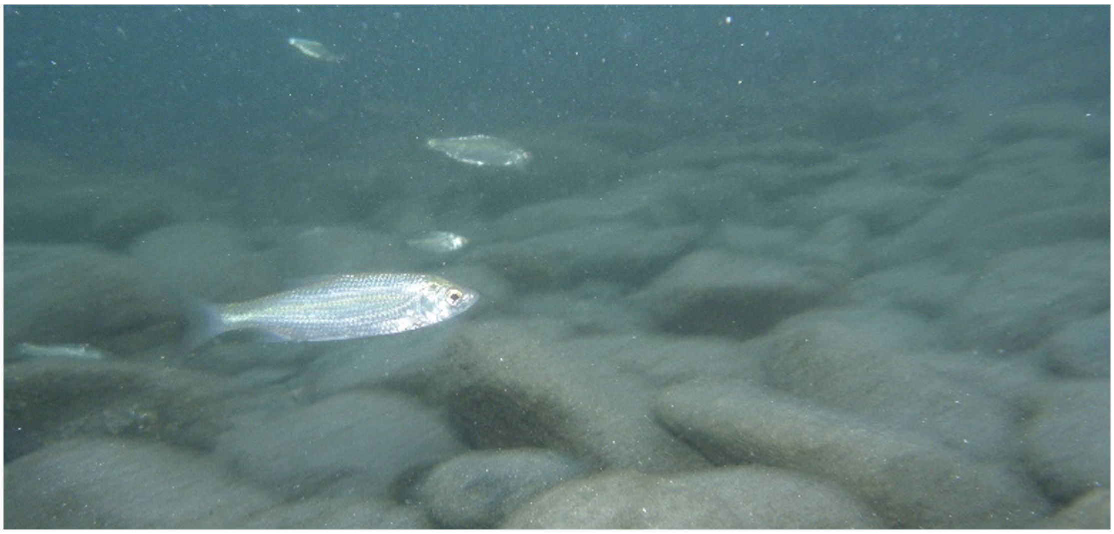

Figure 30: Underwater image of a fish very likely to be *Rutilus pigus* in Lake Maggiore. The photo was taken during Projet Lac sampling. The fish was mixed into a shoal of *Rutilus rutilus*, several individuals of which can be seen in the background.

For species that *were* recorded in Projet Lac, but only represented by one or few individuals, or recorded from only one location, it is highly uncertain whether they would be recorded again the next time that the same sampling were repeated. Estimates of abundance and biomass of these species will also be highly variable between surveys, making it difficult to detect trends in these aspects of the fish community through time. These factors should be kept in mind when interpreting Projet Lac results from this and subsequent rounds of monitoring.

Prospecting for and monitoring rare species

Rather than by randomised, whole-lake sampling, rare species should be looked for and monitored using targeted, non-destructive sampling that concentrates on the habitats where and when the species are most likely to be present. Such non-invasive sampling includes snorkelling, scuba diving and camera traps in littoral habitats, and Remote Operated Vehicles (ROVs) and camera traps in deep habitats. If information on the seasonal changes in the distribution of the species within the lakes is not available, then ecological research should be conducted to obtain this information in order to be able to design an appropriate monitoring program for rare and endangered species. Projet Lac style sampling is complementary to such targeted sampling as it can reveal the presence of previously unknown or recently established populations of the target species. In addition, given that the establishment of targeted monitoring programs for every rare species is probably unrealistic, Projet Lac style monitoring provides the best available information on these rare species in many cases. Environmental DNA (eDNA) methods can be powerful for the detection of rare species too (Deiner et al. 2017), but more method-development is needed for large and deep lakes, and a major limitation in the context of perialpine lake fish assemblages is that distinguishing between closely related species is most often impossible with eDNA.

Variability around estimates of abundance and biomass

Large estimates of abundance and biomass were obtained for some species in single actions in some lakes, which implies that much larger sampling sizes would be needed for the detection of trends in populations based on monitoring with Projet Lac methods. These outlier values occurred where very large numbers of fish were caught in a single or few actions, or where a high biomass of a species was created by a single or a few very large fish in one action. The presence of these outliers is revealed by high variance around average values and/or by comparing patterns in abundance and biomass data, while keeping in mind the average body size of the species.

This issue is particularly influential in the calculation of whole-lake estimates of total fish biomass. In this context, a rare catch of an exceptionally large fish in the open water of a large lake can have a strong influence on the whole-lake biomass estimate, as its effect is magnified due to the large proportional surface area and volume of this part of the lake. This is demonstrated by the large influence of the single, large pikeperch (*Sander lucioperca*) to whole-lake average BPUE in Upper Constance (Figure 7). The issue is less important for species-level analyses of common fish species, since no single fish or action dominates the data. In the analyses presented in this report, the Constance pikeperch was the only instance where a single fish had such a large influence on the whole-lake data. Other seemingly unusual patterns in the biomass, such as the high relative biomass of *Tinca tinca* in Lugano and high relative biomass of *Salmo* spp in Maggiore were driven by multiple fish caught across multiple actions in open water.

Particularly informative aspects of the Projet Lac approach

Several aspects of the Projet Lac approach were particularly informative with regard to species diversity assessment, the ecological state of the fish community and understanding of the lake ecosystems. Electrofishing in the littoral zone recorded a large proportion of the littoral species in each lake and provided site-specific information on the fish community associated with each type of littoral habitat. Benthic gillnets set across a depth gradient into the deep profundal zone were particularly informative for recording the distribution of deep-water endemic species and in determining the capacity of the fish community to populate the deep habitats. An absence of fish from deep habitat may indicate poor environmental conditions or reflect the absence, and often loss, of deep-adapted fish species or both. The high-resolution depth distributions provided by the vertical gillnets gave insights into the potential for ecological interactions among fish species, and between fish and their environment (e.g. water temperature, dissolved oxygen). Multiple, replicate vertical gillnet columns across a range of lake depths to the deepest point and throughout the surface area of the lake helped to confirm the consistency of depth zonation of the fish species. These also provided valuable information on ecologically, commercially and recreationally important fish species living predominantly in open water such as *Coregonus, Salvelinus* and *Salmo.* The vertical gillnets protocol generally provided the most comprehensive impression of the fish community across the whole lake. Finally, the collection of cuvette photos of many fish (see section 'Fish processing and biometry), standard photos of all fish, preservation of many whole fish specimens and tissue samples from every population proved indispensable for reliable species identifications that could be verified, corrected and refined after the end of the field work, and that can be updated if future knowledge gains require this. Misidentifications among closely related species were not uncommon in the field even for very experienced fish biologists in the team. For instance, most *Carassius gibelio* were erroneously recorded as *Carassius carassius* in the field, and most *Cobitis bilineata* as *Cobitis taenia.*

Genetic barcoding was also indispensable for revealing "cryptic" species the presence of which was previously unknown. Microsatellite genotyping and Next Generation Sequencing of thousands of genetic markers were important to assess genetic distinctiveness of newly discovered and previously known sympatric forms, such as the lake versus stream *Cottus* spp, littoral versus profundal *Cottus* spp [41] and all seven species of *Coregonus* in Lakes Brienz/Thun [24]. These genetic methods were also required to determine persistence of genetic differentiation (i.e. reproductive isolation) in sympatry zones between otherwise mostly allopatric species, such as the several species of *Salmo* in lakes Sils and Poschiavo (Figure 46, Figure 47). The value of the collections of well-preserved fish, photos, tissues and published genetic data will further increase with time. These methods are indispensable for a modern biodiversity assessment and should not be economized away in future surveys.

8. Conclusions

Natural and anthropogenic factors influencing lake fish communities

The fish communities of the perialpine archipelagos of lakes

The perialpine lakes system constitutes a region of exceptional richness in endemic freshwater fish in Europe. This system of lakes is unique in Europe south of Scandinavia also in its physical attributes and it is these attributes that are chiefly responsible for the richness in endemic species: Many deep and medium sized to large oligotrophic lakes provide a large diversity of habitats for fish. They are strongly isolated from similar ecosystems (the nearest ones being the large lakes in Sweden and on the Balkans) but only mildly isolated from each other within the four major clusters of Po, Rhone, Rhine and Danube drainage lakes (the latter barely studied in this project). The diversity of uniquely lacustrine habitats biogeographically isolated from similar habitats elsewhere meant there was ecological opportunity for colonizing lineages to radiate into new species within each of the larger lakes. The modest isolation amongst several lakes within each of the three major clusters also generated opportunities for geographical isolation of populations, speciation and subsequent back-colonization, conditions that facilitate the generation of large genetic variation, speciation and the subsequent buildup of species diversity. Each of the four lake clusters constitutes an archipelago of lakes, and the four together make the perialpine lake region a treasure chamber for aquatic biodiversity, quantitatively analysed here for the first time.

Variation in fish communities among lakes

Analyses of Projet Lac data suggest that perialpine lake fish communities, i.e. the species richness, species composition and patterns in species abundances, are influenced by a combination of natural and anthropogenic factors: historical biogeography, isolation, size and morphology of lakes, present and past nutrient state and present and past fisheries practices. Biogeographical history and island biogeography are the primary effects respectively on composition and richness of assemblages.

Despite centuries of human intervention and fisheries management, the identities of the species native to each lake in the region strongly reflect biogeographical affinities. Communities in the major river catchments Rhine and Po (to a lesser extent also Rhone; the Danube was only marginally touched) were distinct, reflecting their connections to different glacial refugia from which they were recolonised after the end of the last ice age. Lakes that had belonged to different catchments at different times in their postglacial history (Constance, Geneva) had these past connections show in the biogeographical affinities of some (Constance) or most (Geneva) of their species. Next to historical biogeography, the position of a lake relative to the Alps (alpine, perialpine or subalpine) had large effects on species composition through effects of altitude on water temperature and connectivity of the lake with the rest of the river network. Alpine lakes got colonised by only very few species that are good climbers and cold-resistant.

The influence of human activities also varied among river catchments, with corresponding effects on the fish recorded in each lake through extinction and the introduction of new species. Anthropogenic eutrophication of the mid-late 20th century resulted in the extinction of many endemic salmonid species in the lakes of the Rhine catchment (particularly in the genera *Coregonus* and *Salvelinus*), especially those in profundal habitats. On the other side of the Alps, the lakes of the Po catchment contain populations of several cyprinid species with narrow north-Adriatic distribution ranges as well as some lacustrine endemics, but these lakes also contain particularly high numbers of non-native fish species, with many introduced from northern perialpine lakes, as well as several from Asia and North America. Many of the regional Adriatic endemics appear to be in strong decline.

Two aspects of lake morphology strongly influence perialpine lake fish communities: lake surface area and lake depth. Lake surface area tightly correlates with the number of fish species occurring in a lake. Larger lakes contain more fish species, with altitude/connectivity also important. Ecological theiry predicts larger lakes to support more fish species due to greater environmental heterogeneity and a wider range of habitats, and because they support a larger overall fish population, which means that a larger number of species have sufficiently large populations to persist against the odds of extinction over longer time scales. Evolutionary theory also predicts larger lakes to have more species because the probability of ecological speciation and adaptive radiation, where species arise through specialisation to different ecological niches within a lake, is scale-dependent. The second aspect of lake morphology, lake depth is an important predictor of endemic richness because water depth is the major ecological gradient along which lacustrine fish populations diverge and speciate. On the northern slopes of the Alps, the Rhine catchment contains far more large and deep lakes than the Rhone catchment, which explains at least some of the differences in species richness between these catchments. Another difference seems to be that Rhone lakes are biogeographically more strongly isolated resulting in fewer species colonizing them after the end of the last ice age.

Consistent with predictions of island biogeography, species-area-relationships were shallow for non-native species, steeper for native species, and steepest for endemic species. Taking into account historically documented extinctions as well as rare species not found in the Projet Lac survey but otherwise recorded in recent years further steepened the species-area-relationships, i.e. more rare and recently extinct species occurred or had occurred in larger lakes. These patterns in the effects of lake size and isolation on species richness imply that fish communities in the perialpine lakes are primarily subject to the ecological and evolutionary rules of isolation and area size. Ecosystem size in this system has strong effects on the evolution of endemic species, on longterm persistence of local populations of more widely distributed species and a weaker, yet detectable effect on the establishment of populations of newly arriving species.

Lake depth, in combination with the nutrient load, influence a lake's productivity. Nutrients are more readily resuspended in shallower lakes and a greater proportion of the water column receives sunlight, enabling primary production (growth of plants and algae). The result is a higher productivity per unit lake area in shallower lakes, as reflected in a higher average fish biomass per unit net area in Projet Lac catches. Smaller, shallower lakes generally also contained a higher proportion of cyprinids such as *Rutilus rutilus* and *Scardinius* spp (Figure 7), reflecting the higher volumetric contribution of shallow benthic habitats, versus pelagic habitats, in these lakes.

Perialpine lakes are naturally oligotrophic, however human activities have increased the amount of nutrients entering many lakes, with a particularly strong increase in the past century, followed by a subsequent decrease in most lakes. Comparing among the lakes, the two most abundant fish taxa in perialpine lakes according to gillnetting, *Coregonus* spp and *Perca fluviatilis*, showed opposing relationships to lake nutrients. The concentration of lake nutrients negatively correlated with the biomass of *Coregonus* caught in the vertical nets of Projet Lac among the larger and deeper perialpine lakes. Lakes with the lowest phosphorus concentrations had the highest biomass (Thun, Walen) and abundance (Walen, Brienz) of *Coregonus*. A large proportion of the *Coregonus* biomass in the low nutrient lakes were smaller fish that are not much exploited by commercial fisheries. *Perca fluviatilis* showed the opposite relationship with phosphorus, with the highest abundance and biomass in the eutrophic lakes.

In the large lakes, the influence of lake nutrients on the fish community differed between the surface waters and the deeper parts of the lake. In the sunlit surface layers, the biomass of benthic fish was higher in lakes with more phosphorus, driven mostly by *Perca fluviatilis* and *Rutilus rutilus*. In the higher nutrients lakes, the fish biomass quickly declined into the deeper parts of the lake. Eutrophic lakes such as Lugano and Zug had almost no fish living below 30 m in either benthic or pelagic habitats due to insufficient oxygen. Low nutrient lakes such as Thun, Brienz and Walen, had a lower biomass of fish in the littoral-benthic zone, but the biomass remained similar into the deeper parts of the lake and fish were abundant even in the deepest sections of these lakes. Importantly, low nutrient lakes that had a recent history of eutrophication and reoligotrophication such as Lake Constance, had lost most or all of their deepwater fish populations during the eutrophic phase, including endemic species, and these lakes have very low or nearly no fish in the deep benthic and pelagic habitat now despite sufficient oxygenation. This is likely because the shallow water species lack the necessary adaptations to occupy those habitats and time since reoligotrophication was too short to recover this functional diversity.

Commercial fishing also seemed to be another important factor influencing differences in the recorded fish communities among lakes. Lakes with commercial fishing had very few large fish of the targeted species. The reduced density of these large fish likely has indirect effects on other interacting species in these lakes. This is something that would require further study.

Distribution of fishes within lakes

The vertical depth distribution of fish in perialpine lakes during Ptojet Lac sampling in late summer, early autumn was associated with gradients in temperature, light, food resources and oxygen. Fish species seemed to distribute themselves along the depth gradient mostly according to their thermal preference and food availability. Peak abundance in open water tended to be deeper in oligotrophic lakes, likely reflecting the broader productive zone resulting from deeper light penetration due the clearer water. Depth distributions were truncated in lakes with present or past hypolimnetic oxygen deficiency. In these lakes, no fish were recorded in the deeper part of the lake during late summer, early autumn, when lakes are generally strongly stratified and have been so for some time. Importantly, this was the case even in lakes that had recovered from eutrophication and are now oligotrophic.

In terms of the horizontal distribution of fishes within the lakes, the highest species richness, abundance and biomass at the time of Projet Lac sampling was close to the shore, in the littoral zone of most lakes. This was mainly due to cyprinids and perch-like fish. In contrast, the largest number of endemic species occurred in the sublittoral, profundal and pelagic zones, and these were mainly salmonids.

The offshore habitat of most large northern perialpine lakes was dominated by *Coregonus* spp, with *Alosa* spp dominating the same habitat in the larger southern lakes Maggiore and Garda. Perch and/or roach were common in the open water in some lakes, particularly those with high nutrient concentrations, such as lakes Zug and Lugano, but also lakes Geneva and Neuchatel. Perch and roach were also often caught in the offshore habitat of smaller perialpine lakes, sometimes with *Coregonus* spp, or without *Coregonus* spp in the case of the very small lakes.

Management challenges

Conservation and management of lake fish communities faces several particularly difficult challenges in the coming years and decades. The effects of climate change on lake ecosystems are likely to become severe, however little can be done about it directly by lake managers. Similarly, established non-native and exotic species are almost impossible to control in the large lakes. In both cases, the only available option is to maintain and restore other aspects of the lake ecosystem to as close as possible to their natural condition to keep the number and severity of simultaneously operating stressors as low as possible.

A further challenge is maintaining ecological and economically sustainable fisheries in lakes that have been returned to their near-natural oligotrophic nutrient regime with the associated lower lake productivity. Additionally, these systems are affected by invasive species, climate change and other threats. In some large perialpine lakes, changes to the lake ecosystem over the past years and decades have resulted in local commercial fisheries not being able to catch enough fish to be economically sustainable. Factors suggested to contribute to this trend include:

- Non-native and exotic fish and invertebrates compete for food and predate upon eggs and larvae of targeted fish species e.g. in Lake Constance [94, 96]
- Decades of eutrophication have resulted in extinction or near-extinction of species that were adapted to deep-water habitats and oligotrophic conditions. This may have resulted in loss of adaptations to oligotrophic conditions in some of the extant target species of a fishery [42, 90]
- Re-oligotrophication leading to reduced lake productivity, which correlates with slower growth in some targeted species [129]
- Re-oligotrophication is also associated with lower biogenic turbidity and clearer water, which extends the productive zone into deeper water [56]. Zooplankton and targeted fish species are then distributed over a greater range of depths, making them less efficient to catch
- Climate change weakens vertical mixing, which contributes to a hypoxic deep zone that reduces the volume of the lake that can be inhabited by fish and invertebrates [50], causes extinction of remaining populations of profundal fish species, lowers lake productivity through weaker upward transport of nutrients [139] and can favour the growth of types of phytoplankton that are not used efficiently by higher trophic levels [64]
- Decades of intense fishing pressure resulted in fisheries-induced evolution, leading to slower growth and earlier maturation in targeted fish species [121, 123, 124] (see section 'Ecological and evolutionary effects of fishing').

The combination of some or all of these factors likely have a significant influence on the population size, density and individual growth rate of targeted fish populations. This in turn influences the livelihoods of professional fishers and the economic sustainability of commercial fisheries on some lakes.

Addressing these challenges requires constructive and collaborative partnerships between lake users, scientists, conservationists and managers of the lake ecosystems and their components. For this to be successful it is important that scientists continue at all times to provide unbiased and objective analyses.

Contributions of Projet Lac

The primary purposes of the Projet Lac surveys was to use standardised sampling and analyses to provide an overview of extant lake fish diversity, describe patterns of species distributions and community composition within lakes and across the perialpine region, and to provide a baseline reference against which future monitoring can be compared to track changes in the fish communities and lake ecosystems.

The different fish sampling methods and the overall approach used in Projet Lac were effective in quantifying the composition of the lake fish community in different lake habitats and throughout the lake, and in compiling a list, based on standardised sampling, of most fish species occurring in each lake. This information allowed quantitative description of the three-dimensional distribution of fishes throughout the lakes, such as the horizontal distribution of fishes among littoral habitats and the vertical distribution by depth. Comparing among lakes data on the fish communities in different habitats and throughout the lake provided insight into the major natural and anthropogenic drivers of differences. This quantitative information is complementary to the observations of management authorities and lake users. Such information can in turn be important for detecting and understanding future changes in distribution, abundance and biomass of species, as well as understanding changes in fisheries catches.

The field surveys, in combination with taxonomic, genetic and phylogenetic analyses of samples collected in Projet Lac, have improved understanding of the diversity and taxonomy of fish across the region. The accurate identification of species and the description of within-species diversity in phenotypically distinct forms and genetic lineages is critical to the conservation and management of fish diversity in the region. This is particularly important for the unique lake-endemic *Coregonus* and *Salvelinus* species of the northern perialpine lakes, and lake- or catchment-endemic *Salmo* species in the Mediterranean and Black Sea catchments. Examples of important contributions of Projet Lac to diversity assessment include providing field data and genetic samples that allowed clarification of the presence of three species of *Coregonus* in Lake Zurich, six species of *Coregonus* in Lake Thun and the documentation of profundal forms of *Salvelinus* in lakes Lucerne, Walen and Thun. The rediscovery of the presumed-extinct profundal char species *Salvelinus profundus* in Upper Lake Constance was another important finding. As was documenting the genetic distinctiveness of lake sculpin from nearby river sculpin (*Cottus gobio* complex), the presence of phenotypically distinct deep water forms of sculpin in lakes that had never been eutrophic, the genetic and phenotypic distinctiveness of roach (*Rutilus rutilus*) in some lakes that had never been eutrophic (Appendix A), and the existence of deeply divergent geographical lineages within *Cottus*, and previously overlooked species within *Barbatula* and *Phoxinus* across the region.

Projet Lac revealed the presence of several species whose presence in the region was not previously known, because they were phenotypically not easy to identify, including the occurrence of *Gobio obtusirostris* in Lake Constance, *Phoxinus septimaniae* in western lakes and *Phoxinus csikii* in most northern lakes. Projet Lac also revealed that some supposedly widespread species had very likely been misidentified for many years in previous work. All *Cobitis* (spiny loaches) recorded in Switzerland and the wider Projet Lac sampling region on both sides of the Alps belonged to the Adriatic species *Cobitis bilineata,* whereas *Cobitis taenia* was not recorded anywhere. All *Carassius* carps recorded across the region were Prussian carp *Carassius gibelio*, while the existence of Crucian carp *Carassius carassius* in the large lakes of the region remains to be confirmed. The widespread and common minnow *Phoxinus* in the lakes of the Aare catchment do not belong to the central European species, *Phoxinus phoxinus,* but to the southeastern European *Phoxinus csikii.*

Finally, Projet Lac revealed the widespread prevalence of non-native species in many lakes across the region. This included the widespread occurrence of southern rudd (*Scardinius hesperidicus*) among the northern perialpine lakes, the high abundance of the French lineage of *Salaria fluviatilis* in Lake Geneva, the exceptionally high abundance, ecological and phenotypic diversity of three-spined stickleback (*Gasterosteus aculeatus*) in Upper Lake Constance, and confirmed the high abundance of northern roach (*Rutilus rutilus*) in some southern lakes. It remains to be investigated whether the recording of exclusively Italian spined loach (*Cobitis bilineata*) in northern perialpine lakes and the absence of spined loach (*Cobitis taenia*), as well as the recording of exclusively Prussian carp (*Carassius gibelio*) and absence of Crucian carp (*Carassius carassius*) are due to anthropogenic translocation, followed by displacement of the native species, or whether this is the original situation.

The establishment of a collection of photographs and tissue samples for genetic analyses, as well as the collection of whole preserved fish at the Natural History Museum of Bern were indispensable components of Projet Lac. These collections allow researchers, taxonomists and conservationists to identify samples with confidence and to revisit the identifications at any point in time, with opportunities to verify, correct and improve these in the light of future data and future insights. Moreover, this material provides opportunities for research in taxonomy, biodiversity and biogeography on these collections beyond what was possible within the limited time, budget and wo/manpower of the project. Finally, and most importantly, the collection offers the first much needed reference to determine and carefully study changes through time in the genetic, morphological and other phenotypic characteristics of many populations of fish across the region. This collection therefore opens the doors for future investigations of responses to changes in the ecosystems or in management at species level, at community and ecosystem level and at the level of the entire archipelago of lakes.

Quantitative and qualitative comparisons among the sampled lakes have allowed to identify the major historical, ecological and anthropogenic drivers and their influence on the fish community. Besides understanding the overall drivers, it is important to recognize that each lake has a unique combination of fish species and populations, a unique set of physical conditions (e.g. lake surface area, water depth, lake shape, water retention time, nutrient transport, oxygen replenishment), a unique biological context for the fish community (e.g. macrophytes, phytoplankton, zooplankton, macroinvertebrates, parasites, birds), and a unique set of past and present anthropogenic pressures. The combination of these components means that every lake and every fish assemblage responds somewhat differently to the various pressures. It also means that it remains difficult to predict in lake-specific detail responses to future changes, such as climate change or changes in nutrients. Comparing the fish community of a lake to itself through time is the most reliable approach for detecting the impacts of changing environments or changing management practices. Continued monitoring using the Projet Lac approach is therefore an important foundation for evidence-based adaptive management in the face of this uncertain future.

9. Glossary

Definition of terms as they are used in this report.

Term	**Explanation**
Abundance	Number of fish.
Alpine	Located within the main central European mountain range e.g. lakes Sils and Poschiavo.
Anthropogenic	Originating from human activity.
Benthic zone	On or close to the lake floor, from shallow to the deepest point of the lake. Defined in this report as within 3 m of the lake floor.
Biodiversity	The variety of life at all its levels. From genes and populations, through to species, communities (combinations of species) and ecosystems.
Biomass	An abbreviation for the amount of biological material ('biological mass'). Used in this report to refer to amount of fish by weight (usually in grams).
Catch per unit effort (CPUE)	Number or weight of fish divided by the sampling 'effort' that was required to catch the fish. For gillnetting, effort is the surface area of net. For electrofishing, effort is the surface area of the shore covered by the electric field.
Comprehensive sampling	Using multiple methods to generate a *complete as possible* picture of the fish community throughout the lake at the time of sampling.
Divergent lineage	A population that is genetically very different from other populations within the same taxonomic species, but where it is currently either unclear whether the divergence justifies to consider them different species, or where the boundaries of these species are unclear.
Ecosystem services	The benefits, in terms of products and services, that humans gain from the natural environment. These are often grouped into 'supporting services' such as primary production, 'provisioning services' such as the provision of fish caught by fisheries, 'regulating services' such as purification of air and water, and 'cultural services' such as the recreational and psychological value of the natural world.
Endemic species	Native species that occur only in a limited geographic area, such as in one lake or in several neighbouring lakes of shared geological origin. These species are of high importance to biodiversity conservation as the local loss of an endemic species often means its global extinction.
Epilimnion	Warmer and generally well-mixed part of the lake above the thermocline. This term is usually used when discussing environmental parameters.
Eurythermic species	Species tolerating a wide range of temperatures.
Eutrophic	A lake with high nutrient concentration and rate of primary production in surface waters resulting from large quantities of nutrients entering the lake. Volume-weighted total phosphorus concentration at winter/spring vertical mix higher than 25 µg / L.
Extinct species	A species that no longer exists anywhere in the world. Also referred to as 'global extinction'.
Extirpated species	A species that is no longer present in a particular area, but exists elsewhere. Also referred to as 'local extinction'.
Exotic species	Non-native species introduced from Asia or North America.
Evolutionary history	How, where and when a species or group of species evolved. 'How' and 'where' relate to the mode of speciation e.g. whether the species evolved through allopatric speciation (populations diverging in geographic isolation e.g. in different river catchments) or sympatric speciation (populations in the same geographic location diverging through ecological specialisation and/or sexual selection). 'When' refers to how long ago the species diverged from closely related species.
Form	A group of individuals that are phenotypically very different from other individuals of a described species occurring in the same lake (e.g. geographical isolation cannot explain the differences), but where it is currently unclear whether the differences are associated with genetic differentiation or caused by phenotypic plasticity.

Genotype	The particular set of genes forming the DNA of an organism or group of organisms.
Genus sp.	Abbreviation 'sp.' is used when it is sure that individuals belong to a particular genus, but uncertain exactly which species. Normally written as 'sp.' but the fullstop is occasionally omitted in this report to improve readability.
Genus spp	Abbreviation 'spp' is used when referring to multiple species within a genus. Normally written as 'spp.' but the full stop is omitted in this report to improve readability.
Habitat	The natural home or environment of an animal, plant, or other organism.
Hypolimnion	Colder and deeper part of the lake below the thermocline. This term is usually used when discussing environmental parameters.
Invasive species	Non-native species that causes ecological or economic harm.
Island Biogeography	The subfield of ecology that examines the factors that affect species richness and composition of insular habitat patches. The field was shaped by Robert H. MacArthur and Edward O. Wilson who coined the term island biogeography in their 1958 landmark paper and subsequent Princeton Monograph. Initially it was conceived to explain variation in species richness on oceanic islands and the effects of area size and isolation. The principles apply to any type of ecosystem that is isolated from similar ecosystems due to being surrounded by unlike ecosystems, including mountain peaks, fragmented forests and large lakes.
Limnetic zone	Sunlit surface waters away from the lake shore. Maximum depth of this zone depends on water transparency, but usually extends to around 20 meters. This term is usually used when discussing animal habitats.
Littoral zone	Shallow area on the edge of the lake. Maximum depth of this zone is often defined by the deepest extent of aquatic vegetation. However, defined as <3 meters in this report for consistency among lakes.
Meristic	Relates to traits that vary in discrete countable units, such as fin spines or scales along the lateral line.
Mesotrophic	A lake with an intermediate nutrient concentration and rate of primary production. Volume-weighted total phosphorus concentration at winter/spring vertical mix between 10 and 25 µg / L.
Native species	Species that arrived in a lake through natural processes, with no human intervention. It can be difficult to differentiate natural and human-assisted range expansions in regions such as Europe with a long history of human translocations. The definition of a native species is therefore often adapted for practicality to mean those species that have been present in a lake for a "long time". The threshold varies among countries and authorities. In line with the Federal Office of the Environment, the threshold A.D. 1500 is used in this report.
Non-native species	Species that have "recently" arrived in a lake or catchment through human-assisted translocation. The threshold varies among countries and authorities. In line with the Federal Office of the Environment, the threshold A.D. 1500 is used in this report. See also 'Exotic species'. The adjective 'invasive' is used where the species has significant impact on the local ecosystem.
Oligotrophic	A lake with a low nutrient concentration and rate of primary production resulting from little nutrients entering the lake. Volume-weighted phosphorus concentration at winter/spring vertical mix less than 10 µg / L.
Pelagic zone	Open water, away from the shore. Includes limnetic and profundal-pelagic zones. This term is commonly used when discussing animal habitats.
Perialpine	On the edges of the Alps e.g. lakes Thun and Lucerne. Unless specified, this term is used in this report to include the pre-alpine area.
Phenotype	Appearance of the organism, including shape, colour, behaviour and any other observable characteristics. The appearance of an organism is determined primarily by its genotype and the effects of environmental factors.
Pre-alpine	Around the Alps. At the edge, but not necessarily within the Alps e.g. lakes Hallwil, Morat.
Profundal zone	Deep part of the lake below the limit of light penetration. Includes profundal-pelagic and profundal-benthic zones. This term is usually used when discussing animal habitats.

Species	In this report, a species is defined as a group of individuals that, under natural conditions and in the absence of geographical isolation, maintains its distinctiveness from other such groups over many generations. This definition is a practical application close to, but not identical to the "Biological Species Concept".
Standardised sampling	Standardised or systematic sampling means to collect data in a way that is well defined to allow comparison to data from sampling adhering to the same standards through time or across space. This is usually by following a protocol that describes the equipment and distribution of effort.
Stenothermic species	Species tolerating a narrow range of temperatures.
Translocation	Introduction of fish by humans into regions where the species or population did not previously occur.

10. Acknowledgements

Institutions

Financial

Eawag – Swiss Federal Institute of Aquatic Science and Technology
Universität Bern
Federal Office for the Environment / Bundesamt für Umwelt / Office fédéral de l'environnement (FOEN / BAFU / OFEV)
Naturhistorisches Museum Bern (NMBE)
Cantons:
Zürich (ZH), Bern / Berne (BE), Luzern (LU), Zug (ZG), Freiburg / Fribourg (FR), Sankt Gallen (SG), Graubünden (GR), Aargau (AG), Thurgau (TG), Ticino (TI), Vaud (VD), Valais/Wallis (VS), Neuchâtel (NE), Genève (GE)
Fischereiforschungsstelle des Landes Baden-Württemberg (FFS)
Internationale Bevollmächtigtenkonferenz für die Bodenseefischerei (IBKF)
Aufsichtskommission Vierwaldstättersee (AKV)
Fédération du Doubs pour la Pêche et la Protection du Milieu Aquatique
Fédération du Jura pour la Pêche et la Protection du Milieu Aquatique
Regione Lombardia

Supporting

AquaBios (environmental consultancy)
Teleos (environmental consultancy)
Naturhistorisches Museum Bern (NMBE)
Internationale Gewässerschutzkommission für den Bodensee (IGKB)
Jagd- und Fischereiverwalter-Konferenz (JFK)
Insitut für Seenforschung (IFS)
Université de Franche-Comté
Commissione internazionale per la protezione delle acque italo-svizzere (CIPAIS)
Office national de l'eau et des milieux aquatiques (ONEMA)
Graia (environmental consultancy)
Consiglio Nazionale Ricerche – Istituto per lo Studio degli Ecosistemi (CNR ISE)

Individuals

Pascal Vonlanthen (AquaBios) –
initiated Projet Lac with Guy Periat and Ole Seehausen, coordinated fieldwork, lead author on several lake-specific reports
Guy Periat (Teleos) –
initiated Projet Lac with Pascal Vonlanthen and Ole Seehausen, coordinated fieldwork, lead author on several lake-specific reports
Begleitgruppe for this report:
Andreas Knutti, Diego Dagani, Daniel Hefti und Baenz Lundsgaard-Hansen (alle BAFU), Michael Kugler (Kanton SG), Peter Ulmann (Kanton LU), Frederic Hofmann (Kanton VD), Danilo Foresti (Kanton TI), Marcel Michel (Kanton GR), Daniel Bernet (Kanton BE), Guy Périat (Teleos), Pascal Vonlanthen (Aquabios), Corinne Schmid (FIBER)
Cantonal fisheries and water quality managers –
support, funding, use of infrastructure and resources
We would also like to acknowledge the following individuals, listed in alphabetical order by surname:
Beatrice Blöchlinger (NMBE) –
collection manager
Jakob Brodersen (Eawag) –
fieldwork, scientific & data exchange with Progetto Fiumi
Andri Bryner (Eawag) –
media works and communication support
Civil servants ("Zivis") –
fieldwork, data entry, incorporating fish into the NMBE collection
Michel Colon (INRA) –
hydroacoustics

Diego Dagani (BAFU) –
financial support, fieldwork, co-author of lake-specific reports
François Degiorgi (Teleos, Université de Franche-Comté) –
fieldwork, gillnetting and electrofishing methods development
Carmela Dönz (Eawag / Universität Bern) –
taxonomic profile for *Salvelinus* and information on *Coregonus*
Reiner Eckmann (University of Konstanz) –
hydroacoustics in lakes Constance, Zurich and Lucerne
Jean-Baptiste Fagot (Fédération du Jura) –
sharing data for several lakes
Philine Feulner (Eawag) –
genetic analyses of Lake Zurich and Walen whitefish
Fishermen and fisherwomen –
support, use of infrastructure and resources
Steve Gerber (Universität Bern) –
bachelor student on fish species co-occurrence
Jean Guillard (INRA) –
hydroacoustics
Reto Hagmann (NMBE) –
collection manager
Marcel Häsler (Universität Bern) –
technical and German language support
Hélène Hefti (Universität Bern) –
masters student on littoral fish-habitat associations
Daniel Hefti (BAFU) –
financial support
Andreas Knutti (BAFU) –
financial support
Kay Lucek (Eawag / Universität Bern) –
information on *Cottus* spp and *Gasterosteus* spp
David Marques (Eawag / Universität Bern) –
information and text on *Gasterosteus* spp
Salome Mwaiko (Eawag) –
phylogenetic tree
Markus Pehr (consultant hydroacoustics) –
hydroacoustics in lakes Constance, Zurich and Lucerne
Timon Polli (Polli Natur + Dienste) –
fieldwork
Jean-Claude Raymond (ONEMA) –
hydroacoustics in lakes of the French-speaking areas
Lukas Rüber (NMBE) –
management of museum collection, DNA barcoding
Erwin Schäffer (Eawag) –
fieldworker extraordinaire
Oliver Selz (Eawag) –
information on *Coregonus* spp
Rosi Siber (Eawag) –
GIS support in all its forms
Petra Teiber-Sießegger (IFS) –
data on littoral habitats and invasive macroinvertebrates for Lake Constance
Andrea Tersigni (Graia) –
collection of samples and photos in Mezzola
Martin Troxler (NMBE) –
taxidermist responsible for inclusion of the Projet Lac collection into the NMBE
Soraya Villalba (Eawag) –
DNA barcoding and database work
Volunteers –
other volunteers not listed here
Jennifer Vonlanthen-Heuck –
German language checking in lake-specific reports
Christine Weber (Eawag) –
feedback on river-related information

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Appendix A – Taxonomic profiles

This appendix discusses groups of fish with unexpected, difficult or uncertain species-level taxonomy. It also provides information on the current state of the taxonomy and/or the available evidence for the identification of species and/or their species status. In cases where species identification was difficult, information on the distinguishing features is provided. The prevalence of the species among lakes and habitats within lakes according to Projet Lac is also summarised. The groups are systematically arranged by order and family following Kottelat and Freyhof [9].

Order Cypriniformes

Family Cyprinidae – carps and minnows

Gobio spp (gudgeon)

Prior to Projet Lac, only one species of gudgeon, *Gobio gobio* was known to occur in Switzerland. *Gobio gobio* is native to much of Europe north of the Alps and was recorded by Projet Lac in most lakes in the Rhine catchment (not recorded in Brienz and Lower Constance and naturally absent from Rousses, Joux and Brenet), as well as Annecy, Bourget and Bret in the Rhone catchment. Although the endangered *Romanogobio benacensis* is the native gudgeon in the Adriatic drainage, and its geographic distribution in Italy touches the borders to Switzerland [140, 141], it has not yet been recorded in Switzerland. And even though *G. gobio* is known to be invasive in much of the Italian Po drainage, no *Gobio* were recorded by Projet Lac in the lakes south of the Alps.

Gobio gobio

Gobio obtusirostris

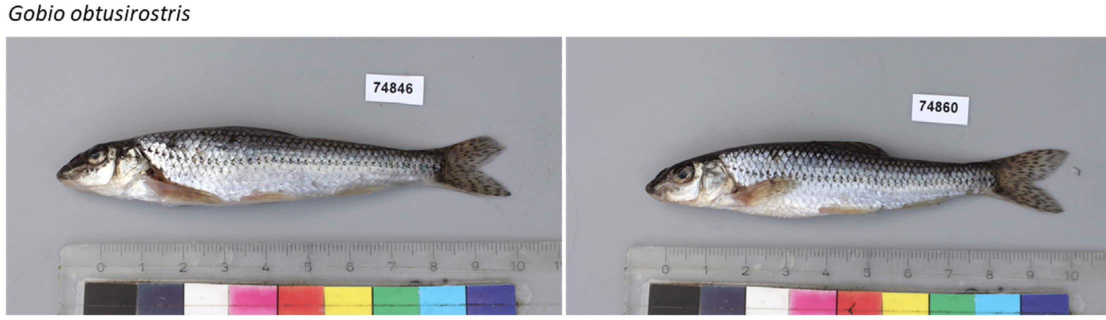


Figure 31: Four adult *Gobio* caught in Upper Lake Constance in the same electrofishing action near the mouth of the Rheintaler Binnenkanal. Genetic barcoding revealed that two individuals had the mitochondrial DNA of *Gobio gobio* (upper) and two of *Gobio obtusirostris* (lower).

In Upper Lake Constance, genetic barcoding of ten *Gobio* caught in Projet Lac, revealed five specimens of the blunt-snout gudgeon, *Gobio obtusirostris* and five *Gobio gobio*. The former species is native to the Danube river catchment and had not been previously recorded in Lake Constance nor in Switzerland. External phenotypic differences between the *G. gobio* and *G. obtusirostris* caught in Lake Constance were small (Figure 31). All *Gobio* in caught in Lake Constance were from fishing actions in the southern corner of the lake between Romanshorn and the mouth of the Rheintaler Binnenkanal. Individuals of both *G. gobio* and *G. obtusirostris* (according to barcoding) were caught together in two fishing actions. One individual of *G. obtusirostris* was also caught by Progetto Fiumi in the nearby Salmsacher Aach, which enters Lake Constance near Romanshorn. The present-day Alpine Rhine originally flowed into the Danube River (until the end of the last ice-age) and Lake Constance is known as a natural contact zone between Danubian and Rhine lineages of several other fish genera (*Barbatula* [142], *Chondrostoma* [143], *Lota* [144]). Projet Lac provided the first such evidence for the two *Gobio* species [9].

Carassius spp (Prussian carp and related species)

Three species of *Carassius* are considered to occur in the perialpine region: *Carassius carassius* (Crucian carp), *C. gibelio* (Prussian carp) and *C. auratus* (goldfish). According to the Ordinance of the Swiss Fisheries Act none of these species are native to Switzerland. *C. auratus* is native to East Asia and has been introduced throughout Europe and most of the world [9]. The native distributions of *C. carassius* and *C. gibelio* are uncertain. *C. carassius* is believed to be native to eastern and central Europe, as far west as the Rhine [9]. *C. gibelio* may be native to the central European lowlands or introduced from Asia [9]. *C. carassius* can be identified by a convex rear edge of the dorsal fin and 31-36 scales along the lateral line, while the rear edge of the dorsal fin in the other two species is concave or straight and they have fewer scales along the lateral line (26-33) [9]. *C. auratus* and *C. gibelio* are distinguished by colour (golden-bronze and silvery brown, respectively). The three species are however often confused with one another.

All *Carassius* caught in Projet Lac except some from Lake Garda, were *C. gibelio*. This species was recorded in all southern perialpine lakes, as well as lakes Rousses, Constance Upper and Morat in the north. In most cases, DNA barcoding was not able to distinguish whether these fish were *C. gibelio* or *C. auratus* (3 from Maggiore, 1 from Lugano, 2 from Constance Upper and 1 from Morat), but clearly ruled out any *C. carassius*. Barcoding did however confirm the presence of two individuals *of Carassius auratus* in Lake Garda.

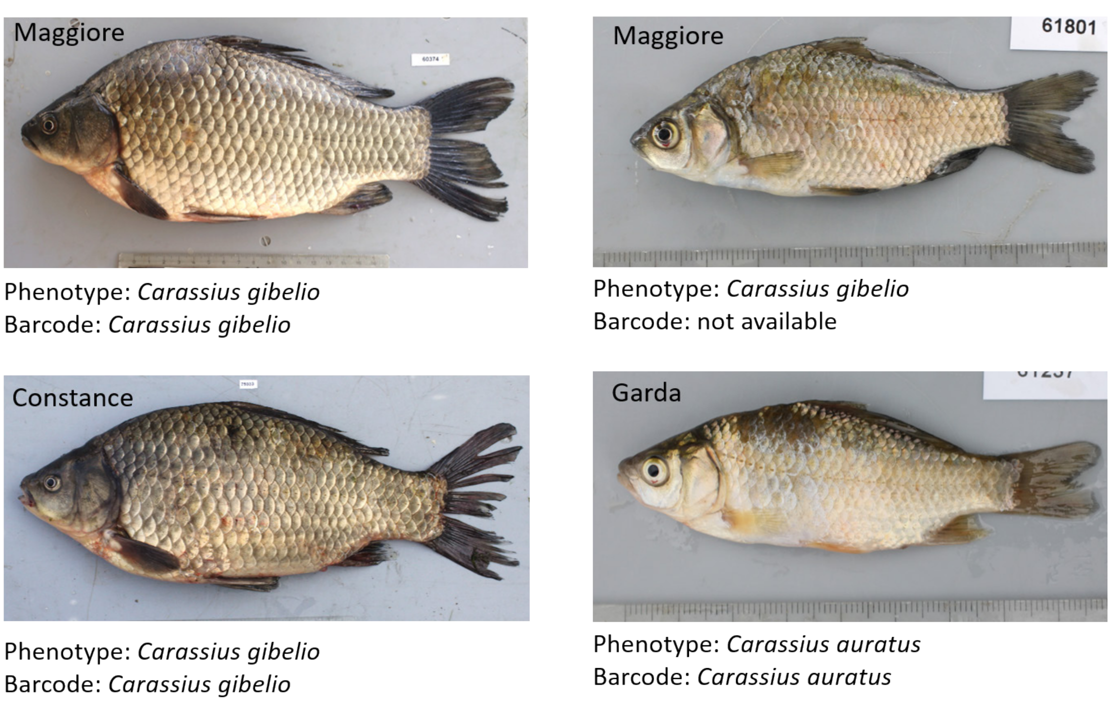


Figure 32: Silvery brown *Carassius gibelio* (Prussian carp) adults (Maggiore, Constance) and juvenile (Maggiore) with golden-bronze juvenile *C. auratus* (goldfish; Garda).

Abramis brama and *Blicca bjoerkna* (breams)

The two cyprinid species *Abramis brama* and *Blicca bjoerkna* appear superficially similar and often hybridise across much of their overlapping distributions. Many fish identified in the field in Projet Lac as *Blicca bjoerkna*, were revealed by genetic barcoding to be *Abramis brama* in their mitochondrial genome. In the other direction, two individuals identified as *A. brama* were *B. bjoerkna* in their barcode. *A. brama* grows to a larger size of 70 cm compared to maximum standard length of 33 cm in *B. bjoerkna* [9]. The species can also usually be distinguished based on the number of lateral line scales (51 – 60 in *A. brama* versus 43 – 46 in *B. bjoerkna*) and branched rays in the anal fin (23 – 30.5 in *A. brama* versus 19 – 23.5 in *B. bjoerkna* [9]), but all these meristic traits are difficult to evaluate in juveniles and small subadults.

Both species were only recorded in the northern perialpine lakes in Projet Lac. *A. brama* was generally more common, recorded in 15 lakes, compared to nine lakes for *B. bjoerkna*. Indeed, *B. bjoerkna* was not recorded in any lakes that did not also have *A. brama*. *A. brama* was recorded in particularly high numbers in Geneva (220 fish) and Lower Constance (69 fish). *B. bjoerkna*, on the other hand, was particularly abundant in Bret (234 fish) and Upper Constance (143 fish). Both species were similarly abundant in Lake Morat (38 *A. brama* and 37 *B. bjoerkna*).

In future monitoring efforts great attention has to be paid to carefully distinguish these species. Genetic work to establish the extent of genetic mixing between the species in Switzerland and the perialpine region would also be worthwhile. Both species are also known to hybridize with *Rutilus* and we recorded several *Abramis brama x Rutilus rutilus* hybrids. Monitoring of this in the future would help understand the drivers and consequences of hybridization among cyprinid species.

Figure 33: *Abramis brama* (above) and *Blicca bjoerkna* (below) from Lake Biel.

Rutilus spp (roach and related species)

Three species of *Rutilus* were recorded by Projet Lac in the perialpine lakes: common roach (*Rutilus rutilus*) is native to the Rhine and Rhone catchments and most of Europe (excluding Italian and Iberian peninsulas and Mediterranean drainages of the Balkan peninsula), while triotto (*R. aula*) and pigo *(R. pigus)* are native and endemic to the northern Adriatic basin, mainly the Po catchment (Figure 34). *Rutilus rutilus* was one of the most common species in Projet Lac, recorded in all northern perialpine lakes. This species was also recorded in a large number of fishing actions within each lake. Usually restricted to the littoral zone, *R. rutilus* also dominated the open water, pelagic zone of some smaller lakes: Remoray, Hallwil, Morat and Brenet. *R. rutilus* populations in the two most pristine oligotrophic lakes, Lake Brienz and Lake Walen, are genetically and – in the case of Lake Brienz – also phenotypically distinct from *Rutilus* in the other northern pre-alpine lakes [145]. Additionally, within Lake Brienz, fish from rocky boulder and cobble habitats are phenotypically distinct from those living over any other substrate type ([145]; Figure 35). We consider these to be different roach populations of high conservation priority. That *Rutilus* from more heavily impacted lakes geographically as distant as Lakes Geneva, Neuchatel and Hallwill are genetically more similar to each other than to those from Lakes Brienz and Walen may imply that *Rutilus* populations have lost parts of their distinctiveness in the course of ecosystem perturbation and stock transfer. In several Rhine lakes we also recorded intergeneric hybrids between *Rutilus rutilus* and *Abramis brama* (Figure 34).

Rutilus rutilus has been introduced into several southern perialpine lakes and was recorded by Projet Lac in lakes Lugano, Maggiore, Varese, Como and Mezzola. *R. rutilus* strongly numerically dominated the native *Rutilus* spp in lakes Lugano and Maggiore, and this northern species was the only *Rutilus* species recorded in Lake Varese. Interestingly, the introduced *R. rutilus* was less abundant than the two native *Rutilus* species in Lakes Como and Mezzola, and it was not recorded in lakes Idro, Iseo and Garda.

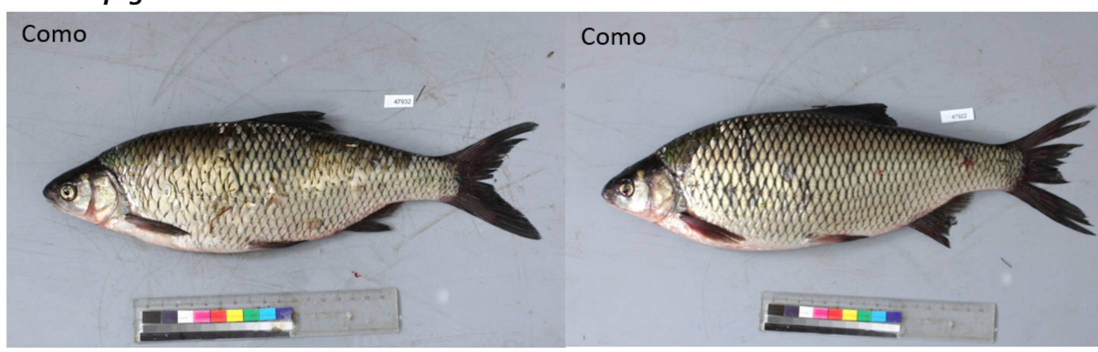
The presence of native triotto (*R. aula)* was recorded in all southern perialpine lakes, except Lugano and Varese. *R. aula* was particularly abundant in lakes Garda and Iseo, and was the only *Rutilus* species recorded in Lakes Garda, Iseo and Idro. In Lake Lugano, on the other hand, the only trace of *R. aula* among the many non-native *R. rutilus* were three individuals with meristic traits of *R. aula* (9.5 branched rays in dorsal and anal fins, versus 10.5 in *R. rutilus),* that though otherwise looked more like *R. rutilus. R. aula* was very rare in Lake Maggiore, with only four individuals phenotypically identified as this species (versus more than one thousand *R. rutilus).* Three of these fish were confirmed as *R. aula* by mitochondrial barcoding (the fourth was not barcoded). On the other hand, one fish from Maggiore that phenotypically matched *R. rutilus* (out of four barcoded *R. rutilus*), had the mitochondrial barcode of *R. aula*. This suggests that hybridisation and backcrossing of hybrids between native *R. aula* and invasive *R. rutilus* is occurring.

Pigo *(Rutilus pigus),* the other *Rutilus* species native to the southern lakes, was recorded in fewer lakes than *R. aula* (Como, Mezzola, and Maggiore), and was everywhere less abundant than *R. aula. R. pigus* was recorded in highest numbers in lakes Como and Mezzola where *R. rutilus* had not become abundant (yet). In Lake Maggiore, only six juvenile fish phenotypically resembling *R. pigus* were recorded. Three of these were confirmed as *R. pigus* by genetic barcoding, while two had the mitochondrial barcode of *R. rutilus* and one had that of *R. aula* (Figure 34). In Lake Lugano, no fish phenotypically matched *R. pigus*, however one adult fish that was phenotypically mostly *R. rutilus* had the mitochondrial barcode and also the lateral line scale count of *R. pigus* (Figure 34). Several other fish also had meristic traits of *R. pigus* (>43/44 lateral line scales), yet otherwise resembled *R. rutilus*. The mismatch between general appearance, meristic traits and mitochondrial barcode again indicates hybridisation and backcrossing between *R. pigus* and *R. rutilus*, and in Lake Maggiore also between the two native species *R. aula* and *R. pigus*.

To our knowledge, this is the first genetic data that show that the dramatic decline of native *R. pigus* and *R. aula* in Lakes Lugano and Maggiore was associated with introgression into the abundant invasive northern *R. rutilus* (as predicted in [92]), but also with introgression between the two native species. It is possibly that the breakdown of reproductive isolation between the native species was mediated by the hyperabundant invasive species. Such complex species interactions deserve further attention by researchers. Another important line of research for the conservation of the native southern *Rutilus* species would address the reasons for the dominance of the invasive *Rutilus rutilus* in Lakes Lugano, Maggiore and Varese, but not in Lakes Como and Mezzola.

There was no evidence for translocation of either of the southern Rutilus species to the lakes in the Rhine or Rhone catchments (several thousand phenotypes inspected, 70 fish barcoded).

Rutilus pigus



Rutilus rutilus

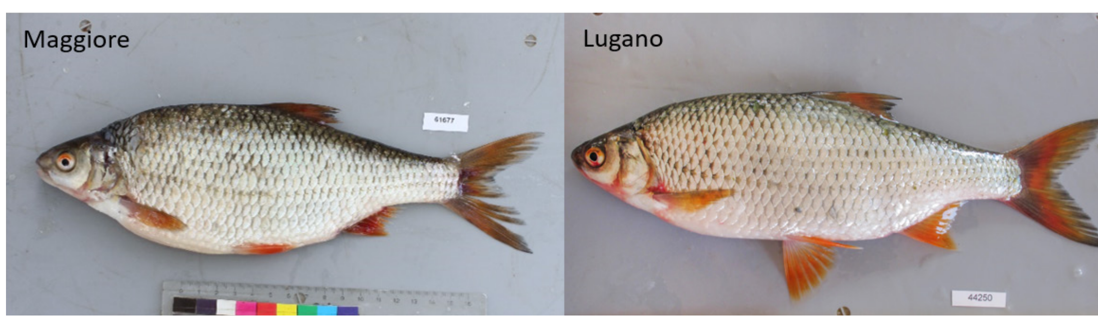


Figure 34a: *Rutilus* species of the perialpine region. *Rutilus aula* (triotto) and *Rutilus pigus* (pigo) are native south of the Alps. *Rutilus rutilus* (roach) is native to the northern perialpine region and is introduced in many southern perialpine lakes, and invasive in several.

Figure 34 b: *Rutilus* species hybrids. Left: phenotypic *R. rutilus* adult with mitochondrial barcode of *R. pigus* from Lake Lugano (a backcross to *R. rutilus*). Middle: phenotypic *R. pigus* subadult with barcode of *R. aula* from Lake Maggiore (a backcross to *R. pigus*). Right: a hybrid between *Rutilus rutilus* and *Abramis brama* from Lake Constance.

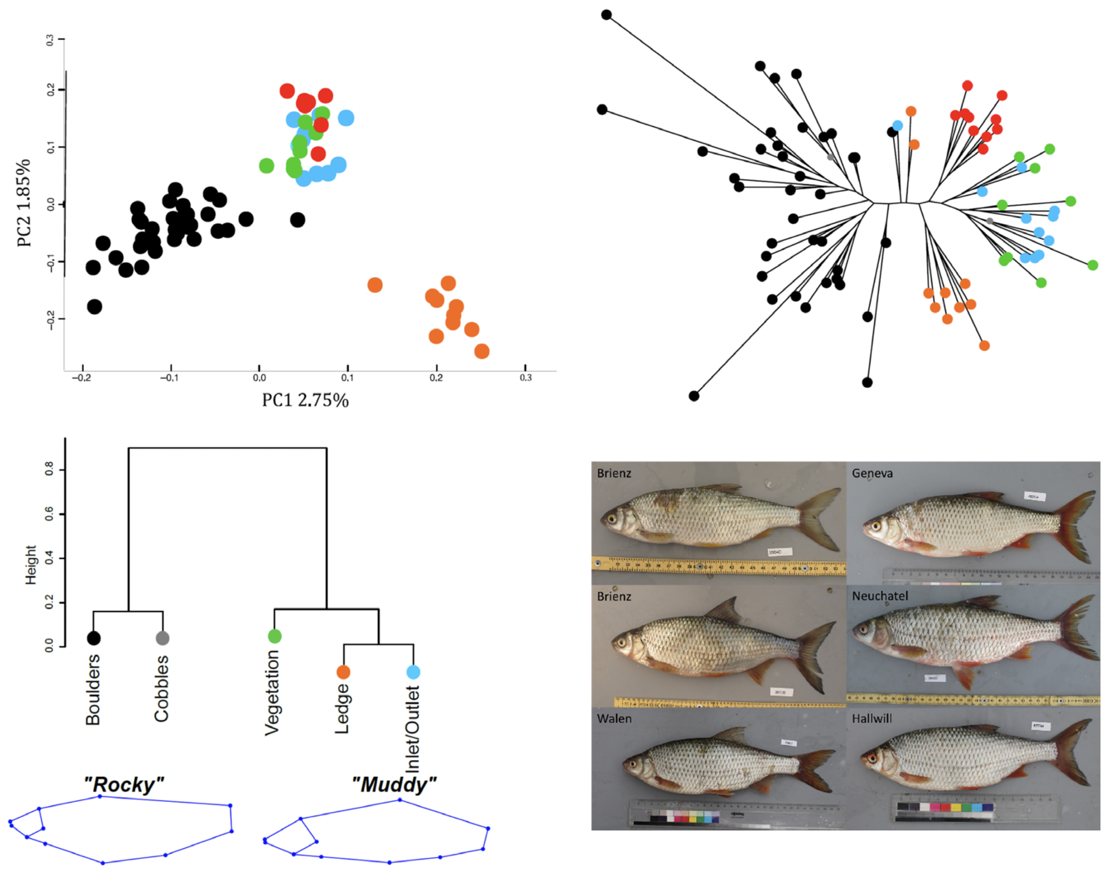


Figure 35: *Rutilus rutilus* population genomic structure across northern perialpine lakes and phenotypic structure within Lake Brienz. Top left: Principal component analysis based on 3,865 polymorphic Single Nucleodide Polymorphisms: black = Lake Brienz, orange = Lake Walen, red = Lake Hallwill, green = Lake Geneva, blue = Lake Neuchatel. Top right: RAxML phylogeny tree depicting the genetic relationship among the individuals from the five lakes. Bottom left: Morphological (Mahalanobis) distances between roach caught over different substrates within Lake Brienz [145]. Bottom right: representative individuals from the five lakes.

Chondrostoma spp (nose carp)

Two species are known from the region: *Chondrostoma soetta* from lakes in the Po catchment and *C. nasus* from lakes and streams north of the Alps (Figure 36). Unfortunately, both species have declined dramatically in recent years. We observed *C. soetta* only in Lake Mezzola, and *C. nasus* only in Lake Sarnen. Both species are likely exterminated in several of the lakes in the Po and Rhine drainage where they were previously recorded respectively. It is possible that *Protochondrostoma genei* occurs or occurred in some of the lakes in the Po catchment, but we did not record it. However, it is noteworthy here to point out that two distinct lineages of *C. nasus* occur in the region, the Danubian lineage confined to the Lake Constance catchment and the Atlantic lineage in the rest of the Atlantic drainage of Switzerland (Figure 37) [143].

Figure 36: Diversity of nose carps (*Chondrostoma*) in periapline systems. Top left: *C. nasus* Atlantic lineage (Wiese, Basel). Bottom left: *C. nasus* Atlantic lineage (Lake Sarnen, Projet Lac). Top right: *C. nasus* Danubian lineage (Alpine Rhine, Lake Constance inlet). Bottom right: *C. soetta* (Lake Mezzola, Projet Lac).

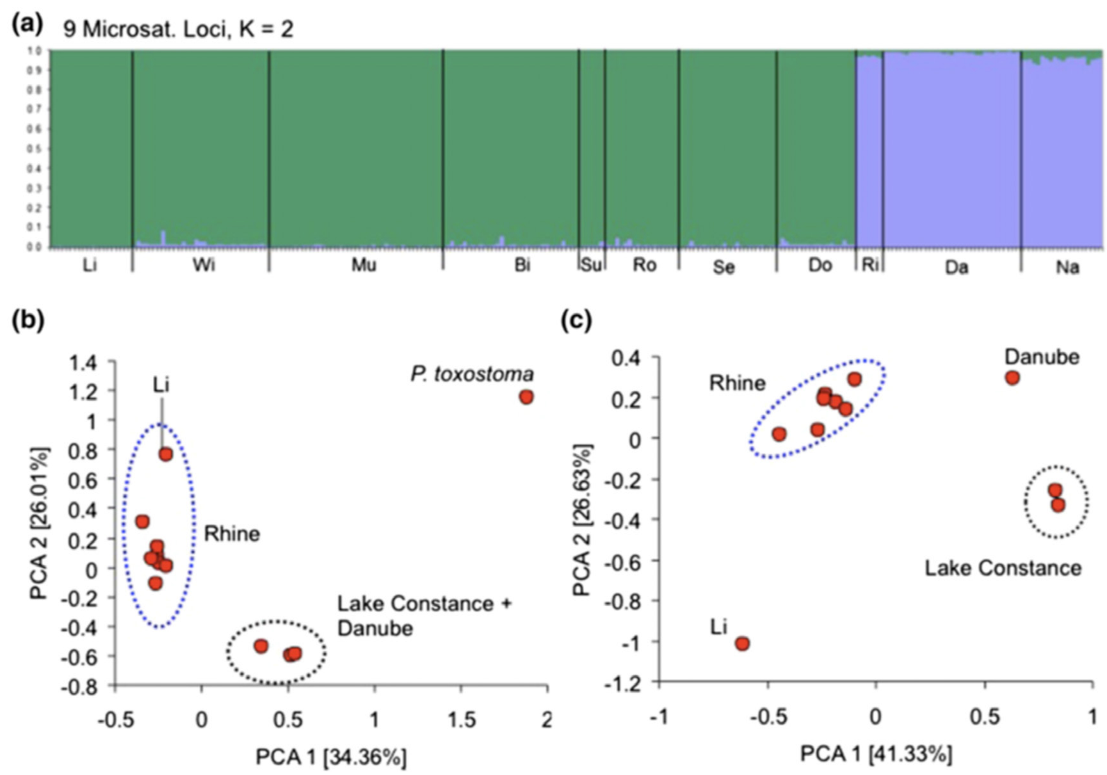


Figure 37: Population structure of nase in Switzerland as inferred from microsatellite data. a) Individual population assignments estimated by STRUCTURE for K = 2. PCA based on population allele frequencies: b) with all populations included; c) *P. toxostoma* excluded. Populations Li, Wi, Mu, Bi, Su, Ro, Se and Do are from various Swiss river stations within Thur, Limmat, Reuss, Aare and Rhine downstream of Lake Constance. Ri is the Alpine Rhine, Da an Austrian inlet to Lake Constance, and Na is a Danubian population. The populations in tributaries to Lake Constance (Ri, Da) belong to the Danubian lineage, whereas all other Swiss populations belong to the Rhine lineage (from [143]).

Scardinius spp (rudd)

Two different species of *Scardinius occur* in the region of this report [9]. *Scardinius erythrophthalmus* is native north of the Alps with a wide distribution across most of Europe except the peninsulas of Mediterranean Europe. *Scardinius hesperidicus* is native south of the Alps, and probably only to the Po river catchment and Adriatic rivers east of the Po (Kottelat & Freyhof). Among other differences, the two species can usually be distinguished as adults by the colour of the fins: red in *S. erythrophthalmus* (particularly the pelvic fins) and dark grey/brown in *S. hesperidicus* (Figure 38).

S. erythrophthalmus was recorded in almost all northern perialpine lakes, except Thun, Brienz, Walen, Upper Zurich and Joux. *S. hesperidicus* was recorded in all southern perialpine lakes. Despite being previously reported in the region, no phenotypes of *S. erythrophthalmus* were recorded in the southern lakes, and all genetically barcoded *Scardinius* from the southern lakes were *S. hesperidicus*. We note that subadult *S. hesperidicus* can have bright orange-red fins, which can lead to confusion with *S. erythrophthalmus*. The presence of the latter species south of the Alps hence remains to be confirmed.

The presence of *S. hesperidicus* (southern rudd) north of the Alps was first revealed by Projet Lac in the first lake sampled by the project (Lake Morat). In the course of the further surveys, the southern species was recorded in a total of 12 northern perialpine lakes, as well as in Lake Sils (Table 16). It was also reported to us with photographic documentation from Lake Poschiavo (Marcel Michel, personal communication). In most lakes, the presence of *S. hesperidicus* was evident from the phenotype, including by the distinct colouration of the fins in adult fish. However, there were also two northern lakes (Thun and Zurich) where the presence of the southern species was revealed only by barcoding of the mitochondrial gene COI. Mismatches between phenotype and barcode were observed in several lakes suggesting some level of hybridization and backcrossing.

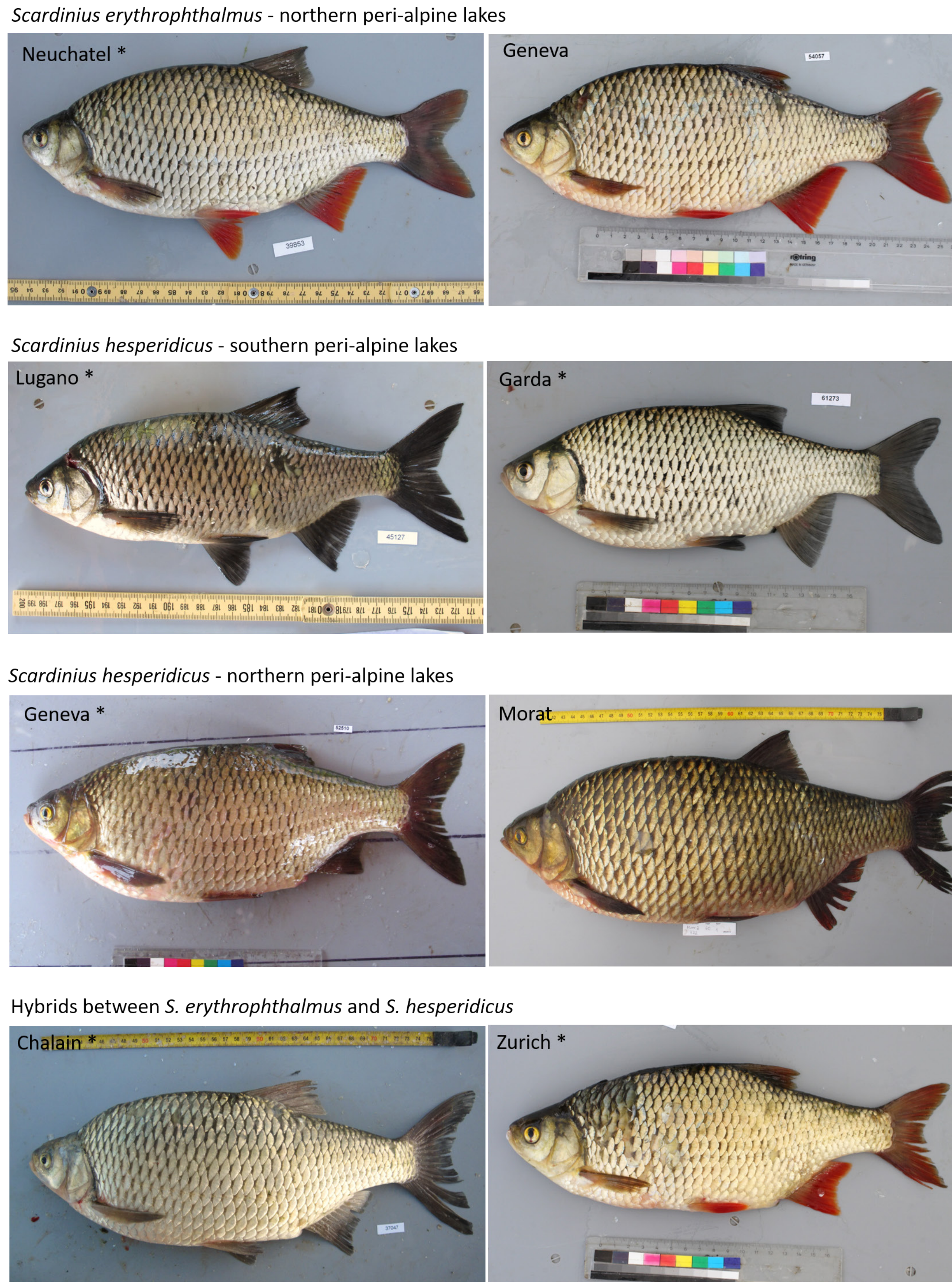


Figure 38: Examples of *Scardinius* spp caught in Projet Lac. Upper panel are northern *S. erythrophthalmus* caught in their native lakes. Upper middle panel are southern *S. hesperidicus* from their native southern perialpine lakes. Lower middle panel are *S. hesperidicus* from northern perialpine lakes. Bottom panel are a phenotypic hybrid from Chalain and a backcross hybrid from Zurich, i.e. a phenotypic *S. erythrophthalmus* that carried *S. hesperidicus* mitochondrial DNA.
* *indicates that the identity was confirmed by DNA barcoding.*

Alburnus spp (bleak)

Two species of *Alburnus* are known from the perialpine region investigated in Projet Lac: *Alburnus alburnus* from Rhine and Rhone catchments, and *Alburnus arborella* from the Adriatic catchment. It is noteworthy that both species were recorded exclusively within their expected native range. The population of *Alburnus arborella* from Lake Lugano was originally described as *Alborella maxima*, Fatio 1882, considered distinctively larger than *A. arborella*, Bonaparte 1841. Buj et al. [146] found that the Lugano population grew indeed much larger than other *A. arborella* and was also meristically distinct. However, because those authors studied East *Adriatic Alburnus* populations plus the Lugano population, but did not include populations from the lakes between these regions, it is difficult to interprete their findings with regard to the status of the Lugano population. Currently, *Alborella maxima* is considered a synonym of *Alburnus arborella*.

Alburnus arborella has unfortunately become very rare in Lake Lugano. Only two individuals were caught in Projet Lac (Figure 38). One was a large (115 mm TL) individual of typical appearance with the high count of lateral line scales that Buj et al. [146] describe for *A. maxima*. The second was of very different appearance, and could not be assigned to *A. arborella, A. maxima* or *A. alburnus*. The COI gene (barcode) was sequenced for both fish. They were separated by several mutations, falling into two distinct subclades within samples currently considered *A. arborella*. The identity and diversity of *Alburnus* from Lake Lugano should urgently be investigated. Our unquantified impression is that the phenotype that corresponds to *A. maxima* is shared with Lake Maggiore whereas the other kind seems to resemble *Alburnus* from Lake Garda.

A second unusual observation in *Alburnus* requires reporting here: we noticed a previously undocumented phenotypic and ecological polymorphism of *Alburnus alburnus* in Lake Brienz. In this lake, we observed considerable variation in shape: on one hand fish with very long snouts, and on the other hand, blunt-snouted fish that resemble *Alburnus alburnus* from other lakes (Figure 39). The long-snouted type was commonly caught near the surface whereas the blunt-snouted type could be caught near the surface or in considerable depths down to 20 m.

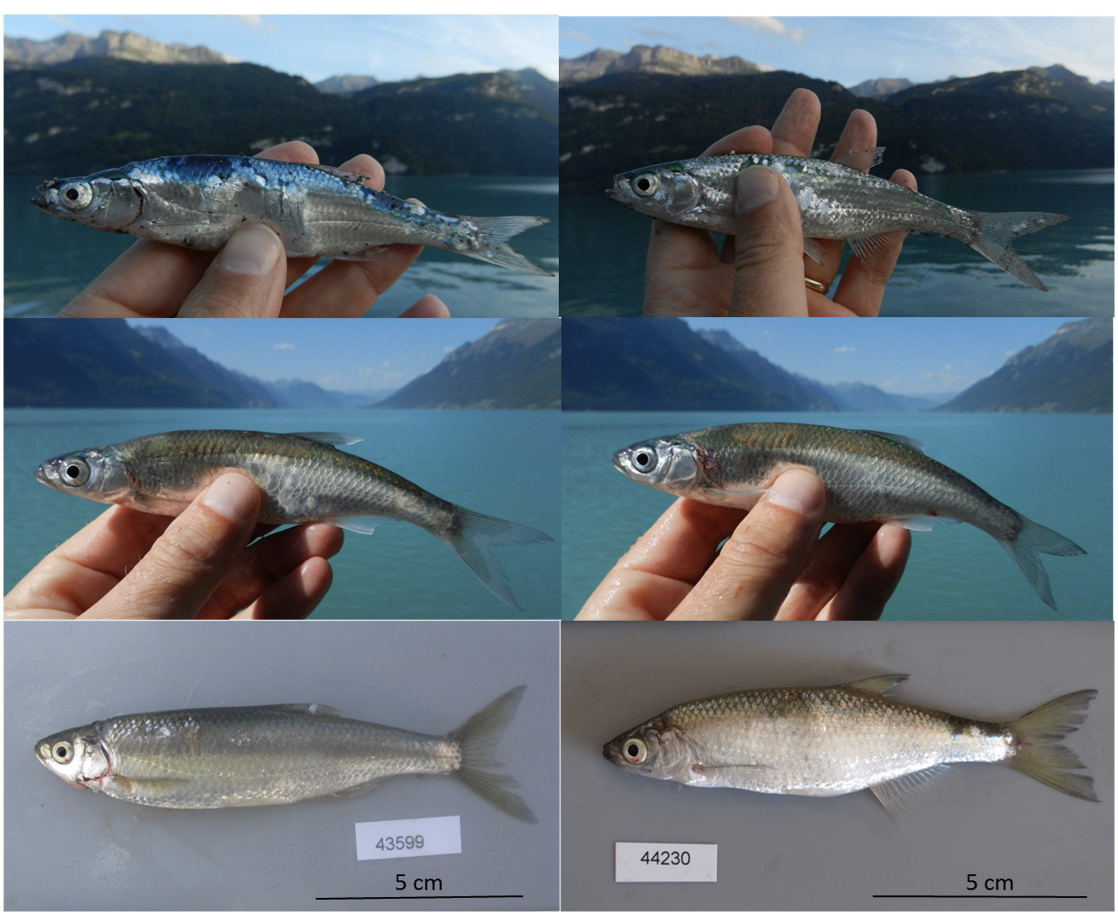


Figure 39: *Alburnus* from lakes Brienz and Lugano. The two individuals top left and middle left were caught in Lake Brienz and represent the form of *Alburnus alburnus* with elongated head and long snout, the fish top right and middle right are also from Brienz and are representative of the blunt-snouted form resembling *Alburnus alburnus* from other lakes. Bottom left: *Alburnus arborella* from Lake Lugano. This fish corresponds meristically to *A. maxima*. Bottom right: unidentified *Alburnus* from Lake Lugano. This fish does not correspond meristically to *A. maxima*, nor to *A. arborella*.

Phoxinus spp (minnows)

Until a recent systematic and taxonomic revision of the European minnows (genus *Phoxinus*), two species were thought to occur in the region sampled by Projet Lac. The species native and widespread in the northern perialpine region was thought to be the central European *Phoxinus phoxinus,* and the species native and widespread in the region south of the Alps was thought to be *Phoxinus lumaireul.* Five other species were known with small distributions in southeastern and southwestern Europe but none of these was thought to occur in the region around the Alps. In 2017, the *Phoxinus* from around Europe were investigated using molecular markers, resulting in a revision of known species and their distribution ranges and the restoration from synonymy and delineation of several additional species that had been considered synonyms of, mostly, *P. phoxinus* [147]. The only samples from Switzerland included in the study were from Lake Geneva and the Ticino. The Ticino sample was identified as *P. lumaireul* as expected. Surprisingly however, the Lake Geneva samples were identified as *P. septimaniae* and *P. csikii*. The former was a known and valid species believed to be restricted to Mediterranean coastal streams in southern France [9]. The latter is one of the species restored from synonymy, and otherwise having a wide distribution covering most of the southern and northern Danube basin. Prior to Projet Lac and the genetic analyses of the samples, it was therefore entirely unclear which *Phoxinus* species occurred in the other lakes of Switzerland north of the Alps.

Phoxinus was not common in Projet Lac catches, despite being previously documented in most lakes across the northern perialpine region. Indeed, among the northern lakes, *Phoxinus* was recorded only in the cool and oligotrophic lakes Walen, Lucerne, Thun, Brienz, as well as in Neuchatel and Chalain. Additionally, *Phoxinus* were collected from lakes Sils (Danube catchment) and Poschaivo (Po catchment). Barcoding of *Phoxinus* collected from these lakes and from several streams sampled by Progetto Fiumi in all major catchments revealed the existence of four deeply divergent mitochondrial lineages of *Phoxinus* that conform to three of the described and valid species plus one lineage that was defined by Palandačić et al [147] but remains undescribed.

The *Phoxinus* of all lakes and streams of the Aare system correspond to *P. csikii*. This extension of the previously known distribution range is complimentary to the data of Palandačić et al [147], filling the gap between the previous records in Bavaria and those in Lake Geneva that were previously appearing isolated. The new distribution range data is consistent with the expansion out of a Danubian refugium [147] and into the Swiss midlands via the old postglacial Danubian connections of Lakes Walen and Constance that were subsequently captured by the Rhine catchment. *P. csikii* is hence, likely the native minnow of the Swiss Rhine and Aare catchments, possibly including Lake Geneva.

The *Phoxinus* of Lake Chalain in the Jura region of the Rhone drainage, as well as those from tributaries of the Doubs (sampled in Progetto Fiumi), were revealed to be *P. septimaniae*. This is consistent with the known range of this taxon that was recently extended from the Pyrennees to the Jura Rhone [147]. More surprisingly, Progetto Fiumi data revealed that P. septimaniae, nearly completely absent from the lakes in the region, does occur in most streams of northern Switzerland, often together with P. csikii. The exception is the Alpine Rhine (and Lake Constance) where the species seems absent. Interestingly, of all our northern Swiss lake samples, only one individual from Lake Thun was barcoded as *P. septimaniae* whereas 45 were *P. csikii*. This is in contrast to Lake Chalain in the Rhone drainage, where *P. septimaniae* lives in the lake in the absence of *P. csikii*, and also in contrast to the two alpine lakes, Sils and Poschiavo, where both species co-occur.

South of the Alps, the expected Italian minnow, *P. lumaireul* was recorded by Projet Lac only in Lake Garda. No *Phoxinus* were recorded in the other northern Italian and Ticino lakes. Barcoding of some individuals caught in Progetto Fiumi in the Ticino River near Breggia and La Spiagetta did confirm the presence of P. lumaireul in the Swiss Po drainage, but other Progetto Fiumi samples from the Ticino River near Breggia, turned out to be a north-central European taxon, informally referred to as *Phoxinus* sp. "morella" [147]. These are almost certainly due to translocation from northern central Europe to Ticino. The true remaining distribution of *P. lumaireul* in Ticino and its interaction with other *Phoxinus* taxa will need to be addressed in future projects.

Surprisingly too, some samples from a tributary of Lake Geneva (Stockalper Canal; Rhone drainage) were identified as *P. lumaireul,* implying that three different lineages currently co-occur in the Lake Geneva region (*P. csikii, P. septimaniae, P. lumaireul). P. lumaireul* has most likely been translocated to Lake Geneva from the southern Alps by humans. It is important to emphasize that *Phoxinus phoxinus,* previously thought to be the common minnow in the northern prealpine region, was not recorded at all in Projet Lac (nor in Progetto Fiumi).

In the Alpine region, the large phenotypic variation of *Phoxinus* in lakes Sils and Poschiavo was tentatively interpreted in the field as indicating the presence of two species, assumed to correspond to *P. lumaireul* and *P. phoxinus* [148] before the genetic work. However, barcoding revealed that the two species were actually *P. septimaniae* and *P. csikii,* with both species occurring in both lakes (the only native species likely being *P. csikii* in Sils). Underwater observations in Lake Poschiavo revealed that shoals dominated by one species occurred in close proximity to shoals dominated by the other species, with some mixed shoals in the very shallow littoral zone.

Regarding the physical appearance of the minnow species, *Phoxinus csikii* of the Aare lakes appear to be phenotypically distinct from *P. septimaniae* and *P. lumaireul*. *P. csikii* is smaller, more slender, with a less blunt head, more silvery and less yellow colouration, has more and smaller blotches along the midlateral line and very dark, metallic, green-black male coloration. Males and females of *P. septimaniae* often appear deep yellow, both with very yellow fins. The few large males of *P. lumaireul* obtained in Lake Garda also appeared yellow (Figure 40). Future work is needed to investigate the ecological relevance of phenotypic differences between the *Phoxinus* species, determine the extent of distribution range overlap between them and to quantify possible gene flow and morphological and ecological differences between these species and their ecological interactions where they co-occur within a lake / stream system. Further work should also investigate the identity of the many minnow populations in smaller alpine lakes that were not sampled in Projet Lac or Progetto Fiumi.

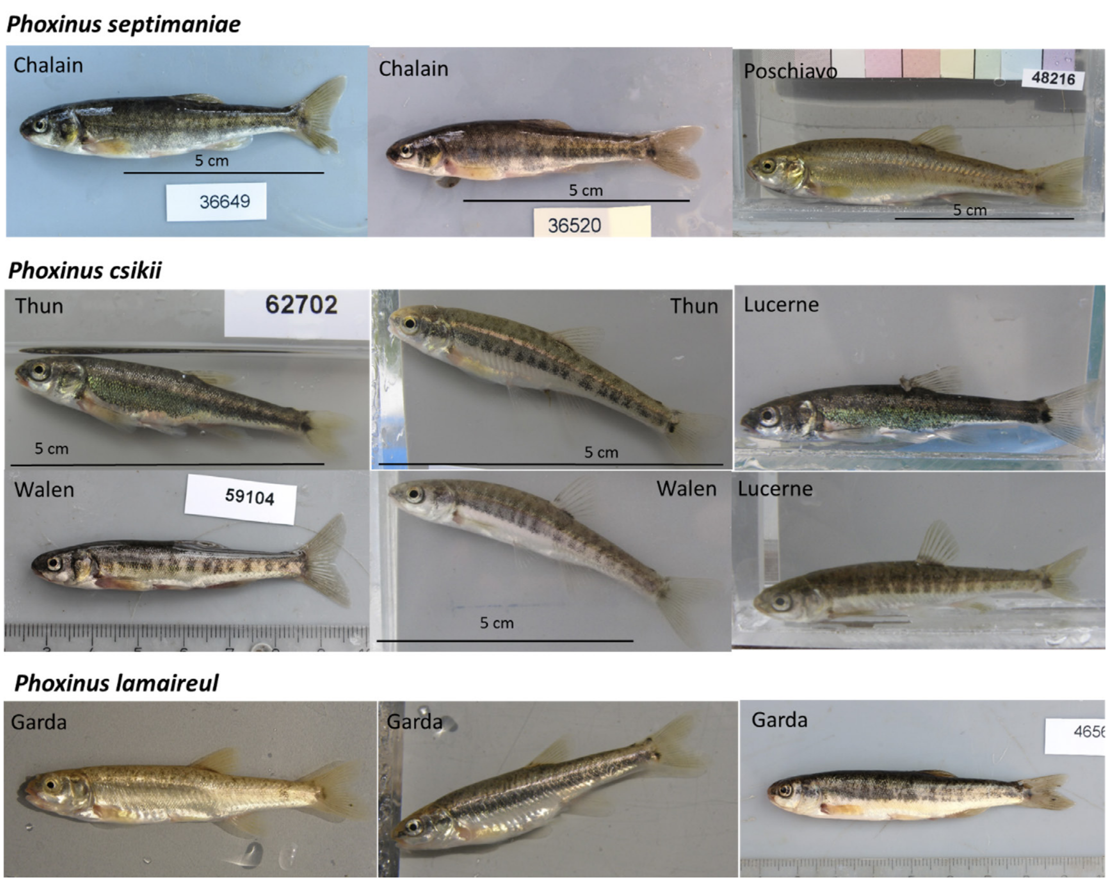


Figure 40: The three different *Phoxinus* species recorded in Projet Lac. *P. septimaniae* from lakes Chalain and Poschiavo. *P. csikii* from lakes Thun, Lucerne, Walen. *P. lumaireul* from Lake Garda.

Family Cobitidae – spined loaches

Cobitis spp (spined loach)

Two species of spined loach (*Cobitis*) are often considered to be native around the central Alps: *Cobitis bilineata* is native to the Po river catchment, while *C. taenia* has a wide geographic range north of the Alps [9]. In Switzerland, the spined loach of the northern perialpine and midland region was often assumed to be *C. taenia* (Fish atlas), but Kottelat & Freyhof [9] reported *C. bilineata* as introduced to northwstern Switzerland [9]. All *Cobitis* recorded by Projet Lac phenotypically resembled *C. bilineata* (Figure 41). This included those in the northern perialpine lakes Neuchatel, Morat and Biel (excluding one distinct phenotype in Lake Biel, see below), and all lakes south of the Alps that had Cobitis (Como, Mezzola, Iseo, Garda, Maggiore and Varese). Similarly, all *Cobitis* recorded by Progetto Fiumi on both sides of the Alps resembled C. bilineata. Among other distinguishing features, *C. bilineata* has two black spots on the base of the tail and *C. taenia* has only one spot on the upper section of the tail. The identity of Projet Lac and Progetto Fiumi samples as *C. bilineata* was confirmed by DNA barcoding, which revealed identical barcodes in the fish analysed from north and south of the Alps, consistent with reason range expansion. Thus, no *C. taenia* were recorded in Swiss lakes and rivers north of the Alps and it is unclear whether *C. taenia* ever occurred in the northern perialpine region, or whether *C. bilineata* has recently invaded and displaced a putatively native species. We inspected *Cobitis* samples from the Lake Biel region from the 1930s in the Natural History Museum of Bern. Many of these fish were so strongly bleached that their melanin pattern was reduced to invisibility, but the few that could be identified were clearly *C. bilineata*. In this regard it is also important to note, that *C. taenia* seems absent from the entire upper Rhone catchment in France northwest of Switzerland [149] and has only isolated occurrences in southwestern Germany (Baden Württemberg south of Karlsruhe), mostly confined to the Rhine valley. Populations from the Seine catchment (Yonne, Figure 41) and the Karlsruhe region are very clearly *C. taenia* [150].

Cobitis species are often diagnosed based on distinctive features in the shape and arrangement of melanic blotches and stripes. Among our samples from Lake Biel was one fish with a pattern very different from *C. bilineata* and *C. taenia* (Figure 41). Instead of dark blotches that are squared or longer than high, and separated by gaps about as wide or wider than the blotch itself, this fish had blotches that were higher than long and were separated by gaps clearly narrower than the blotch. It also had more vertical lines of black spots on the caudal fish than most *C. bilineata*. It seems most likely that this fish is a deviant phenotype of *C. bilineata* but it could be a different species, especially since the taxonomy of the *Cobitis* in eastern Europe is very poorly resolved. More samples will be needed from Lake Biel to answer this question.

Figure 41: All *Cobitis* caught in Projet Lac in lakes north and south of the Alps resembled *Cobitis bilineata*, except one fish from Lake Biel that was phenotypically distinct from *C. bilineata* and also from *C. taenia* (fishec number 168747). Photo of *C. taenia* from the Yonne river (Seine, France) is provided for comparison (photo from Guy Periat).

Family Nemacheilidae – stone loaches

Barbatula spp (stone loach)

Six species of *Barbatula* (stone loach) are currently known from Europe: *Barbartula quignardi* from northern Spain and southern France; *B. leoparda* from a tiny Mediterranean drainage in French Catalonia; *B. sturanyi, B. zetensis* and *B. vardarensis* all have small distribution ranges on the Balkan region; and *B. barbatula* from the rest of Europe. Large morphological variation within *B. barbatula* has long been suspected to indicate the presence of several additional, undescribed species [9]. Indeed, a phylogeographic study by Sediva et al [151] revealed that *B. barbatula* consisted of many, deeply divergent mitochondrial lineages, with some originating in the Pleistocene (2.6 million – 12 thousand years ago) and even the Miocene (23 – 5 million years ago). The three described Balkanian species are phylogenetically all nested within this large group of lineages commonly referred to collectively as *B. barbatula*. Prior to Projet Lac, it was not known which of these lineages occurred in Switzerland and around the perialpine region.

Barbatula were recorded in Projet Lac in lakes Chalain, Geneva, Constance, Walen, Zurich, Zug, Lucerne, Biel and Neuchatel. Large variation in colour pattern and head shape were evident among the collected fish, both within and among lakes. Sequencing the COI mitochondrial gene (barcode) and comparison with sequences on GenBank (an online database of genetic sequences) revealed the presence of *Barbatula quignardi* in the Rhone catchment in lakes Chalain and Geneva, as well as in the fish collected by Progetto Fiumi from the Allaine River. Morphologically, populations of *B. quignardi* tended to differ from the others by having a deeper caudal peduncle.

The remaining barcoded *Barbatula* consisted of two distinct lineages. One lineage was recorded by Projet Lac in the lakes of the Aare-Rhine (including Limat and Reuss river subcatchments; Neuchatel, Biel, Walen, Zurich, Lucerne, Zug), while in Progetto Fiumi, the only river that this lineage was recorded from was the Sense River. Populations of this lineage are referred to in this report as *Barbatula* sp. Lineage I. Fish of this lineage seem to be mostly composed of smaller fish with blunt snouts and high-contrast, large, dark blotches (although those in Lucerne were somewhat paler and larger).

The second lineage was widespread among the streams and rivers of the Aare-Rhine (including the River Sense; based on Progetto Fiumi), but was recorded in Projet Lac in only one lake of this catchment (Lake Zürich Obersee). On the other hand this was the loach recorded in lakes Geneva and Constance outside the Aare-Rhine catchment. This lineage is referred to in this report as *Barbatula* sp Lineage II. These fish appeared to grow larger than most fish we collected of the populations of *Barbatula* sp. Lineage I. The fish of Lake Constance were particularly variable, with enormous differences in colour pattern and head shape. Barluenga et al [142] had previously described the unusually large genetic variation and very high genetic differentiation between some populations of *Barbatula* in Lake Constance. It is not impossible that there are two different species in Lake Constance and this situation requires attention in the future.

Barbatula sp. "Lineage II" and *B. quignardi* turned out to be sister taxa in the barcode tree, whereas *B.* sp. "Lineage I" was the sister lineage of both of these together and all three belonged to the Western clade of Sediva et al [151]. The most surprising finding here is that *B.* sp. "Lineage I" and *B.* sp. "Lineage II" are geographically fully sympatric in the Aare-Rhine, but seem to partition the macrohabitat between them with Lineage I mostly confined to the streams (only exception Lake Zürich Obersee) and Lineage II mostly confined to the lakes (only exception the Sense River). This situation requires further investigation in the future.

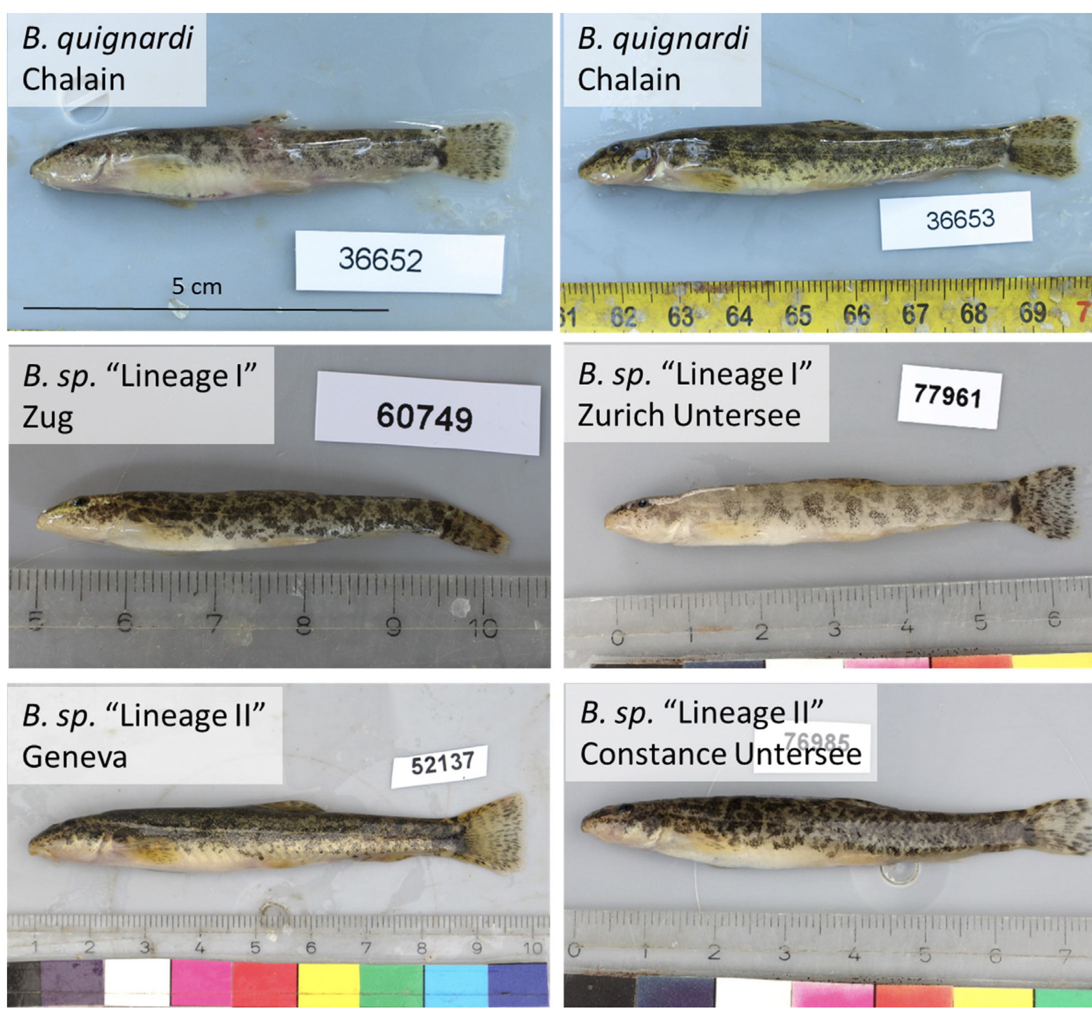


Figure 42: *Barbatula* species identified using genetic barcoding. Note that the scale differs among the photos.

Family Esocidae – pikes

Esox spp (pike)

Two species of pike in the genus *Esox* are considered native to Switzerland. The northern pike *Esox lucius* is widespread in cooler fresh and brackish water across the northern hemisphere. The second species *Esox cisalpinus* was described from lakes south of the Alps in 2011 based on genetic and phenotypic evidence [152, 153]. It was described under two different names by two author teams in the same year, with the name *E. cisalpinus* considered to have precedence over *E. flaviae.* The formal description suggested that adult *E. lucius* exhibit only the round-spotted phenotype, while *E. cisalpinus* shows mostly diagonal bars or stellate spots, with some fish showing vertical or horizontal bars [153]. The number of scales along the lateral line also seems to distinguish the two species, with *E. cisalpinus* ranging from 101 – 115 scales and *E. lucius* generally from 125 – 148 scales [153]. Figure 43 shows the phenotypic variability of *Esox* caught in Projet Lac. Indeed, all very large *E. lucius* (> 60 cm) exhibited the round-spotted pattern. Intermediate-sized adults were more variable, for example the fish from Lake Walen with stripes and spots arranged in diagonal bars. Multiple round-spotted phenotypes, matching *Esox lucius,* were also recorded in Projet Lac in some southern lakes (Maggiore and Lugano), corresponding with previous reports of the northern species in these lakes as a result of stocking [153]. Among the DNA-barcoded *Esox* from the southern lakes, one fish from Lugano was genetically identified as *E. lucius* (corresponding with its northern phenotype; Figure 43). All other pike from the southern lakes were *E. cisalpinus* in their mitochondrial sequence (5 from Lugano, 3 from Maggiore, 3 from Garda, 1 from Como, 1 from Mezzola), despite some having the northern, round-spot pattern (Figure 43). Interbreeding between *E. cisalpinus* and stocked *E. lucius* may have caused this disconnection between phenotype and mitochondrial genotype (barcode).

Considerable genetic divergence emerged among the barcoded *E. lucius* from the northern lakes, between the fish of the western lakes of the sampled region (Chalain, Annecy) compared to other northern lakes. Despite evidence suggesting the additional presence of *E. cisalpinus* in Lake Geneva in the first half of the 19th century (barcoding of historic samples from a museum collection) [154], all ten *Esox* barcoded from Lake Geneva in Projet Lac were genetically *E. lucius*. Two lineages were apparent among the Geneva pike however, with five of the fish sharing the lineage of a historically sampled *E. lucius* (also collected in the first half of the 19th century) [154] [4]. This lineage was also shared with two pike from Lake Joux. The five other *E. lucius* from Lake Geneva shared a lineage with fish of other northern perialpine lakes (including also one fish from Lake Joux). Another distinct lineage of *E. lucius* contained all barcoded pike from Chalain (3 fish) and one from Annecy. This lineage clustered with GenBank reference samples mostly from Canada (as well as other parts of Europe) and may reflect the translocation of fish for stocking.

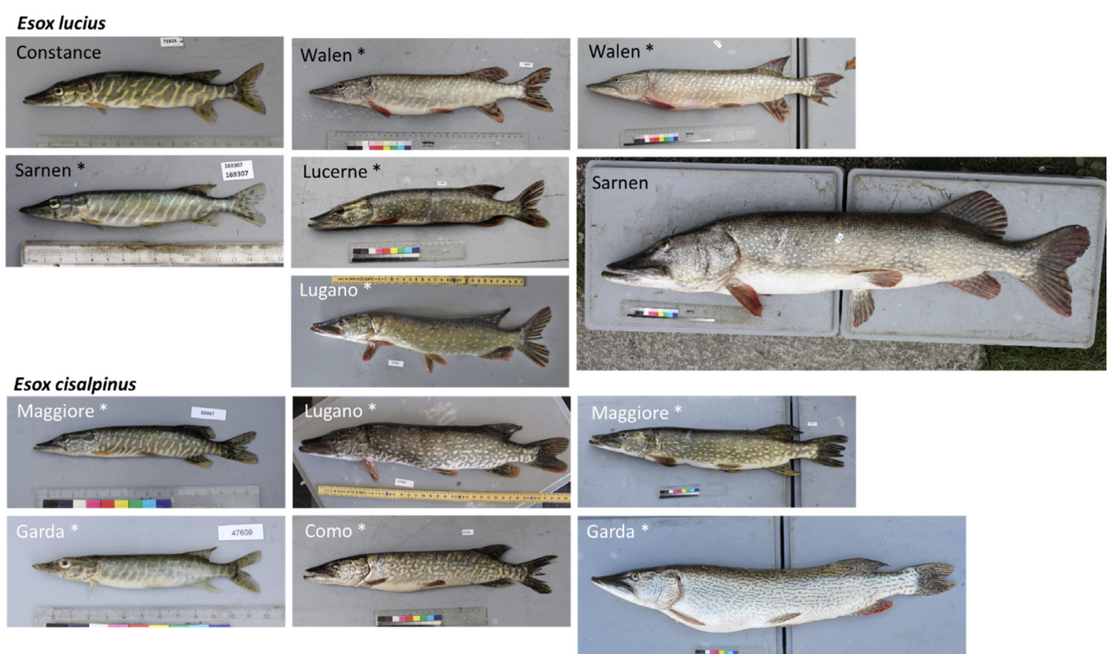


Figure 43: Comparison between the appearance of *Esox lucius* and *Esox cisalpinus* in lakes north (black text) and south (white text) of the Alps. Fish in each column are shown approximately to scale relative to each other. The two largest specimens display characteristic patterns for the two species respectively.
** indicates that the species identity is based on genetic barcoding.*

[4] Interestingly, the numbers of scales along the lateral line of both historically collected *Esox* from Lake Geneva corresponded to *E. cisalpinus* (111 and 113 scales) [154].

Order Salmoniformes

Family Coregonidae – whitefishes

Coregonus spp (whitefish)

Since recolonization of the lakes after the retreat of the ice-sheets across Europe around 15,000 years ago, whitefish (*Coregonus*) have diversified into different ecological niches within each larger lake or set of connected lakes [155]. This has resulted in up to six ecologically differentiated species within a lake [24, 48]. At least 25 perialpine lakes were known to support native *Coregonus* species, the majority of which were endemic [42]. The ecosystem changes resulting from eutrophication in the second half of the 19th century led to extinction and speciation reversal of *Coregonus* species in many lakes [42]. Almost 40% of *Coregonus* species went extinct across the region. Detailed information on the diversity of perialpine *Coregonus* species and the effects of human activities is available in Vonlanthen et al [42], with two key figures provided in Figure 24.

Coregonus spp can occupy many different spatial habitats, from the shallow benthic to open pelagic and the profundal zone down to 300 m of depth. No other group of fish occupies such a wide range of habitats in these lakes. Known ecologically relevant differences among *Coregonus* species include body size and growth rate, number, length and shape of gill rakers, eye size and visual pigments, diet and spawning habitat. The most distinct ecological types are the following:

1. large, fast growing, sparsely gill rakered, benthivorous species, which spawn in shallow water, referred to as "Balchen"-type whitefish (e.g. *Coregonus duplex* in Zurich/Walen, *C. alpinus* in Thun/Brienz, *Coregonus litoralis* in Lucerne, *C. arenicolus* in Constance, *C. suidteri* in midland lakes and *C. palaea* in Neuchatel).
2. small sized, slow growing, densely rakered, zooplanktivorous species that live in the pelagic zone and spawn in deeper water, referred to as "Albeli"-type whitefish (e.g. *Coregonus heglingus* in Zurich/Walen, *C. albellus* in Thun/Brienz, *C. muelleri* in Lucerne).
3. small or medium sized, slow growing, sparsely rakered, benthivorous species that live and spawn in the deep profundal zone of lakes (e.g. *Coregonus gutturosus* in Constance, *C. profundus* in Thun).

Species with other combinations of these or other characteristics occur in lakes with more than three Coregonus species. For instance a type that is in many regards intermediate between the "Balchen"-type and "Albeli"-type whitefish, referred to as "Felchen"-type (e.g. *Coregonus fatio* in Thun, *C. zuerichensis* in Zürich, Walen, *C. macrophthalmus* in Constance), or large-bodied, fast growing, densely rakered pelagic zooplanktivores such as the Blaufelchen, *C. wartmanni* of Lake Constance. Reproductive isolation among members of lake radiations is maintained by differences in spawning depth, spawning season, possibly mate choice [39, 156] and possibly natural selection against intermediate phenotypes resulting from hybridisation [157, 158].

Coregonus spp were recorded in Projet Lac in all northern perialpine lakes, except Bret. The highest number of *Coregonus* species recorded in the same lake was in Lake Thun, where all six species known to occur in the lake were recovered [24, 159]. All four species known from Lake Brienz were also recorded in Projet Lac [24, 160]. Three *Coregonus* species were recorded in Upper Constance, Upper Zurich, Lucerne and Biel. *Coregonus* spp were most commonly caught between 10 and 40 meters and dominated the biomass in the open water of many lakes. One species of *Coregonus* presumed to be extirpated in one lake was re-discovered in that lake in Projet Lac. In upper Lake Zurich, genetic analyses of samples collected in Projet Lac revealed the presence of three species, *C. duplex, C. zuerichensis* and *C. heglingus* [161], whereas *C. heglingus* was previously thought believed to have been extirpated in Lake Zurich [42]. In Lake Lucerne, one individual resembling the deep-water adapted *Coregonus nobilis* (Edelfisch) was also recovered in Projet Lac. This species had also almost gone extinct (and was at some point believed to be extinct) during eutrophication, but was rediscovered in 2004 [162]. None of the other believed extinct *Coregonus* species, such as the profundal *C. gutturosus* in Lake Constance, *C. fera* and *C. hiemalis* in Lake Geneva, or *C. restrictus* in Lake Morat were recorded by Projet Lac.

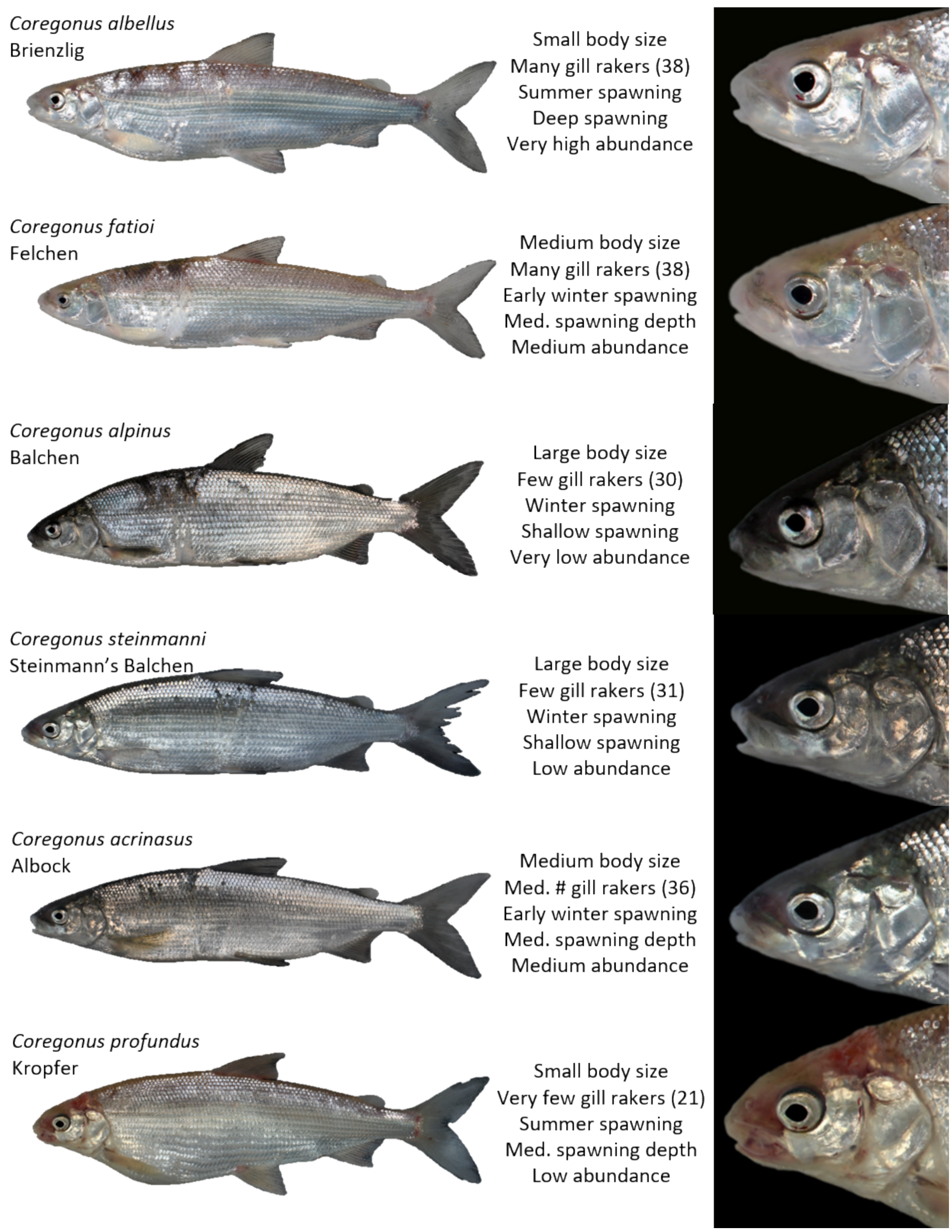


Figure 44: Lake Thun contains a diverse assemblage of *Coregonus* species, with all except Albock having evolved from common ancestors within the lake. Albock contains genetic material from fish introduced from Lake Constance in the 1930s and might be a hybrid species. Brienzlig, Felchen and Balchen also occur in Lake Brienz. Steinmann's Balchen appears tob e restricted to Lake Thun, but a phenotypically similar species occurs in Lake Brienz that may have an independent origin. Gill raker numbers are the average values for the populations of Lake Thun. The number of gill rakers reflects the diet of the species: species with many gill rakers are more efficient at feeding on zooplankton, while species with few and coarser rakers are better at feeding on larger prey, such as larger invertebrates that they obtain by sifting sediment from the lake floor. Local fishermen and previous reports [48, 163] describe a late-winter (February/March) spawning form of *C. albellus*, however it's status remains unknown. Most information taken from [24, 42]. Gill raker numbers and photos from Oliver Selz.

Family Salmonidae – trouts and charrs

Salmo spp (trout)

Species of trout (*Salmo* spp) were recorded in most lakes surveyed by Projet Lac. *Salmo* spp dominated the fish biomass in the littoral and benthic zones of the alpine lakes Sils and Poschiavo. In the perialpine lakes, trout were most frequently caught in the inflowing streams and rivers. In Zug, Hallwil, Lower Constance, Chalain and Lucerne trout were only caught in adjacent streams and rivers, and not in the lake itself. Large, silvery lake forms of *Salmo trutta* caught in the pelagic zone ("lake trout" sometimes called *S. trutta* forma lacustris) were most common in Lake Geneva, with some also caught in lakes Walen, Upper Constance, Brienz, Sarnen, Neuchatel, Morat, Saint-Point and Joux.

Atlantic trout (*Salmo trutta*) are native in the northern perialpine lakes and probably also in Lake Sils in the alpine section of the Inn-Danube catchment. Atlantic trout were recorded in all lakes in the Rhine catchment except Upper Zurich, Biel and Rousses. In the Rhone catchment, Atlantic *S. trutta* have been widely introduced, any may be native only in Lake Geneva. In the Rhone lakes this species was missing from Projet Lac catches of only the smallest lakes: Remoray, Bonlieu and Bret. It is not known which of these lakes may have hosted the native Rhone or zebra tout *Salmo rhodanensis* in the past, and what happened to these populations.

Atlantic trout *S. trutta* has also been introduced into all surveyed southern perialpine lakes, as well as Lake Poschiavo. Indeed, *S. trutta* were recorded in every lake of the Po catchment, except Varese (which did not have any trout). *Salmo trutta* is known to hybridize with southern *Salmo* species in some water bodies where they have been introduced, and remain distinct in others. The massive stocking of *S. trutta* into southern drainages is thought to have led to nearly complete displacement of the native species in some drainages [164]. This makes the proper assessment of trout diversity in southern drainage systems very important, but also complicated.

Projet Lac recorded Atlantic trout *Salmo trutta* and three Adriatic-endemic *Salmo* species in the southern lakes: *Salmo marmoratus* (marbled trout) in lakes Maggiore, Lugano and Poschiavo, *Salmo cenerinus* (northern Italian brook trout) only in Lake Poschiavo, and three individuals resembling *Salmo carpio* (carpione) in Lake Garda. "Engadiner trout" were also identified in Lake Sils, characterized by very few large black spots and genetically belonging to the Danubian *Salmo labrax*. This taxon coexists with *Salmo trutta* in Lake Sils as two genomically distinct species (Figure 46). Finally, a local lake trout type was documented in Lake Poschiavo, with an unusual pattern of very dense large black spots. This taxa genetically resembled *S. marmorata* in the mitochondrial barcode, but *Salmo cenerinus* at microsatellite markers, with considerable introgression from *Salmo trutta* (Figure 47). This likely native form of lake trout in Poschiavo and is referred to in this report as *Salmo* sp. "Blackspot". Based on information from local fisheries authorities, this trout form spawns in the lake, where an annual spawn fishery takes place. This makes it ecologically unique in Switzerland. The only other known lake-spawning trout in the perialpine region is *S. carpio* of Lake Garda, which is interestingly of similar hybrid origins (mitochondrially *S. marmoratus*, otherwise mostly *S. cenerinus*) [165].

It is noteworthy that Projet Lac recorded lake trout forms of *S. marmorata* in Lake Maggiore. The highest abundance and diversity of trout was recorded in the alpine lakes Sils (Danube catchment) with two native species, and Poschiavo (Po catchment) with three native and two non-native species. The *Salmo labrax* (Danube trout) phenotype was recorded in both lakes. This lineage is native to the Danube catchment, and has been introduced into Lake Poschiavo. *Salmo* sp. "Blackspot" was recorded also in Lake Sils where it was possibly introduced from Lake Poschiavo. In Poschiavo, the two species native to the Po river catchment, *Salmo cenerinus* and *Salmo marmoratus* were confirmed as genetically distinct from one another and from *S. trutta*, but with strong signs of hybridization (Figure 47), possibly associated with the arrival of *S. trutta* and *S. labrax* in the lake. Some genetic differences remain that correspond to the different phenotypes (Figure 47).

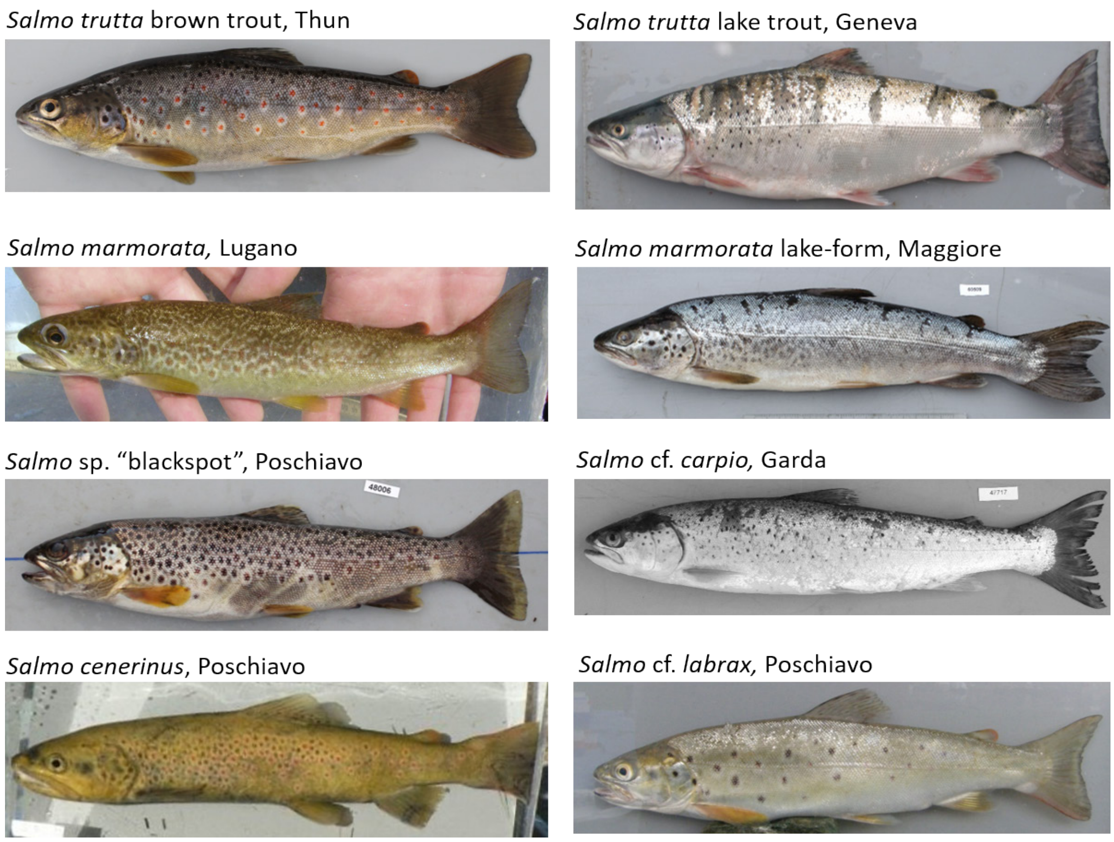


Figure 45: Diversity of *Salmo* spp recorded in Projet Lac.

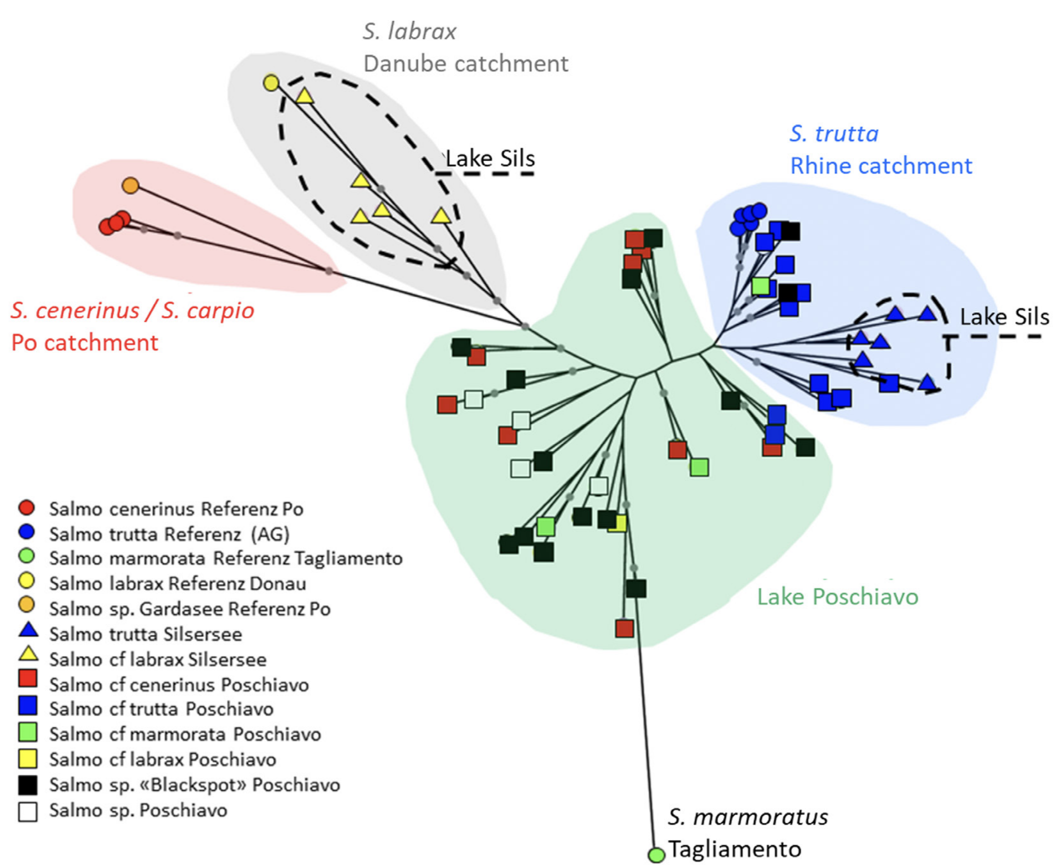


Figure 46: RAxML phylogeny tree depicting the genetic relationship among individual trouts from Lakes Sils and Poschiavo and reference populations of the five species *S. trutta, S. marmorata, S. labrax, S. cenerinus* and *S. carpio* based on several thousand Single Nucleodide Polymorphisms. Note that phenotypic *S. trutta* from Poschiavo are genetically close to *S. trutta* from reference populations in the Rhine, whereas phenotypic *marmorata, cenerinus* and "blackspot" from Poschiavo are genetically intermediate between nonintrogressed *S. trutta, S. marmorata* and *S. cenerinus* references.

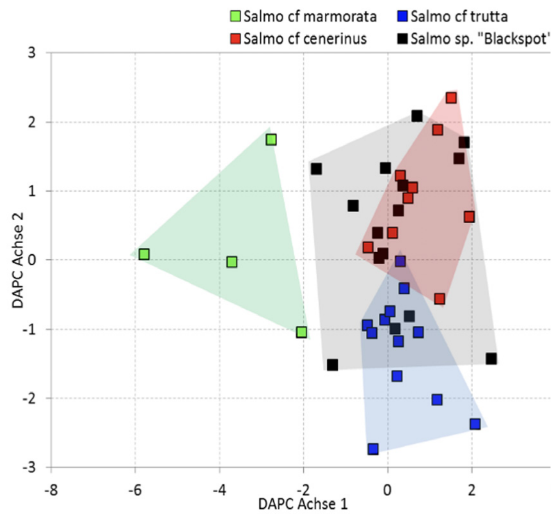


Figure 47: Weak genetic differences among phenotypically assigned trout populations in Lake Poschiavo. Discriminant Analysis of Principal Components based on several thousand Single Nucleodide Polymorphisms.

Salvelinus spp (lake char)

The perialpine lakes of Switzerland form the southern geographic range limit of the genus *Salvelinus* (lake char). Officially, one species of *Salvelinus* is currently native to Switzerland according to federal law (VBGF): *Salvelinus umbla*. This species naturally occurs in all deep perialpine lakes north of the Alps, and was introduced into many alpine and southern perialpine lakes, beginning in medieval times and extensively in the 19th–20th century [9]. Two additional endemic species of *Salvelinus* once occurred in Switzerland: a deep-water adapted (profundal) species in each of lakes Constance (*Salvelinus profundus*) and Neuchatel (*Salvelinus neocomensis*). These species were considered to have been driven extinct by the negative effects of lake eutrophication.

The genus *Salvelinus* is renowned for its diversity of ecologically distinct forms in northern latitude lakes, for example Iceland, Scandinavia and Siberia, often with multiple forms occurring within the same lake [80]. In several cases, these forms have been shown to be genetically distinct sympatric species [80]. A considerable diversity of forms also occurs in some deep perialpine lakes in Switzerland. The Swiss naturalist Konrad Gessner already described three forms of *Salvelinus* in 1575 [13] (Figure 48). Gessner mostly focused on the strong size differences between the forms, and named them accordingly: *Umbla minor, Umbla major*, and *Umbla maxima*. However, with the exception of the two profundal species of lakes Constance and Neuchatel, the diversity of *Salvelinus* has not been studied since the birth of modern taxonomy.

A large variety of forms can still be found among *Salvelinus* in some Swiss lakes (Figure 49). A widespread "generalist" form lives in many smaller lakes, as well as in some larger lakes as the single known surviving form (such as Geneva, Zug and Zurich; Figure 50), and often has a bright red belly. Four other ecologically specialized forms[5] can be distinguished in several lakes: limnetic (living in open water), benthic (near the lake floor), profundal (deepwater) and piscivorous giant (fish feeding). Limnetic forms are characterized by a slender body and a rather small head, and often exhibit an orange belly during the spawning period. Benthic forms of *Salvelinus* have a bulkier body shape with a long, wide head. Profundal forms are adapted to live in the deep zones of the lake, with especially large eyes, pale body coloration, and often have inflated bellies when brought to the surface. Piscivorous giant forms are mainly characterized by their large body size and often by large jaws. All four specialized forms can co-occur in the one lake, as is the case in Lake Thun[6] (Figure 49). Lake Thun has several additional forms that are currently being investigated using morphological and genetic methods (Doenz, Seehausen et al, in prep [25]).

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5 Also called "morphs" or "ecotypes" in the char literature.

6 Only two of the specialised forms could be distinguished among Projet Lac catches in Lake Thun.

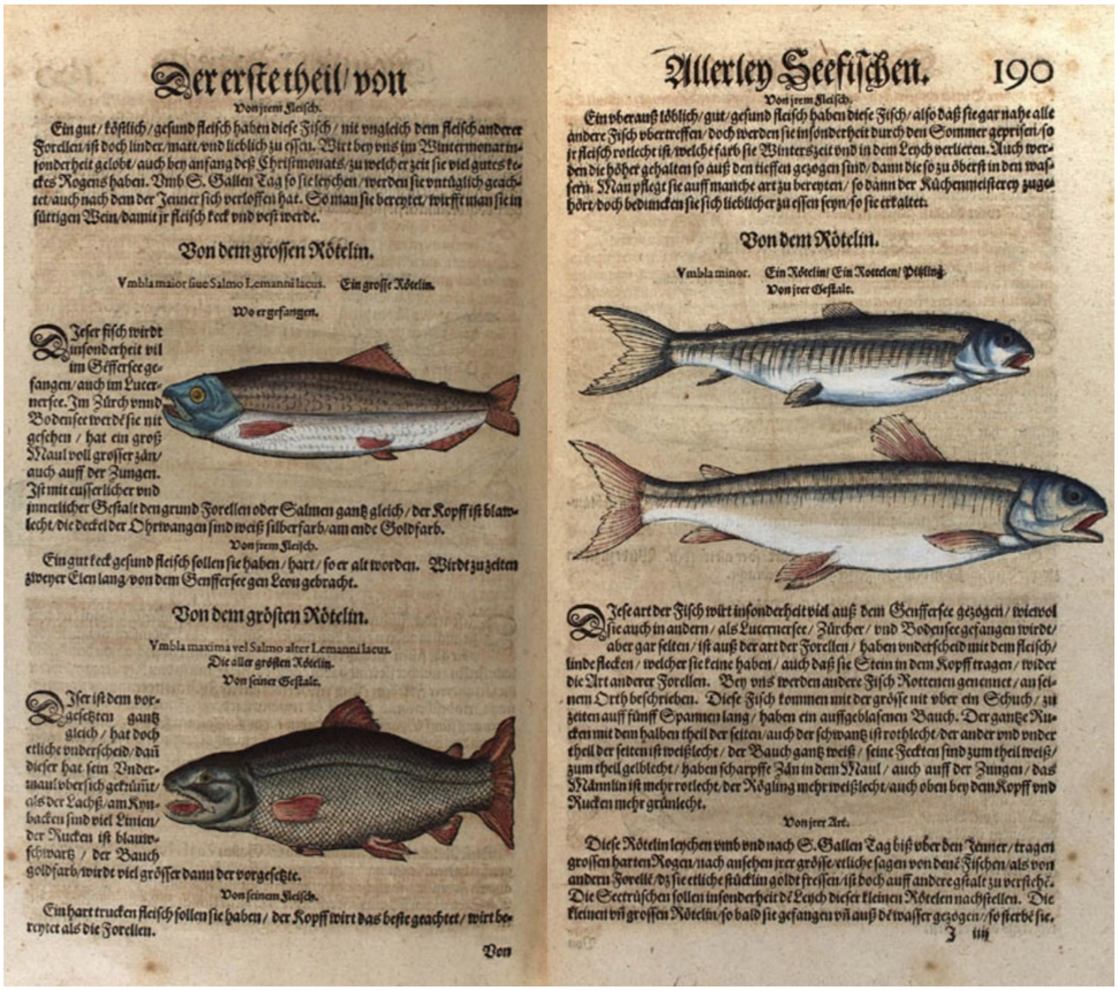


Figure 48: The three forms of *Salvelinus* in Swiss lakes described by Konrad Gessner in 1575.

It is currently unclear whether and which of the *Salvelinus* forms are different species. It is also unknown how many different species there used to be in Switzerland. In lakes where *Salvelinus* has been extensively studied and where many individuals of each of the different forms are available, genetic differentiation has been shown between coexisting forms. For example, such studies show that *S. profundus* is clearly a distinct species from *S. umbla*, and also suggest that there are several species in Lake Thun [25].

In Projet Lac, native *Salvelinus* were caught in lakes Thun, Brienz, Walen, Upper Constance, Upper Zurich, Lucerne and Zug in the Rhine catchment, and Geneva and Annecy in the Rhone. *Salvelinus* was also recorded as a non-native species in the two alpine (Sils and Poschiavo) and several southern perialpine lakes (Iseo, Lugano, Como, Mezzola). The highest diversity of *Salvelinus* was observed in lakes Thun, Lucerne and Walen, each with three forms (Figure 49). At least two other distinct forms are known from lakes Thun and Brienz, with at least one other disctinct form known from Lake Lucerne [25]. The rediscovery of the presumed extinct *S. profundus* in Upper Lake Constance was particularly remarkable. It was caught in nets set at the location where this species was last documented in 1974 [166].

Several samples of *Salvelinus* from Projet Lac have been used for genetic investigations (i.e. lakes Thun, Walen, Lucerne, Constance, Geneva, Sils and Poschiavo). While these analyses are not yet complete, it can already be said that the data show that several genetically differentiated forms coexist in some lakes. The results also show that biogeographical context, ecological adaptation, as well as past stocking practices must be considered in order to understand the origins of the sympatric forms, and the wider phylogenetic relationships among the *Salvelinus* species and forms in the region. *Salvelinus* introduced into lakes Sils and Poschiavo from Austrian populations (Figure 51) are genetically very different from the native *Salvelinus* in Swiss perialpine lakes [25]. Genetic data also indicate that each lake originally harbored its own char populations, and that individuals of different forms from the same lake were often more closely related to each other than the same forms in other lakes [25, 167]. However, analyses of the same genetic data also showed clear traces of stock transfer among lakes (Figure 51). For example, the original *Salvelinus* populations of lakes Constance, Thun and Brienz have been strongly mixed with introduced populations from other lakes. The native population in Lake Neuchatel, seems to have been completely replaced by a population introduced from Lake Geneva ([25]; no Salvelinus were caught by Projet Lac in Neuchatel). Detailed analyses are underway to characterize what remains of the native populations in these lakes.

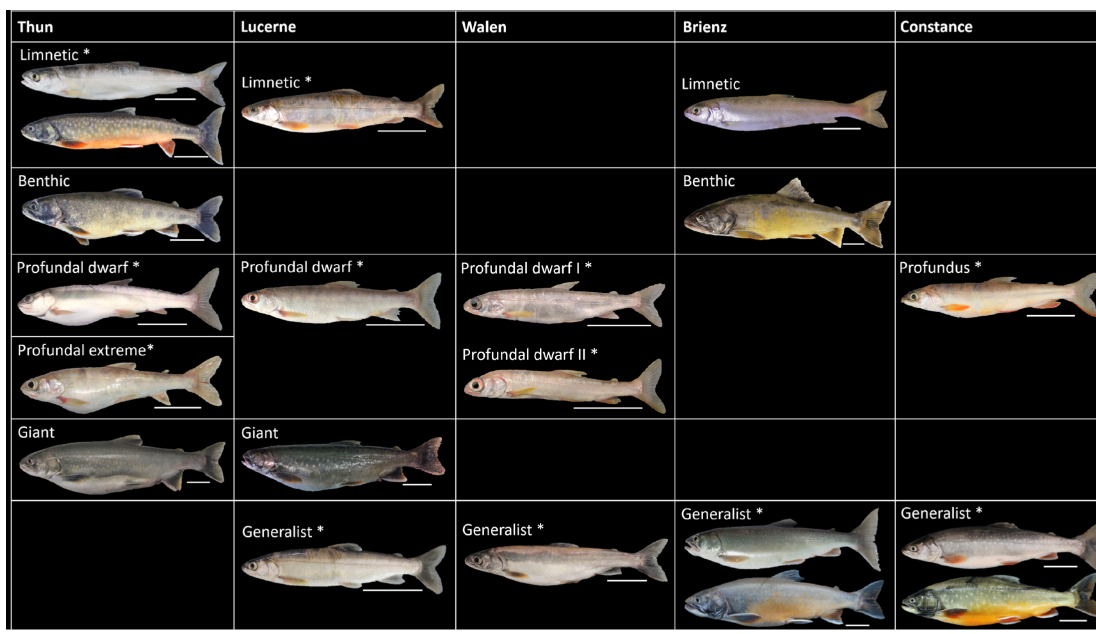


Figure 49: Diversity of *Salvelinus* in Swiss lakes with more than one surviving form (based on current scientific knowledge). Forms that were caught during Projet Lac are indicated by *. The generalist form is treated as *S. umbla* in this report and the specialized forms as distinct taxa. Additional photos of the forms during the breeding season are shown where available (individuals with more orange belly). Horizontal white bar indicates 5 cm. Photos by Projet Lac, Carmela Doenz and local fishermen.

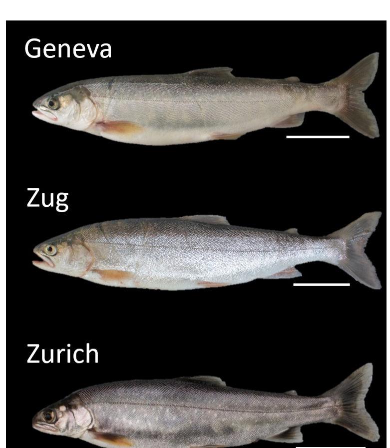


Figure 50: Generalist forms of *Salvelinus umbla* in lakes with only a single known surviving form. Two genetically distinct clusters of *S. umbla* occur in Lake Zurich. The pictured fish was caught by Projet Lac in Upper Lake Zurich and is genetically and phenotypically similar to the generalist form from Lake Walen. On the other hand, *Salvelinus* analyzed from Lower Lake Zurich (none caught in Projet Lac) tend to be genetically and phenotypically more similar to *S. umbla* from Lake Zug (Carmela Doenz, personal communication).

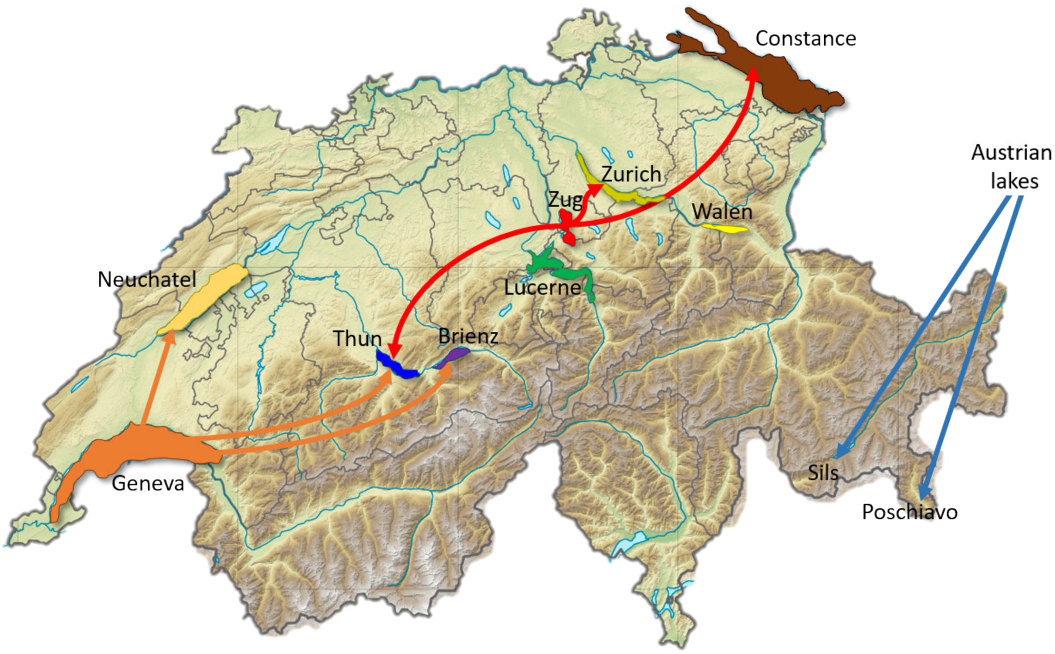


Figure 51: Genetic traces of stock transfer of *Salvelinus* spp among investigated Swiss and Austrian lakes detected using genetic methods (Doenz, Seehausen et al, in prep [25]). These traces indicate that when stocks were introduced to lakes that had native char, the introduced char populations hybridized with the native populations.

Family Gasterosteidae – stickleback

Gasterosteus spp (three-spined stickleback)

Three-spined stickleback (*Gasterosteus* spp) were recorded in six lakes in Projet Lac (Table 11). *Gasterosteus gymnurus* is native to Switzerland in Lake Maggiore and in the Rhine near Basel. Although currently included in *G. gymnurus,* the native populations in lakes Maggiore and Garda[7] belong to the northern Adriatic lineage. This lineage is morphologically and genetically distinct and should be recognised as a separate species [168, 169, 170]. *G. gymnurus* recorded by Projet Lac in Lake Geneva were not native to the lake. This species was first documented in the lake in 1872 [171] and belongs to a West-European (middle Rhone) lineage [172].

Also not native to Switzerland, *Gasterosteus aculeatus* was recorded in lakes Constance (Upper and Lower lakes), Biel and Lucerne. *G. aculeatus* was first recorded in the Lake Constance catchment in 1870 in streams on the Austrian side of the lake (see [173] and references in [174]). Genetic analyses suggest that the *G. aculeatus* in Lake Constance derive mostly from a genetic lineage found in the Baltic drainage (Poland)[172]. *Gasterosteus* across the middle of Switzerland, such as those caught in lake Biel, are a hybrid mixture of the native upper Rhine and non-native Baltic lineages of *G. aculeatus*, as well as the non-native middle Rhone lineage of *G. gymnurus* [175].

The *Gasterosteus aculeatus* of Lake Constance, and especially those of Upper Lake Constance, were far more abundant, larger and were found in a wider range of lake habitats than stickleback caught in the other lakes sampled by Projet Lac (Table 11, Figure 52). More than 2,500 *G. aculeatus* were recorded in the littoral zone, benthic zone and pelagic zones of Upper Lake Constance, to around 45 meters deep. This species formed 96% of the number of fish and 30% of the biomass caught in the CEN pelagic nets in Upper Lake Constance and formed around 50% of the fish caught in the vertical gillnets (volume-weighted, whole-lake NPUE). The *G. aculeatus* of Upper Lake Constance have many and large bony plates covering the entire side of their body and thereby resemble both their freshwater-Baltic and marine ancestors[176]. Most other lineages of *G. aculeatus* reduced their number of bony plates as they adapted to freshwater habitats, such as streams, rivers, small lakes or the littoral zone of larger lakes[177]. However, freshwater lineages of *G. aculeatus* in the Baltic[176], as well as several other lineages around the world [178, 179] have maintained the full set of bony plates. This may provide them with an adaptive advantage in the habitats of large lakes where piscivorous fish are the dominant predators[180]. The strong and highly developed armour of the Upper Lake Constance *G. aculeatus*, inherited from their marine ancestors, may be part of the reason why they are able to colonise the pelagic zone of such a large waterbody.

7 *Gasterosteus* spp were not recorded in Garda by Projet Lac.

Gasterosteus aculeatus were also abundant in the pelagic zone of Lower Lake Constance, constituting almost 65% of fish caught in the CEN pelagic nets. *G. aculeatus* caught in Lower Lake Constance were on average 2 cm smaller than those caught in the Upper Lake (average total length 47 mm compared to 67 mm). The smaller body size of *G. aculeatus* in Lower Lake Constance meant that very few were caught in the vertical nets in this lake. Analyses of gillnet mesh size selectivity show that the smallest mesh size of the vertical nets (10 mm) only starts to become efficient at catching stickleback over 60 mm in length. The smaller size of the stickleback in the Lower Lake therefore resulted in very few of this species being caught in this vertical net protocol.

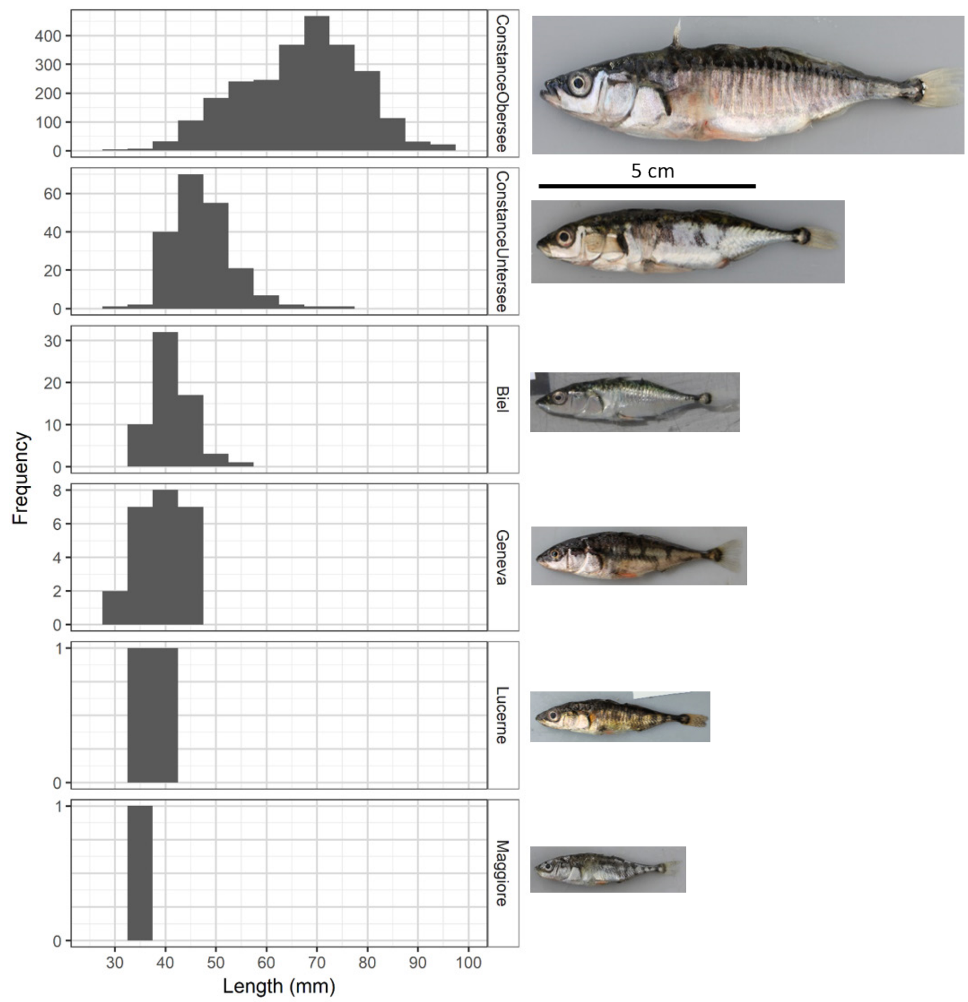


Figure 52: Stickleback were dramatically larger in Upper Lake Constance compared to other lakes. Length frequency distribution of all *Gasterosteus* spp caught in Projet Lac. Scaled photos on the right show one of the larger individuals from each lake.

Table 11: Overview of lakes surveyed by Projet Lac where *Gasterosteus* spp were recorded.

Lake	Species	Number Gasterosteus spp caught in Projet Lac	Habitats occupied by stickleback	First stickleback recorded in catchment (lake)
Constance – Upper	*G. aculeatus* Lake population predominantly Baltic lineage; *G. gymnurus* and hybrids in streams [181]	2,527	Littoral / benthic / limnetic	1870 (1930)
Constance – Lower	*G. aculeatus* Lake population predominantly Baltic lineage; *G. gymnurus* and hybrids in streams [181]	249	Littoral / benthic / limnetic	1870
Biel / Bienne	Hybrid swarm between *G. aculeatus* (Baltic), *G. gymnurus* (middle Rhone) and *G. gymnurus* (upper Rhine) [172]	63	Littoral / benthic / limnetic	Early 1900s
Geneva	*G. gymnurus* Mostly middle Rhone lineage (introgression from *G. aculeatus* in the NE) [182]	24	Littoral / benthic	1872
Lucerne	*G. aculeatus* Lineage undetermined	2	Littoral	?
Maggiore	*G. gymnurus* Endemic northern Adriatic lineage	1	Littoral	Native

Family Cottidae – sculpins

Cottus spp (sculpin)

The sculpin, *Cottus gobio* is a taxon with wide and irregular distribution across Europe and considerable phenotypic and genetic variation between populations that may well comprise of several species [9, 183]. *Cottus* was caught in the benthic zone of many lakes across a wide range of depths from the littoral zone to the deepest point. Along the depth gradient, two peaks in abundance were evident in many lakes, in the shallow littoral and in the profundal, with a gap at intermediate depths. *Cottus* were common in the Rhine catchment, naturally absent only from the higher-altitude Jura lakes Brenet, Joux and Rousses, and were notably missing from Projet Lac catches in the lakes Zug, Morat and Constance Untersee. In the Po catchment, *Cottus* were caught in Poschiavo, Como, Mezzola, Garda and Maggiore, while in the Rhone catchment, this species was only caught in Geneva, Annecy and Chalain.

Genetic differences among catchments, and between lake and stream populations in the Aare-Rhine
Analysis of *Cottus gobio* collected in Projet Lac and an earlier Eawag project "BioChange" identified that the populations of *Cottus gobio* in the Rhine (Aare, but also including Geneva), Rhone (Doubs, but not Geneva) and Po catchments showed substantial genetic differentiation (Figure 55) [41]. The similarity of the *C. gobio* in Lake Geneva to populations in the Rhine catchment had already been shown in earlier work [184] and is attributed to fish crossing from the Upper Rhine to Rhone through ephemeral waterways formed at the retreating edge of the Rhone glacier in the early Holocene (c. 11,000 years ago).

In addition, lake populations of *Cottus* within the Aare-Rhine catchment were genetically distinct from stream populations, whereas lake populations were more similar to each other than to geographically intervening stream populations [41]. Lake and stream *Cottus* in the Aare catchment thus seem to belong to two distinct evolutionary lineages, possibly representing two separate colonisations (with lakes Constance and Geneva belonging to the stream lineage). This suggested that recolonization of Switzerland after deglaciation occurred in two waves, with the stream lineage representing the first wave of colonization. The lake lineage only arrived in the Aare after lakes Constance and Geneva had become inaccessible for colonisation of fish from the Aare; respectively by the Rhine falls in Constance and the retreat of the Rhone glacier further into the Alps for Geneva [41].

Phenotypic and genetic differences between littoral and profundal forms
Phenotypically distinct forms of *Cottus* were recorded in the profundal zone of lakes in the Aare and Po-Adriatic catchments to almost the deepest point of several lakes. In the Aare catchment, *Cottus* were caught to 209 m deep in Lake Thun (lake max depth Z_{max} = 217 m), to 214 m deep in Lake Lucerne (Z_{max} = 214 m) and to 145 m in Lake Walen (Z_{max} = 151 m). Also in the Po-Adriatic catchment, *Cottus* were caught to 125 m deep in Lake Maggiore (Z_{max} = 372 m) and to 290 m deep in Lake Garda (Z_{max} = 350 m). The deep-caught fish were paler in colour and tended to have flatter heads compared to the fish caught in the littoral zone of the same lakes (Figure 53). In the Po-Adriatic lakes the profundal fish corresponded to *Cottus ferrugineus* (described by Heckel & Kner in 1858), currently considered a synonym of *C. gobio* (Figure 54).

Parts of the genomes of profundal and littoral individuals from lakes Thun, Walen and Lucerne were analysed in detail [41]. Significant genomic differentiation between littoral and profundal *Cottus* existed in Lake Walen, but not in lakes Lucerne or Thun. However, several genetic loci showed substantial genetic differentiation between the profundal and littoral populations, especially in Lake Thun, suggesting that the very small number of profundal fish that were available for analysis (e.g. n = 5 in Lake Thun) may have limited the ability to detect genome-wide differentiation [41]. Alternatively, it is possible that the phenotypic differences are the result of plasticity (i.e. the ability of one genotype to produce different phenotypes when exposed to different environments) and further research with a greater number profundal fish is required to properly understand the situation. Sufficient numbers of profundal fish from lakes Maggiore and Garda were not available to test for genomic differentiation [41]. However, DNA barcoding revealed that three profundal fish from Maggiore and Garda belonged to a different mitochondrial lineage than the one barcoded littoral fish from Lake Maggiore and two stream fish from the Maggia (collected by Progetto Fiumi).

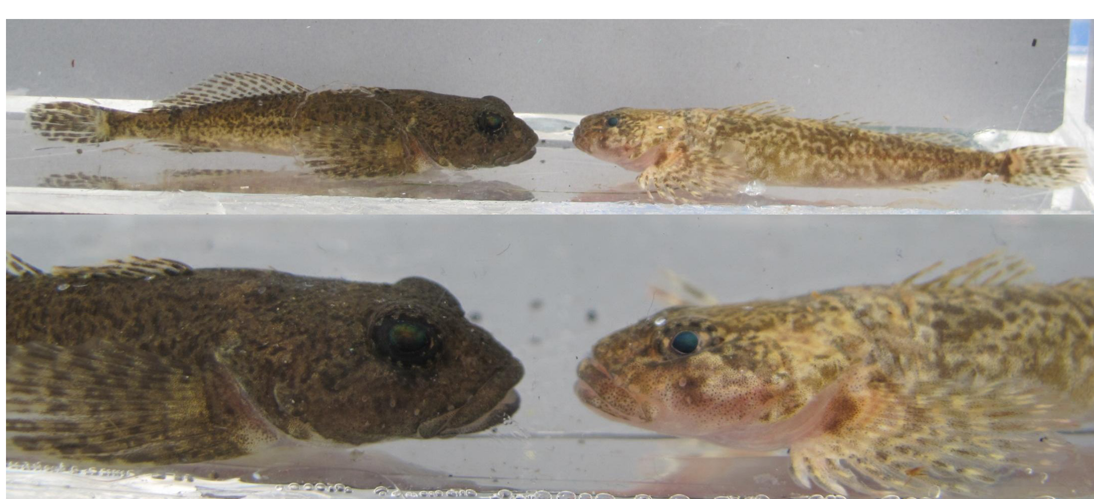


Figure 53: Littoral (left) and profundal (right) Cottus were phenotypically distinct in lakes Thun (shown in photos), Walen and Lucerne in the Rhine catchment and lakes Garda and Maggiore in the Po catchment.

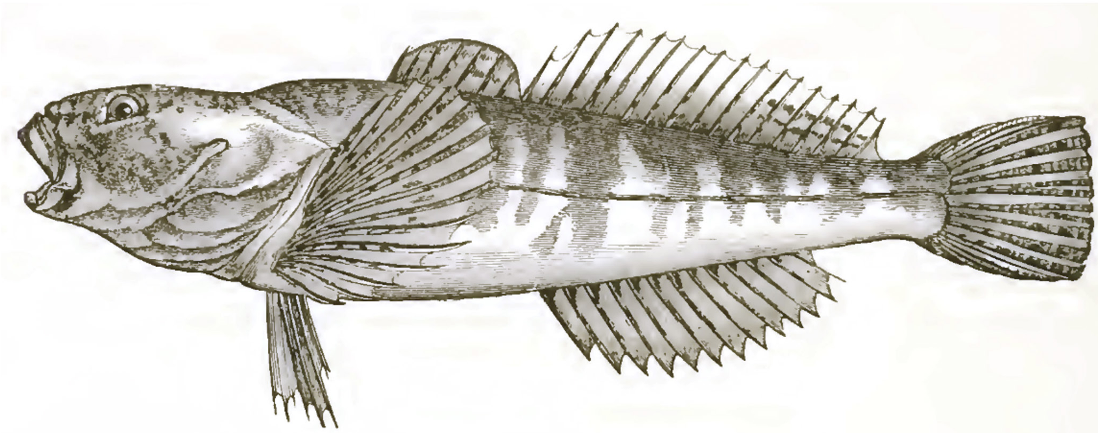


Fig. 18.—COTTUS GOBIO (CUVIER).

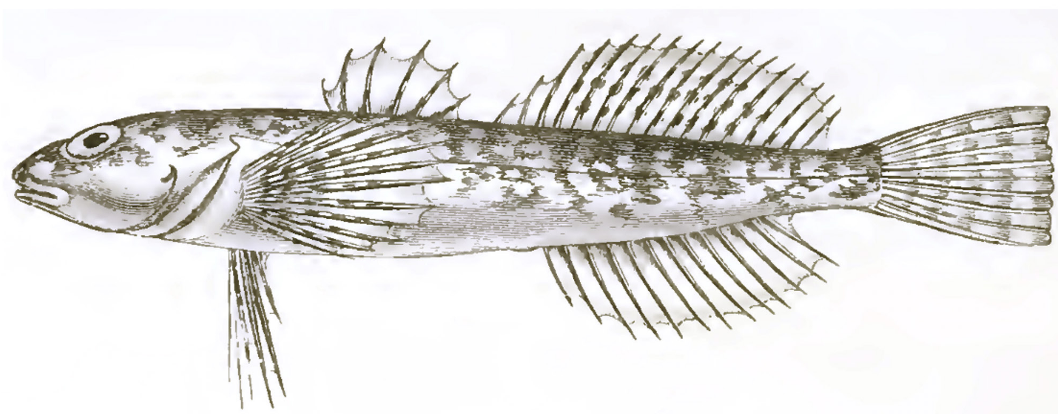


Fig. 22.—COTTUS GOBIO, VARIETY FERRUGINEUS (HECKEL AND KNER).

Figure 54: Phenotypic differences between littoral and profundal *Cottus* were consistent with the distinction between *Cottus gobio* (top) and *Cottus ferrugineus* (bottom) in Seeley [185].

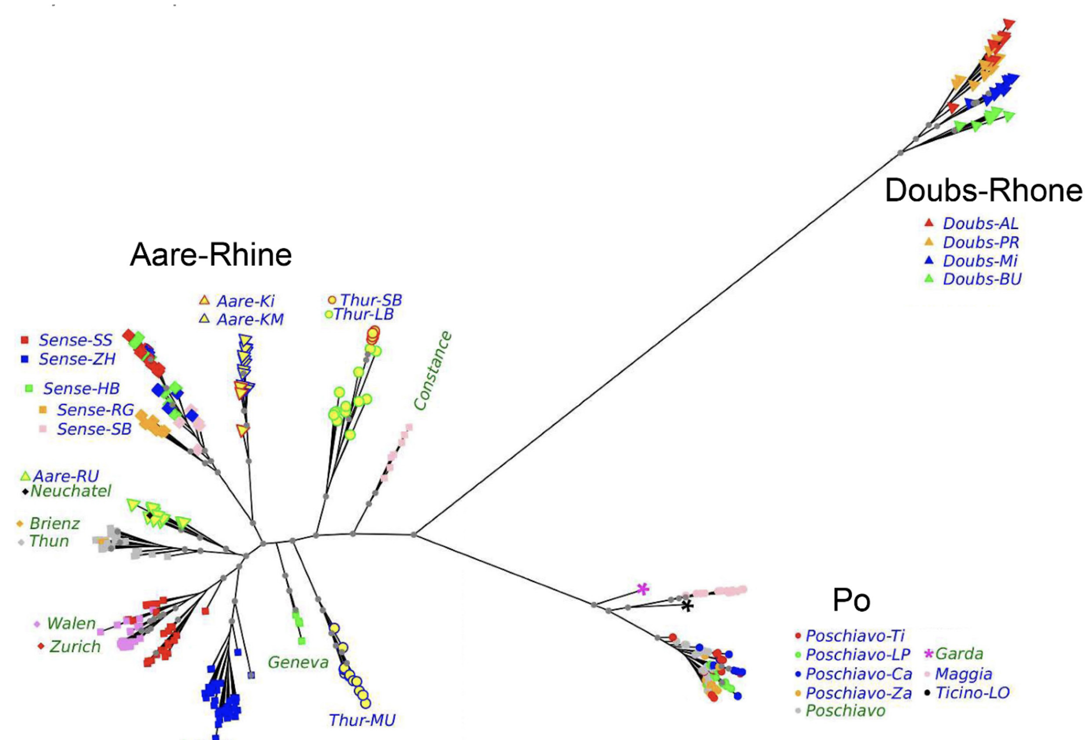


Figure 55: Phylogenetic relationships of *Cottus* from perialpine lakes (green labels) and streams/rivers (blue labels). RAxML tree with 100 bootstrap replicates. Grey dots on nodes indicate >50% bootstrap support. Adapted from Lucek et al. [41].

Family Percidae – perches

Perca spp (European perch)

European perch (*Perca fluviatilis*) were recorded in all except the alpine lakes (Sils and Poschiavo) and was the most abundant species caught in Projet Lac. Across most of central Europe, *P. fluviatilis* typically have red fins and four to six vertical bars (some of which are often V-shaped). Perch populations in lakes across Switzerland exhibited unusually large variation in fin colour (common and extremes of fin coloration), as well as in the number of vertical bars within and among lakes. Most lakes were dominated by fish with yellow-orange or yellow fins, but highly distinct red-finned forms were found along with the yellow-finned forms in Lugano, St-Point, Geneva, Walen and Constance (Figure 56, Figure 57). Many *Perca fluviatilis* recorded in Projet Lac also exhibited unusually large variation in the vertical striping, ranging from four bars to eight or more.

Figure 56: Variation in morphology, banding and fin colour in *Perca fluviatilis*. Figure 2 from [186].

In Lake Constance, yellow-finned perch with many vertical bars was the more common phenotype caught in Projet Lac, whereas red-finned fish with few vertical bars, resembling classical central European perch, were much rarer. DNA-barcoding of Constance perch as part of Projet Lac showed that yellow-orange finned perch were genetically distinct from red-finned fish. This corresponded with previous genetic analysis of perch in Lake Constance using microsatellite DNA, which also revealed significant genetic variation between yellow-finned and red-finned individuals [187]. The earlier study also showed that the yellow-finned perch were more vulnerable to infection by several parasites (tapeworm *Triaenophorus nodulosus* and gill worm *Ancyrocephalus percae*), which do not generally cause damage to the red-finned perch and populations elsewhere. The combination of the significant genetic differentiation and different immune responses between the red-finned and yellow-finned perch in Lake Constance suggest that these are two genetically distinct species with different evolutionary histories.

An additional level of genetic and taxonomic variation among perch in Switzerland is again best demonstrated by earlier work in Lake Constance. This work revealed strong genetic differentiation between the populations of *Perca fluviatilis* living in Lower and Upper parts of Lake Constance (Untersee and Obersee) [188]. The two populations most likely originate from different glacial refugia that met in Lake Constance during range expansion after the last glacial period, and persist as two distinct species with little hybridisation [189]. Experimental evidence suggests that divergence between the two populations may be maintained by postzygotic isolation through genetic incompatibility [190]. It is not yet clear whether and how the variation and differentiation between fin colour types is related to this historical differentiation of lineages. Further work is needed to clarify the status and species diversity in Lake Constance perch.

Fin coloration was recorded for most perch collected in Projet Lac and lakes were determined to contain only the common yellow/orange-finned form, or both yellow/orange- and red-finned forms. The assignment as such is not meant to imply that yellow- and red-finned perch are distinct species in every lake. However, the phenotypic diversity in many lakes and in the region overall, is unusual compared to places elsewhere in Europe, and the situation requires careful genetic, ecological and phenotypic analysis. Until the situation is properly understood, a precautionary approach to conservation should treat red- and yellow-finned perch as two different management units. The likely outcome will be that red- and yellow-finned perch are distinct species in some lakes, but not in others.

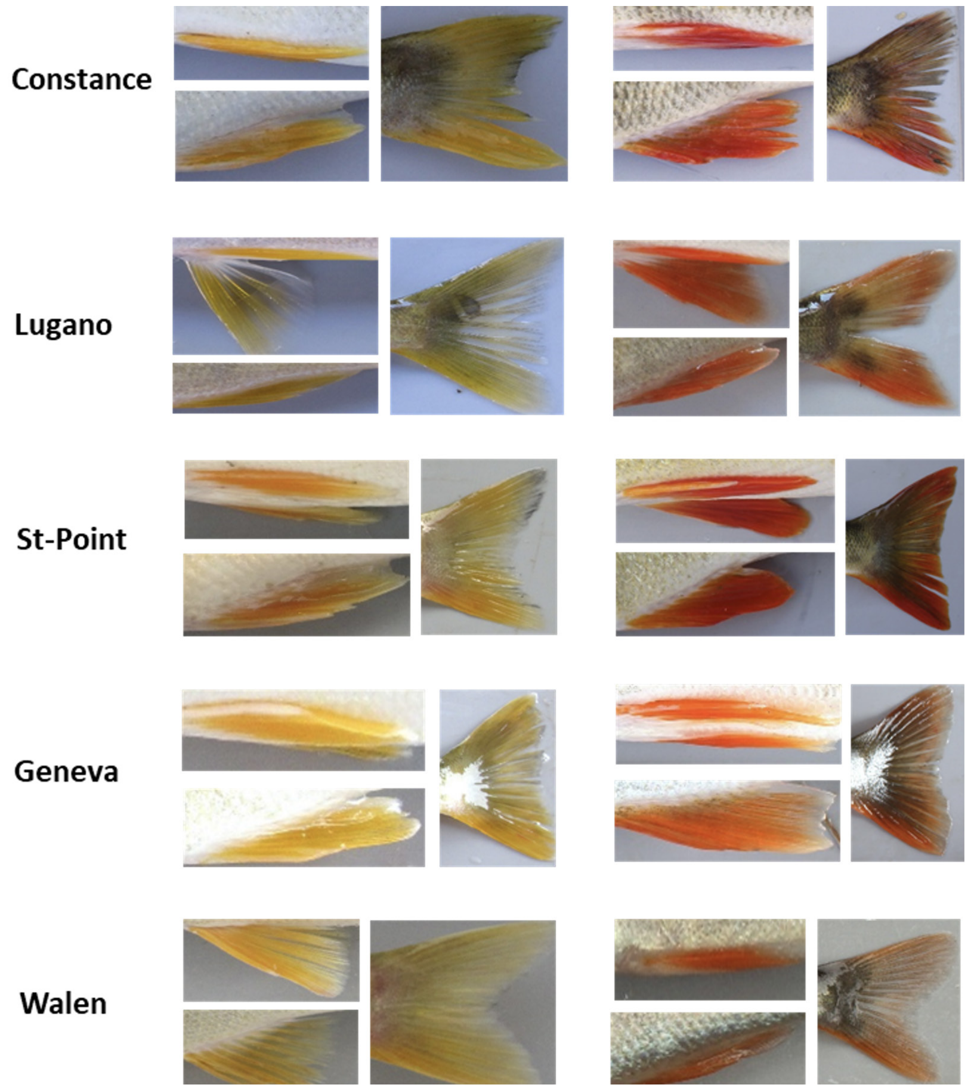


Figure 57: Extremes of variation in fin colour in *Perca fluviatilis* within and among lakes.

Family Blenniidae – blennies

Salaria spp (freshwater blenny)

The freshwater blenny *Salaria fluviatilis* is native to the lakes and streams south of the Alps. *Salaria* were recorded by Projet Lac in lakes Garda, Maggiore, Lugano and Como. *Salaria* were also recorded in the northern perialpine lakes Geneva and Annecy. The population in Lake Geneva is phenotypically distinct from the southern perialpine populations in several key traits, including features that are used to distinguish between the species in this genus [191] (Figure 58). For instance, males of the populations of the southern perialpine lakes have blue cephalic pores on the lower part of the cheek, while those from Lake Geneva lack these pores. Barcoding of *Salaria* from all Projet Lac sampling sites revealed that the Lake Geneva population is genetically distinct from the populations of the southern perialpine lakes. This indicates that Lake Geneva was not colonised from southern Swiss or northern Italian populations of *Salaria*, but most likely from populations further down the Rhone in France. Following the identification key of Doadrio et al [191], the Lake Geneva population would be diagnosed as typical *Salaria fluviatilis*, whereas the populations from the lakes south of the Alps would not (given the presence of blue cephalic pores on the lower cheek, which they share with *S. atlantica*).

Projet Lac sampling in Lake Maggiore revealed, besides the common phenotype of *Salaria*, a rare and previously unknown phenotype that is highly distinct in its colour pattern. Three individuals were documented by underwater photography and one of these was collected by hand net. The new phenotype has marbling on the head instead of the diagnostic head stripes of *S. fluviatilis* and has a broad, dark midlateral band instead of vertical bars on the flank (Figure 59). *S. economidisi* from Lake Trichonis in Greece has a similar midlateral stripe pattern. Further work with additional collections is required to understand this situation.

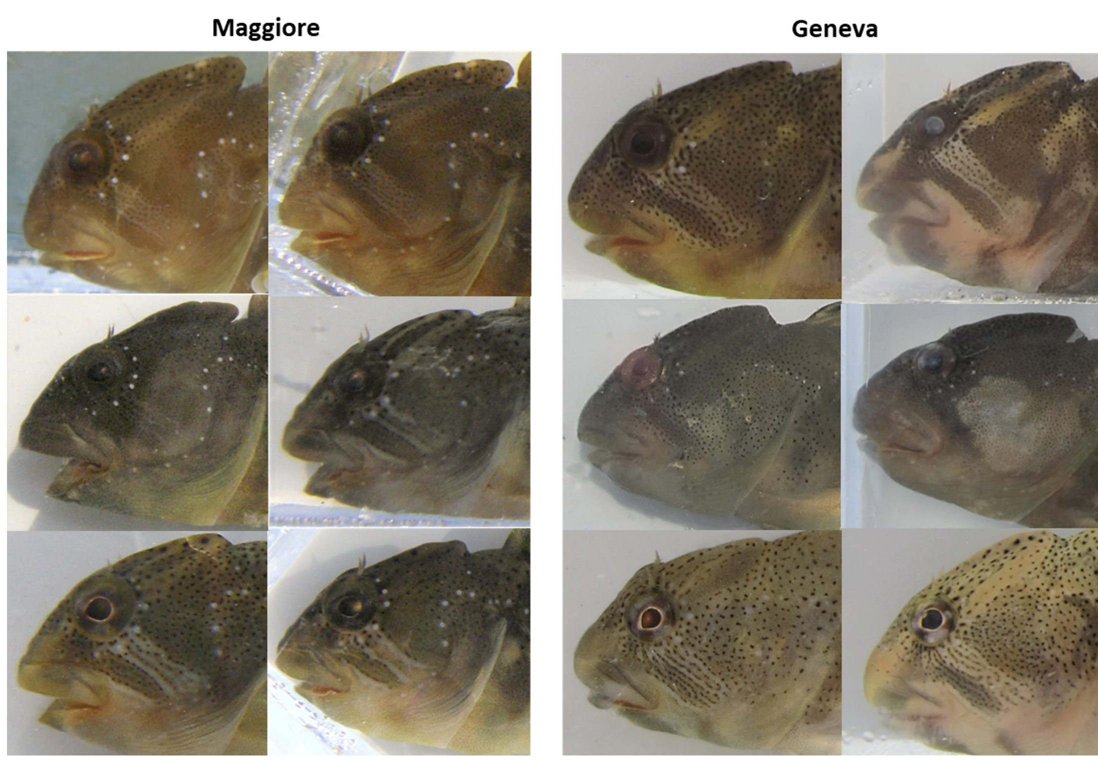


Figure 58: *Salaria* in Lake Geneva were phenotypically and genetically distinct from those in the southern perialpine lakes. Males of the populations of the southern perialpine lakes, such as Lake Maggiore, have blue cephalic pores on the lower part of the cheek, while those from Lake Geneva (and Annecy) lack the blue iridescence of these pores.

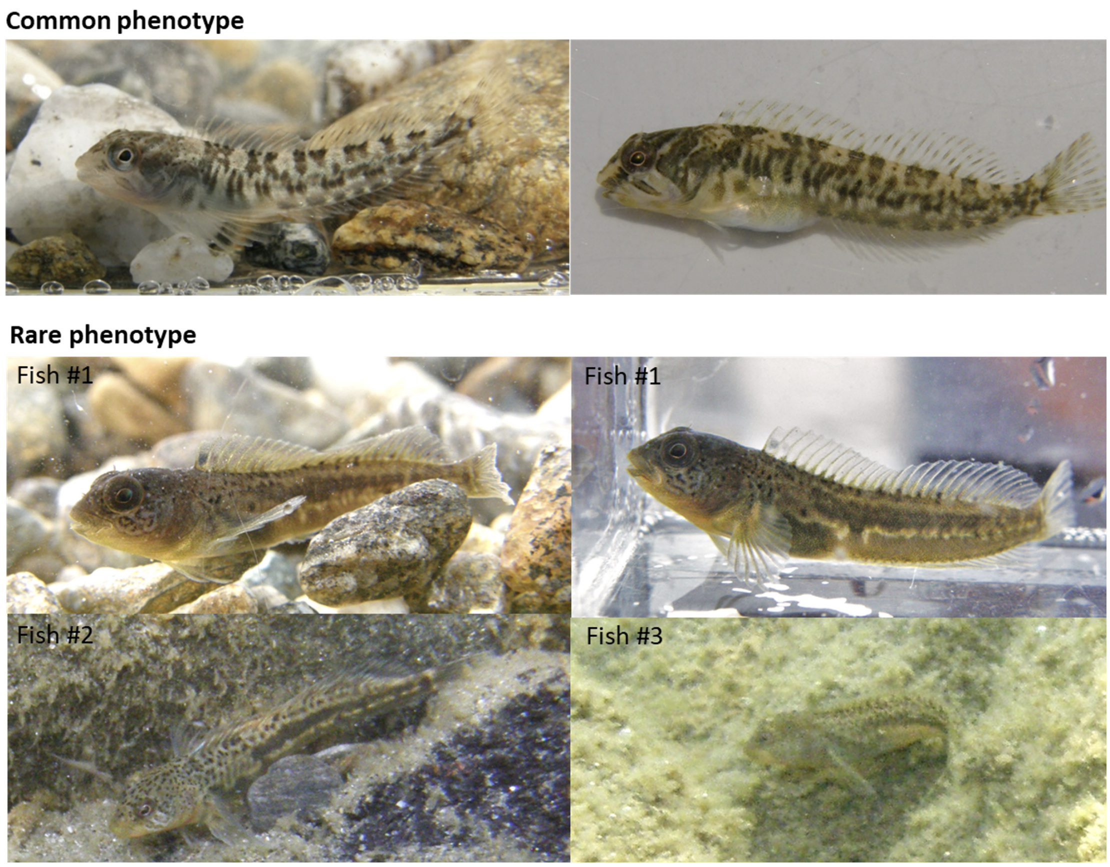


Figure 59. Comparison between common phenotype of subadult *Salaria fluviatilis* and the new, rare phenotype in Lake Maggiore. The upper four photos were taken with the fish in cuvettes with (left) and without (right) gravel. Lower two photos are of additional individuals of the rare phenotype in their natural habitat. Note the marble pattern on the cheek on the rare phenotype, instead of the diagonal face stripes in the common phenotype. Also the broad, dark midlateral band running along the flank instead of paired vertical bars.

Appendix B – Supporting information

The following section contains information to support the publication Umwelt Zustand: “Biodiversity, distribution and community composition of fish in perialpine lakes – “Projet Lac” synthesis report” (www.bafu.admin.ch/uz-2102-e).

Details of Projet Lac methods

Littoral habitat mapping

Littoral habitats to approximately 3 m deep were mapped by boat prior to the fish sampling based on aerial or satellite photos in mapping software (ArcGIS, QGIS, MAPINFO). The classification of habitat types was based on Degiorgi [192]. This classification considers the composition of the substrate (i.e. leaf litter, silt, sand, cobble, boulders, bedrock), the presence and type of vegetation (living/dead, floating, emergent or submerged macrophytes) and the proximity to in- or outflowing rivers or streams.

Table 12: Criteria used to classify the lakeshore habitat types. Similar habitats were combined for most analyses (reflected by duplication in the column ‘Habitat name’).

Description	Habitat name	Composition
Inflow	Inflow	Flowing
Outflow	Outflow	Flowing
Rock slab, ledge (solid rock/bedrock, no interstitial space)	Rock slab	Mineral
Rocks, boulders (larger than 150 mm)	Blocks	Mineral
Boulders with no interstitial spaces (e.g. embedded in mud)	Blocks	Mineral
Cobbles (100 – 150 mm)	Cobbles	Mineral
Cobble with interstitial sediments	Cobbles	Mineral
Cobbles and gravel	Gravel + cobbles	Mineral
Gravel (5 – 30 mm)	Gravel	Mineral
Sand (mineral 0.5 – 5 mm)	Sand	Mineral
Fine mineral sediment (smaller than 0.5 mm)	Fine sediment	Mineral
Fine organic sediment (smaller than 0.5 mm)	Fine sediment	Plant
Leaf litter	Leaf litter	Plant
Floating water plants + other cover	Floating plants	Plant
Sparse reeds (more than 10 cm between stems)	Reeds	Plant
Dense reeds (less than 10 cm between stems)	Reeds	Plant

Description	Habitat name	Composition
Sparse hydrophytes	Macrophytes	Plant
Dense hydrophytes	Macrophytes	Plant
Wood or trees (roots or branches in or touching water)	Wood or trees	Plant

In addition to mapping the distribution of the different littoral habitat types, it was noted whether the shoreline appeared to be in a near-natural state or whether it was artificial or heavily modified by human activities. Examples of artificial habitats included harbours, solid concrete walls and boulders used to stabilise the lakeshore.

Gillnet sampling

Multi-mesh, monofilament gillnets were one of the main methods used in Projet Lac to sample the lake fish community. These were near-transparent, nylon mesh nets, usually stretched vertically between float and lead lines. The nets were set at a location and required the fish to swim into the net and become entangled. Projet Lac used two gillnet sampling protocols, each designed to representatively sample the fish community throughout the whole lake.

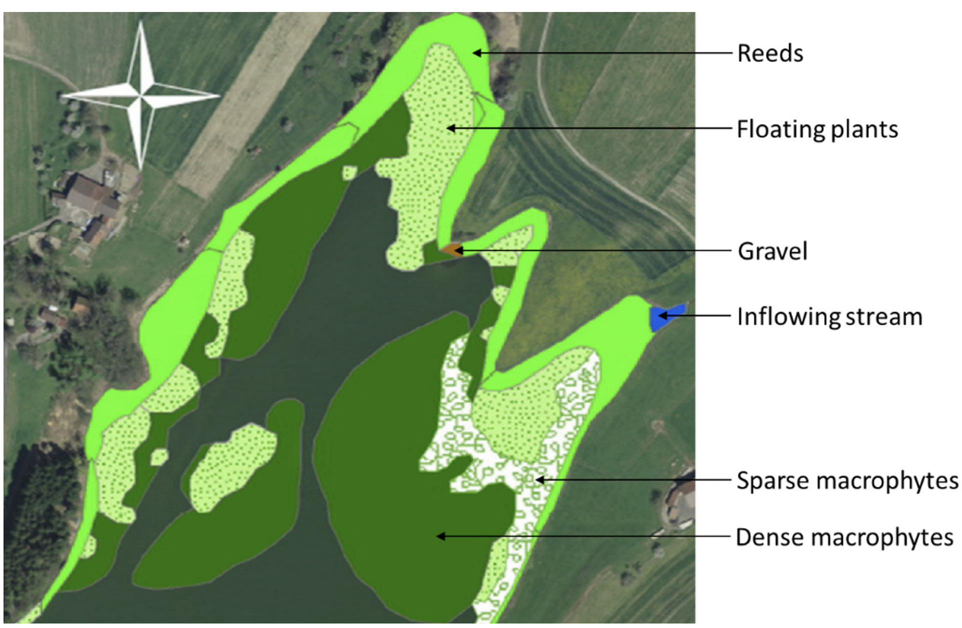


Figure 60: An example of a littoral habitat map from Lake Bret.

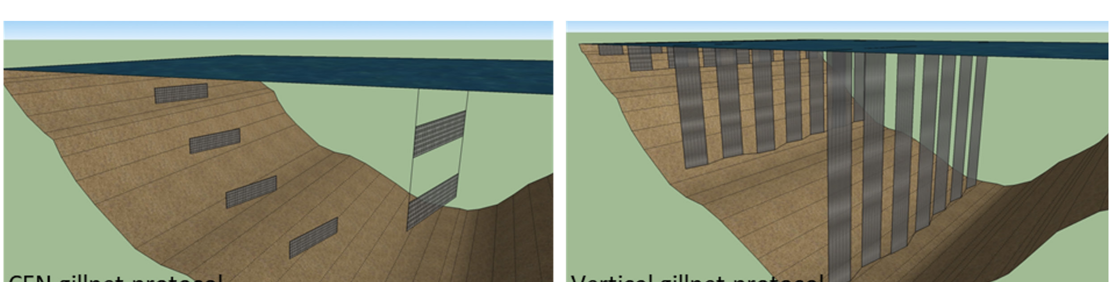


Figure 61: Two gillnet protocols used to sample all major lake habitats. The European standard, also called the CEN protocol, uses separate, horizontally-oriented nets to sample the benthic and pelagic zones. The vertical protocol uses columns of nets that simultaneously sample the fish community from the surface to the lake floor.

CEN protocol

The European standard for gillnet sampling lake fish (CEN 14757 [193]; hereafter referred to as the CEN protocol or CEN gillnets) prescribes horizontally-oriented gillnets consisting of twelve contiguous panels of different mesh sizes deployed in benthic and pelagic habitats (Figure 62). For nets used to sample benthic habitats, each mesh panel was 1.5 m high by 2.5 m wide. Mesh sizes were 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm (measured knot-to-knot; overall net dimensions 1.5 × 30 m). Benthic nets were randomly distributed within depth zones (0–3, 3–6, 6–12, 12–20, 20–35, 35–50, 50–75 m deep) with replication in each zone prescribed in the protocol based on maximum depth and area of a lake. The CEN protocol requires sampling to a depth of 75 m, with optional setting of deeper nets. Given the great depth of many prealpine lakes, multiple benthic nets were set deeper than 75 m. CEN nets sampling pelagic habitats consisted of contiguous mesh panels 6 m high and 2.5 m wide following the same series of mesh sizes as the benthic nets, but excluding the 5 mm panel. Pelagic nets were deployed in the column of water above the deepest point of a lake in the same depth zones as the benthic nets (albeit with the first zone 0–6 m instead of 0–3 m) to 75 m deep. The CEN protocol was developed for lakes with surface area up to 5,000 ha (50 km^2), however many lakes sampled by Projet Lac were larger than this. In these lakes, the replication of nets in each depth zone was increased according to lake area within boundaries imposed by practical constraints (time, budget).

Vertical net protocol

The vertical net protocol prescribes vertically oriented gillnets that simultaneously sample from the lake surface to the lake floor. This type of vertical nets was first used in the USA for studying depth distribution of fishes in lakes and reservoirs (e.g. [194]). The vertical netting protocol was developed by Degiorgi et al. [195, 196] and describes the use of vertical nets to sample whole-lake fish communities. Mesh sizes of nets used in this protocol were 10, 15, 20, 30, 40, 50, 60 mm. Each mesh size was set as a separate column of net, with the full set of net-mesh columns referred to as a 'battery'. Net columns for each mesh were 2 m wide, with the height of the vertical axis of the net corresponding to water depth. In littoral habitats (to 5 m depth), net columns of different mesh sizes were attached to the same float and lead lines with adjacent columns separated by gaps of 2 m width. For deep-set nets, each net column was deployed as a separate net, with columns of different mesh size placed as close together as practical i.e. usually within a radius of 50 m (Figure 63).

Netting effort under the vertical net protocol was allocated to the littoral and deeper habitat zones. Littoral habitats were determined by the littoral habitat mapping (see section 'Littoral habitat mapping') and deep/pelagic habitats were identified on bathymetric maps and defined according to the maximum depth of a lake (Z_{max}; Table 12, Table 13). Some deep habitat categories were not present in the lake if Z_{max} was less than 40 m. In each lake, at least three replicate net batteries of the full set of mesh sizes were deployed within each habitat category.

CEN and shallow-set vertical gillnets were deployed for around 14 hours from evening until the next morning. Vertical gillnets in the deeper parts of the lakes were also set in the evening and were collected after between 15 and 24 hours in the water.

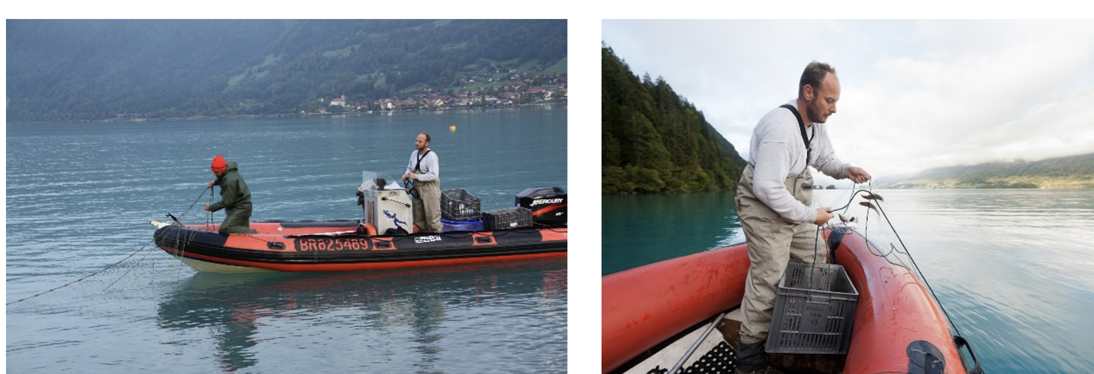


Figure 62: Retrieval of CEN gillnets. Photos: Andri Bryner, Eawag (left); Stefan Kubli, Eawag (right).

Electrofishing

Electrofishing was conducted in the littoral habitats that were identified by the habitat mapping (see section 'Littoral habitat mapping') [197]. Each littoral habitat type was sampled at least three sites by either wading or from a boat (Figure 64). An estimate of the length and width of the electrofished area was used to calculate estimates of fish density. Electrofished stretches were usually around 2 meters wide and 15 meters long. Electrofishing conducted by GRAIA and CNR-ISE (Consiglio Nazionale delle Ricerche – Istituto per lo studio degli ecosistemi) in Como, Idro, Iseo, Mezzola and Varese used a point sampling approach where the anode was immersed for 5 seconds at each location [198].

Table 13: Depth zones used in the vertical gillnet protocol to allocate sampling effort. The littoral zone was further divided into habitat types based on substrate composition, presence of vegetation and proximity to flowing water (see Table 12). Z_{max} refers to the maximum depth of the lake.

Depth habitats	Details
Littoral	< 5 m
Sublittoral	5 m – 10 m
Deep sublittoral	10 m – 30% Z_{max}
Min pelagic / profundal	30% Z_{max} – 60% Z_{max}
Med pelagic / profundal	60% Z_{max} – 90% Z_{max}
Max pelagic / profundal	90% Z_{max} – Z_{max}

Figure 63: Retrieval of vertical nets in open water. Photos: Andri Bryner, Eawag (left), Projet Lac (right).

Figure 64: Electrofishing from boat (left) and by wading (right).

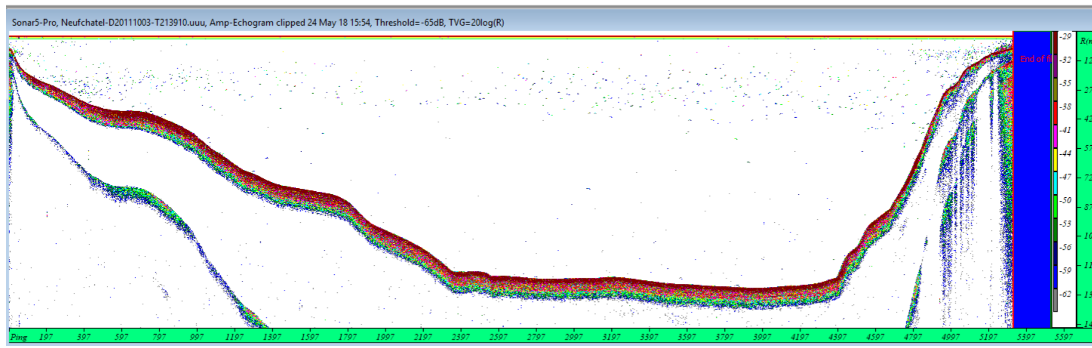


Figure 65: Example of a hydroacoustic transect showing a cross-section of Lake Neuchatel from south-east, near Font (canton Fribourg/Freiburg; left side of figure) to north-west, near Vaumarcus (canton Neuchâtel; right side of figure). The red-brown band represents the lake floor. Hydroacoustic echoes of single fish are visible in the open water, particularly in the upper 25 m (depth-scale shown in green on the right hand side).

Hydroacoustics

Hydroacoustic investigations were mostly conducted by INRA Thonon, while the surveys for lakes Lucerne, Zurich and Constance were carried out by the University of Constance. Lakes were covered by parallel transects during the day and the night (Figure 65). The depth sounder used by INRA was a SIMAD EK60 split-beam sonar operating at a frequency of 70 kHz. The system used for lakes Lucerne, Zurich and Constance was a Simrad EY60 split-beam sonar operating at a frequency of 120 kHz. The raw data were analysed with the software Sonar 5 [199] to produce estimates of abundance and biomass of fish per hectare.

Fish processing and biometry

Fish caught in the deep-set vertical nets were removed from the nets on the boat as the nets were retrieved (Figure 63). Fish that were alive were euthanized. Fish caught by electrofishing were processed on the boat and returned alive to the water. Fish from electrofishing destined for a collection were euthanized and taken to the field lab on land for processing. CEN gillnets and shallow-set vertical nets were retrieved from the water and brought back to a makeshift field lab on the lakeshore (Figure 66). There, the fish were removed from the nets, placed in boxes labelled with the net number and mesh size and passed on to the biometry station. At the biometry station, each fish was:

1. assigned a unique code, the "fishec number",
2. identified to species level where possible,
3. measured for total length (tip of snout to tip of tail) to the nearest millimetre,
4. measured for wet-weight to the nearest gram,
5. photographed in the standard way: lateral view (left side) of the fish from above, including a scale bar, colour bar (for colour correction) and the fishec number (Figure 66, Figure 67).

Figure 66: Recording weight, measuring total length and taking a standard photograph in the field lab.

Where many small fish of the same species and size were caught in the same mesh or the same electrofishing action, the fish were processed together as a batch. The number of fish, total weight, minimum and maximum lengths of fish in the batch were recorded. In some cases, it was not possible or practical to measure the weight of the fish e.g. fish caught by electrofishing, processed on the boat and returned to the water. In these instances, only the length of the fish was recorded, and weight was estimated based on the length-weight relationship for the species based on other individuals for which length and weight had been measured.

In addition to the standard photo, cuvette photos of fish in water were taken of fish of particular interest in some lakes, whenever possible again from the left side (Figure 67). Cuvette photos were particularly useful for small and dark fish such as sculpins, blennies and gobies where details of shape and colour cannot be distinguished in standard photos. For larger fish, this type of photo also provided more natural and life-like colours.

A piece of the pectoral fin and/or muscle tissue was taken for genetic studies from the right side of as many individuals of each species in each lake as practical. This was taken either in the field or during the preservation of the specimen at the museum. The tissue sample was immediately placed in 100 % technical ethanol and later frozen at -80 °C for long-term storage at Eawag, Kastanienbaum or the Natural History Museum of Bern.

Up to thirty individuals of each species from each lake were selected for inclusion in the collection of the Natural History Museum of Bern. Fish were frozen in the field and later transferred to the museum where they went through an extensive preparation process for long-term preservation (Figure 68). These specimens are available for future research projects and taxonomic studies.

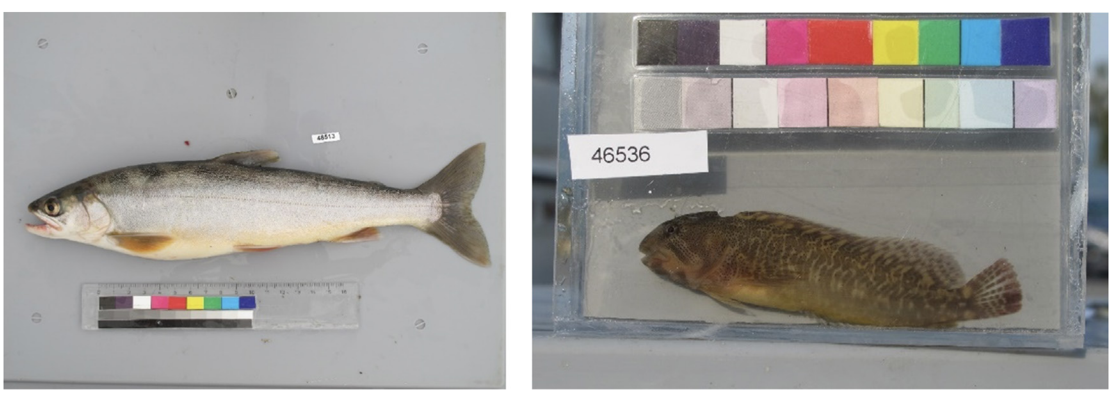


Figure 67: Standard photos (left) were taken of almost all sampled fish, while cuvette photos (right) were taken of fish of small, benthic fish and fish of particular interest in some lakes.

Figure 68: Fish from Projet Lac being prepared by museum staff for long-term preservation.

Environmental data

Chemical and physical parameters of the water routinely measured by cantons or research institutions were used in this report to investigate the ecological state of the lake habitats available to the fishes. The time series of this environmental monitoring data was also used to understand how the lake ecosystem has changed through time, particularly in response to the effects of humans such as eutrophication, reoligotrophication and climate change. Phosphorus concentrations used in analyses were generally depth-integrated average concentration of total phosphorus during the winter-spring vertical mixing period of the year of the fish sampling. In addition to the cantonal monitoring, Projet Lac used temperature loggers in several lakes to obtain high temporal resolution information on the surface water temperature. The loggers were generally deployed for 1 – 3 years at one location.

Data analysis

The sampling methods used by Projet Lac provide a multitude of perspectives on the fish community and a large range of options for analysis. For example:

- Abundance, biomass
- All fish lengths, length-limited (e.g. only fish > 25 cm)
- Raw numbers (how many fish, fish species, etc), relative numbers (% of the fish community)
- Focus on single species, groups of species (e.g. taxonomic or trophic groups), multivariate assemblage composition (more influenced by dominant fish species, by the diversity of species, or by rare species)
- Littoral, benthic, pelagic, depth-limited (e.g. only surface waters), whole-lake
- Whole-lake: volume-weighted, surface area-weighted
- Average catch corrected by net area, average (uncorrected) catch among nets
- CEN gillnet protocol, vertical gillnet protocol, electrofishing, hydroacoustics
- Analyse all lakes together, subsets of lakes separately (e.g. different river catchments, small/shallow vs large/deep lakes)

There is no perfect or universally correct way of handing the data. The best approach depends on the question or aspect(s) of the fish community that are of most interest. The results presented in this report are based on what we consider the most appropriate approach for the context and have proven to be robust, in that the pattern has withstood critical examination from multiple perspectives.

Catch per unit effort (CPUE)

For most analyses, the amount of fish caught in each electrofishing or gillnet action (i.e. each sample) was divided by amount of "effort" put in to catch these fish. This is referred to generally as catch per unit effort (CPUE). Biomass corrected by effort is referred to as biomass per unit effort (BPUE), abundance as number per unit effort (NPUE). For electrofishing, the 'effort' was the surface area of the shore (in m^2 electrofished area) covered by the electric field. For gillnets, 'effort' was the area of the net (in m^2 of net area).

Further correcting the gillnet catches by the amount of time that the nets were in the water (known as 'soak time') was also an option. It was assumed however that the number of fish did not change significantly (and certainly did not increase linearly) with the comparatively small differences in soak time before the nets were collected in the morning after the nets had already been in the water for 12 hours since the prior evening. Finally, to avoid discussing very small values, CPUEs in this report are generally multiplied by 100 and therefore represents abundance or biomass per 100 m^2 of net or electrofished area.

Catch per unit effort is also known as 'catch rate', and can be thought of as reflecting the density of fish. For example, the number or weight of fish per cubic meter. In reality, CPUE is influenced by many factors relating to the sampling methods, the fishes and their environments (see section 'Strengths and limitations of individual sampling methods'). The simplification of CPUE to fish density can be useful however to understand what is meant by these values.

Whole-lake catches

A single value representing the fish community throughout the whole-lake can be informative for comparisons across the full spectrum of lakes. An average catch for the whole lake based on raw catch data will be influenced by the distribution of sampling effort throughout the lake [200]. For example, the CEN protocol prescribes that an approximately similar surface area of gillnet should be set in the benthic and pelagic zones. Thus, an average catch calculated on the raw catches of this protocol will be approximately equally influenced by the fish community in the benthic and pelagic zones. However, the benthic zone constitutes only a very small proportion of the volume of large perialpine lakes. A representative measure of the whole-lake fish community should be influenced by the catches in the different habitats, with their contribution weighted by the availability of the habitat within the lake. In this manner, the whole-lake estimate provides an indication of the average catch if multiple nets were set randomly throughout the lake.

The basis of the whole-lake calculation is to determine the fish catches in particular habitats and then scale up to the whole lake based on the availability of the habitat within the lake. This approach requires reliable estimates of the fish community in the individual habitats, particularly those forming a large proportion of the lake. The vertical gillnet protocol is generally most appropriate for whole-lake calculations in large perialpine lakes because this protocol prescribes more rigorous spatial sampling of the fish community in the high-volume, open-water habitat [201].

Whole-lake catches were calculated in two ways, each providing different insights into the fish community: catch per net area and catch per vertical net battery.

Catch per unit net area

Whole-lake catch per unit net area (CPUE) reflects the biomass or number of fish per area of net, averaged across the entire lake. This calculation divided the lake into depth-based compartments and weighted the whole-lake CPUE for each species by their catch rates in each depth-compartment, according to the volumetric contribution of the compartment (i.e. the volume of the compartment as a proportion of the volume of the lake)[201]. Compartments were defined according to the depth strata used by the vertical net protocol to allocate sampling effort (Table 13). The resulting value is crudely equivalent to weight or number of fish per unit water volume. This tends to be naturally lower in deeper lakes due to the larger volume of the less productive profundal zone.

Catch per vertical net battery

An alternative whole-lake estimate, that is more analogous to fisheries catch statistics (usually reported in kilograms per hectare), acknowledges that a battery of vertical nets simultaneously samples the fish of the entire column of water at a particular location. This approach does not correct for net area and therefore does not penalise for the less productive profundal zone. It instead considers the catch of fish in a vertical net battery as a depth-integrated sample. Similar to the whole-lake CPUE, a weighted average was used to obtain the value for the whole lake, this time weighting the average catch in each depth-habitat (Table 13) by the surface area of the depth-habitat as a proportion of the surface area of the lake.

Comparisons among lakes

By applying the same sampling equipment, in the same way, across all large lakes of the region, the Projet Lac approach provides the opportunity to look at how the fish community varies between lakes with different environmental factors. Investigating correlations among lakes between variables reflecting the fish community and other factors in the lake can be useful to provide predictive insight to how the fish community in a particular lake might change with changes in environmental conditions. The results of this standard scientific approach must be interpreted cautiously however when applied to such large entities as the large and deep perialpine lakes. The lakes are complex systems where many important biological, physical and human-based factors interact to shape the ecosystem and the fish community observed in a survey. For this reason, and given the modest number of lakes, only the ecological factors exerting the greatest/most general influence on the fish communities, such as lake morphology and productivity, can be investigated with quantitative statistical analyses. The influence of other factors on the fish community will generally only be detectable if their effects are greater than these major factors across the majority of lakes in the dataset. Descriptive analyses considering combinations of ecological factors can also provide insights into the lake ecosystems, particularly to identify single lakes or sets of lakes that deviate from otherwise strong relationships, which can be a first step in looking for explanations. Strong dominance of particularly ecological processes with a unique situation in a lake may offer such explanations, for example the influence of high turbidity resulting from glacial sediment on the productivity of Lake Brienz.

Strengths and limitations of individual fish sampling methods

Standardised fishing in each lake was conducted using multiple sampling methods. Each method has strengths, weaknesses and biases. The combination of methods used in Projet Lac was selected to give the most robust picture of the lake fish community possible with the finite sampling resources available.

Gillnetting

Gillnetting provides a relative estimate of fish abundance/biomass, which is proportional to actual abundance/biomass via a fish's "catchability". The catchability of a fish reflects the probability that an individual fish will encounter the net, be caught in the net and that it stays in the net until it is retrieved. The catchability therefore varies between species (e.g. more mobile, spiny or deep-bodied fish are more likely to be caught), within species (e.g. fish body depth relative to net mesh size), with environmental conditions (e.g. net may be seen and avoided by the fish in clear water), with predation (e.g. fish may be removed from the net by predators) and through time (e.g. daily and seasonal differences in movement patterns [202]). Other factors influencing catchability include the physical characteristics of the gillnets (e.g. mesh size, net material, hanging ratio, net spacing, age of the net), their orientation in the water column and the distribution of fishing effort between littoral, benthic and pelagic habitats. The CEN gillnet protocol provides robust information on the fish of benthic lake habitats [200], while the vertical net protocol provides better estimates of pelagic and whole-lake catch per unit effort [201].

Electrofishing

Electrofishing is an active sampling method where the person operating the electrofishing equipment moves through the habitat. The electric current causes a reaction in the fish that results in most species swimming toward the operator. Electrofishing is therefore more effective in capturing small, slender and less mobile species, that may be under-represented in the gillnets. Electrofishing is also useful for obtaining fish that still show their live coloration, as colours are often lost in fish that have been in gillnets for some time. The live coloration can be important for species identification, particularly to distinguish between closely related species. A major advantage of electrofishing is that fish are stunned in the catching process and can be returned alive to the water. Electrofishing is only effective in shallow areas however, and so was only used to sample the littoral zone of the lakes. Another disadvantage is that catchability is influenced by fish behaviour, in that some species do not swim towards the anode, but rather the stunned fish fall into vegetation or rock structure. Larger, highly mobile fish may also escape before the current reaches them. Finally, the data collected by this method can be influenced by the behaviour of the operator, i.e. the different ways that people operate the electrofishing device to sample the fish of the lakeshore.

Gillnets and electrofishing involve physically catching the fish and so can provide accurate information on species identification, length and weight, as well as the potential to take additional samples or information, such as photographs, scales to determine the age of the fish, tissue samples for genetic analyses, stomach contents and to preserve the fish for accurate morphological and taxonomic work and as a reference for future research.

Table 14: The two main sampling methods used by Projet Lac to sample littoral habitats, gillnets and electrofishing, vary in when and how they sample, and the types of fish that they tend to catch in greater numbers.

		Gillnets	**Electrofishing**
Sampling details	**Period**	**Overnight**	**Daytime**
	Duration	Long: approx. 14 hours	Short: 5 – 10 minutes
	Method	Passive	Active
Fish selectivity	Mobility	More mobile	Less mobile
	Shape	Deeper-bodied	Non-selective
	Spines	Hard spines	Non-selective
	Size	Larger	Smaller
	Predatory behaviour	Active	Ambush
	Defence strategy	Flight	Hide

Hydroacoustics

Hydroacoustic surveys are useful to produce estimates of the fish biomass, abundance or size structure without being influenced by the catchability bias that affects gillnets and electrofishing. Hydroacoustic sampling has the additional advantage that it is non-destructive and does not interfere with the fish. Vertical hydroacoustic surveys are effective in open water, but are blind to fish in important habitats, including the littoral and benthic zones, as well as in the uppermost 1.5 m of the water column. This method also cannot provide reliable information on species identification.

Strengths and limitations of the Projet Lac approach

Aim of the Projet Lac sampling approach

The Projet Lac sampling approach aimed to provide standardised estimates of the fish community in all major habitats at the time of sampling (e.g. different littoral habitat types, different depths of benthic and pelagic zones). Fishing actions were distributed randomly within each habitat and the number of actions was determined with the aim of overcoming most of the sampling variation (within practical limitations), meaning that the estimate should not change substantially with further sampling of the habitat. The sampling protocols used in Projet Lac are designed such that the results are reproducible, meaning that differences in the results between surveys are assumed to be primarily due to changes in the fish community [192, 193, 203].

Overall, this approach provides a picture of the fish community according to the sampling methods at the time of sampling. The sampling methods have certain biases (see section 'Strengths and limitations of individual sampling methods') and the picture obtained by sampling is not exactly the same as the actual fish community. However, conducting the sampling according to the protocols and sampling all lakes around the same time of year provides standardised, and therefore repeatable and comparable information. An important caveat is that the effort invested into species identification and the identification skills of the survey teams must also remain consistent.

Sampling all major habitats is also important to reduce the chance of overlooking species or aggregations of individuals that only occur in certain habitats at that time of year. Scaling up to an average catch throughout the whole-lake using an appropriate statistical approach (see section 'Whole-lake catches') reduces the effect of the uneven distribution of sampling effort throughout the lake. Recording the amount of effort required to catch each fish is also particularly important to ensure the comparability of the data through time and between lakes.

Lake ecology in late summer – early autumn

The picture of the fish community provided by Projet Lac, particularly in terms of the distribution of fishes among habitats within a lake, is that of late summer and early autumn and is not representative of the spatial distribution and size structure in the lake at other times of the year. Fish move among habitats throughout the year, for example using particular littoral habitats for spawning in summer and moving deeper into the lake in winter as in warmwater-adapted cyprinids and perch, or vice versa for coldwater-adapted *Coregonus* spp Some species also move between lakes and rivers in different seasons. At the time of Projet Lac sampling, most species had finished spawning, with the exception of the coldwater salmonids that spawn mainly in winter. Surface water temperatures are generally warmest around July-September in most lakes. This is therefore the period when summer stratification is strongest and when oxygen depletion below the thermocline becomes severe. These factors influence the distribution of fish throughout the lakes. In order to ensure comparability to this first series of Projet Lac surveys, future monitoring should also be conducted in late summer – early autumn.

Length frequency distribution

The mesh sizes used in the two gillnet protocols influence the picture one obtains of the size distribution of fish within species and across all species within a lake. The geometric series of the CEN gillnet mesh is particularly suited to minimise the bias of net selectivity [200]. Net selectivity becomes weaker (i.e. the range of fish sizes frequently caught in a particular mesh becomes wider) with increasing mesh size, so the increment between successive meshes in the CEN protocol increases with the mesh size. The size of the panels of each mesh remains the same however (1.5 x 2.5 m), meaning that the number of mesh-holes in the panels, and thereby the maximum number of fish that can be caught in the panel, decreases with increasing mesh size. Saturation effects, whereby fish already caught in the net deter other fish from coming near the net, are also stronger in larger fish and large-mesh panels. As such, the resulting length-frequency distribution does not necessarily reflect that of the actual fish assemblage in the lake. Larger fish will tend to be under-represented compared to medium-small fish. Very small fish (< 4 cm total length) are also not effectively caught in gillnets and will be under-represented by this sampling method. Gillnetting is, however, the only method available to obtain estimates of fish sizes in all major habitats in a lake. Since the same mesh sizes and area of each mesh size was used in all lakes, the length frequency distributions are comparable across lakes and repeated sampling following the same gillnet protocols will mean that the results can be compared through time.

Random sampling

The decision to distribute the fishing actions at random within each habitat is based on the principles of statistical sampling. The main objective was to determine the average state of the fish community in a habitat. This approach provides numbers that can be compared among habitats as well as between lakes and also through time within a lake. It also allows scaling-up to a whole-lake picture of the fish community based on the average catches in each habitat and the availability of the habitat within the lake (see section 'Whole-lake catches').

The alternative option is using local knowledge of fishers and fisheries authorities to identify fishing locations. This can efficiently identify locations within a lake with the highest catches of a particular species, and can, in some cases, be used to locate rare or localised species. However, the level of local knowledge, and the sampling operators access to the knowledge, differs among lakes and habitats (e.g. littoral vs profundal habitats), and may change through time (e.g. with changing generations of fishers). Thus, the numbers obtained through this approach are not standardised nor objective, and therefore cannot be reliably used for lake fish monitoring or ecological research involving comparisons among lakes.

Absence of species

The presence of a species in a Projet Lac survey obviously indicates that the species is present in the lake. However, the absence of a species in the standardised catches does not necessarily mean that the species is not present in the lake. If a species is absent from Projet Lac catches, it could either mean that 1) the species was not present in the lake at the time of sampling, or 2) that the species was present in low numbers and/or only occurred in a few locations, or 3) the species was not efficiently sampled by the methods (e.g. *Anguilla anguilla* in gillnets), and was therefore overlooked by the sampling. There are multiple examples where species were not recorded by Projet Lac, but were recently observed by local authorities in the lake. The true absence of a species from a lake where it was previously recorded could be due to 1) local extirpation of the species, 2) a seasonal migration of the species between rivers and lakes, such that it was absent from the lake at the time of sampling, or 3) seasonal absence of adult life stages and presence only of juveniles that could not be retained in the nets at the time of sampling. In each lake-specific report, local knowledge was used to determine whether a species was likely still present in the lake or had been extirpated.

Habitat relationships

A further strength of the Projet Lac approach was the collection of habitat information regarding whether the fish was caught in open water, on the lake floor or in which type of littoral habitat. Spatial coordinates (latitude/longitude) and catch depth of each fish also provided the three-dimensional position of the fishes within the lake. This provides information on relationships between fish and their habitats, on how these relationships vary among and within species, as well as through time when results are compared with those of future sampling events. This information thereby allows spatially explicit identification of the ecological state of the habitats, and may reveal options for rectifying deficiencies.

Comparison to fisheries statistics

Fisheries catch statistics allow exploration of fish catch trends in a lake through time. Analyses of these data can reveal how fisheries catches change over years with changing environmental conditions. However, fisheries catch statistics represent only a small proportion of the fish species in a lake and do not accurately reflect changes in fish populations through time. Changes in fishing effort (e.g. number licences, number of net-nights), equipment technology (e.g. introduction of nylon nets or use of echosounders), market trends (and other incentives) and fisheries management regulations (e.g. changes in permitted mesh sizes) dramatically influence the link between fisheries catch statistics and trends in the actual fish populations. Fisheries catch statistics also offer little or no information on the spatial distribution or use of habitats by fish in a lake. For all of these reasons, standardized monitoring is required for evidence-based management of lake fish.

Table 15: Overview of Projet Lac sampling methods among lakes.

Catchment	Local name	Short english name	Country	Sampling year	CEN benthic	CEN pelagic	Electro-fishing	Vertical nets	Hydro-acoustics	Littoral map	Museum fish	Fish photos	DNA barcodes
Rhone	Lac d'Annecy	Annecy	FR	2010	✓	✓	—	—	✓	?	✓	✓	✓
Rhone	Lac de Bonlieu	Bonlieu	FR	2013	✓	✓	✓	✓	—	?	✓	some	—
Rhone	Lac de Bret	Bret	CH	2014	✓	✓	✓	✓	—	✓	✓	✓	✓
Rhone	Lac de Chalain	Chalain	FR	2011	✓	✓	✓	✓	?	✓	✓	✓	✓
Rhone	Lac de Remoray	Remoray	FR	2012	✓	✓	✓	✓	?	Degiorgi	✓	✓	✓
Rhone	Lac de Saint-Point	Saint-Point	FR	2012	✓	✓	✓	✓	?	Degiorgi	✓	✓	✓
Rhone	Lac du Bourget	Bourget	FR	2010	✓	✓	—	—	✓	?	✓	✓	✓
Rhone	Lac Léman	Geneva	CH FR	2012	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Bodensee Obersee	ConstanceObersee	CH DE AT	2014	✓	✓	✓	✓	✓	ISF	✓	✓	✓
Rhine	Bodensee Untersee	ConstanceUntersee	CH DE	2014	✓	✓	✓	✓	✓	ISF	✓	✓	✓
Rhine	Brienzersee	Brienz	CH	2011	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Hallwilersee	Hallwil	CH	2012	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Lac Brenet	Brenet	CH	2011	✓	✓	✓	✓	—	✓	✓	✓	✓
Rhine	Lac de Bienne / Bielersee	Biel	CH	2017	✓*	—	✓	✓*	—	—	✓	✓	some
Rhine	Lac de Joux	Joux	CH	2011	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Lac de Morat / Murtensee	Morat	CH	2010	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Lac de Neuchâtel	Neuchatel	CH	2011	✓	✓	✓	✓	✓	✓	✓	✓	?
Rhine	Sarnersee	Sarnen	CH	2017	✓ *	✓	✓	✓ *	—	✓	✓	✓	some
Rhine	Thunersee	Thun	CH	2013	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Vierwaldstättersee	Lucerne	CH	2014	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Walensee	Walen	CH	2012	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Zugersee	Zug	CH	2013	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Zürich Obersee	ZurichObersee	CH	2014	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rhine	Zürich Untersee	ZurichUntersee	CH	2014	✓	✓	✓	✓	✓	✓	✓	✓	✓
Po	Lago di Como (Lario)	Como	IT	2014	GRAIA	GRAIA	GRAIA	—	—	—	✓	some	some
Po	Lago di Garda (Benaco)	Garda	IT	2013	✓	✓	✓	✓	—	—	✓	✓	✓
Po	Lago di Lugano (Ceresio)	Lugano	CH IT	2011	✓	✓	✓	✓	✓	✓	✓	✓	✓
Po	Lago di Mezzola	Mezzola	IT	2013	GRAIA	GRAIA	GRAIA	—	—	—	✓	some	some
Po	Lago di Poschiavo	Poschiavo	CH	2012	✓	✓	✓	✓	✓	✓	✓	✓	✓
Po	Lago d'Idro (Eridio)	Idro	IT	2014	GRAIA	GRAIA	GRAIA	—	—	—	✓	some	some
Po	Lago d'Iseo (Sebino)	Iseo	IT	2014	GRAIA	GRAIA	GRAIA	—	—	—	✓	—	some
Po	Lago Maggiore (Verbano)	Maggiore	CH IT	2013	✓	✓	✓	✓	—	—	✓	✓	✓
Danube	Silsersee / Lej da Segl	Sils	CH	2012	✓	✓	✓	✓	✓	✓	✓	✓	✓

— Data not available.
Degiorgi Littoral habitat mapping conducted by François Degiorgi (Teleos / Université de Franche-Comté).
ISF Littoral habitat mapping conducted under contract to Institut für Seeforschung, Landesanstalt für Umwelt Baden-Württemberg (LUBW).
* Sampling conducted by AquaBios and Teleos.
GRAIA Fish sampling conducted by ecological consultancy GRAIA (Gestione e Ricerca Ambientale Ittica Acque srl) and CNR-ISE (Consiglio Nazionale delle Ricerche – Istituto per lo studio degli ecosistemi) under contract to Regione Lombardia.

Details of fish species diversity in perialpine lakes recorded by Projet Lac

Species diversity among lakes surveyed by Projet Lac

Table 16: Fish species recorded across all lakes surveyed in Projet Lac: ● species is native to the lake, 🟢 species is endemic to the lake, 🟠 species is non-native to the lake, 🟡 exotic species. Open circles reflect where a species was know to occur in the lakes from other Eawag studies. ■ records from the Swiss Fish Atlas [38] (Swiss lakes only).

Order	Family	Scientific name	Common name	Annecy	Bourget	Bret	Bonlieu	Chalain	Saint-Point	Remoray	Geneva	Rousses	Joux	Brenet	Neuchatel	Morat	Biel	Thun	Brienz	Zug	Lucerne	Sarnen	Hallwil	ZurichObersee	ZurichUntersee	Walen	ConstanceObersee	ConstanceUntersee	Garda	Idro	Iseo	Maggiore	Lugano	Varese	Como	Mezzola	Poschiavo	Sils	Projet Lac records	Total records
Cypriniformes	Cyprinidae	*Abramis brama*	Common bream		●	●					●				●	●	●	▪	▪	●	●	●	●	●	●	▪	●	●				▪							14	18
		Alburnoides bipunctatus	Spirlin					●			▪					▪	●		▪	▪	▪		●		▪		▪												3	10
		Alburnus alburnus	Common bleak			▪					●		▪		●	●	●	●	●	●	●	●	▪	●	●	●	●	●											14	17
		Alburnus arborella	Alborella																										●		●	●	●		●	●			6	6
		Barbus barbus	Common barbel								●				▪	●	●	●	▪	▪	●	●	●	●	▪	▪	▪	●											9	15
		Barbus plebejus	Padanian barbel																										●			●	▪						2	3
		Blicca bjoerkna	White bream		●	●					▪				●	●	●	▪		▪	▪	●	▪	▪	▪	▪	●	●											8	16
		Carassius gibelio	Prussian carp									🟠			🟧	🟠	🟧								🟧		🟠	🟠	🟠	🟠	🟠	🟠	🟠	🟠	🟠	🟠			12	15
		Carassius auratus	Goldfish			🟨					🟨				🟨										🟨			🟨	🟡										1	6
		Chondrostoma nasus	Common nase												▪	▪	▪	▪			▪	●			▪	▪	▪												1	9
		Chondrostoma soetta	Italian nase																													▪	▪			●			1	3
		Cyprinus carpio	Common carp			●					●	●	▪		●	●	▪	▪	▪	●	▪	▪	●	▪	●	▪	●	●	●	●	●	●	●		●				16	24
		Gobio gobio	Gudgeon	●	●	●					●				●	●	●	●	▪	●	●	●	●	●	●	●	●	▪				▪	▪						16	20
		Gobio obtusirostris	Blunt-snout gudgeon																								●												1	1
		Leuciscus leuciscus	Common dace				●	●			●	▪	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●											19	20
		Phoxinus septimaniae	Mediterranean minnow					●			○							🟠																			🟠	🟠	4	5
		Phoxinus csikii	Danube minnow								○	▪	▪	▪	●		▪	●	●		●				▪	●	▪	▪									🟠	●	7	15
		Phoxinus lumaireul	Italian minnow																										●										1	1
		Pseudorasbora parva	Stone moroko																										🟡										1	1
		Rhodeus amarus	Bitterling												●	●	●											▪	🟠	🟠	🟠	🟠				🟠			8	9
Cypriniformes	Cyprinidae	*Rutilus rutilus*	Common roach	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●				🟠	🟠	🟠	🟠	🟠			30	30
		Rutilus aula	Triotto																										●	●	●	●	▪		●	●			6	7
		Rutilus pigus	Pigo																													●	▪		●	●			3	4
		Scardinius erythrophthalmus	Common rudd	●	●	●	●	●	●	●	●	●		●	●	●	●	▪	▪	●	▪	●	●	▪	●	▪	●	●											19	24
		Scardinius hesperidicus	Southern rudd		🟠		🟠	🟠	🟠	🟠	🟠	🟠		🟠	🟠	🟠	🟠	🟠							🟠				●	●	●	●	●	●	●	●		🟠	22	22
		Squalius cephalus	European Chub	●	●	▪		●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●											22	23
		Squalius squalus	Italian chub																										●		●	●	●		●	●			6	6
		Telestes souffia	Riffle dace					●								▪	▪				▪						▪												1	5
		Telestes muticellus	Italian riffle dace																										●		●	●	●		●	●			6	6
		Tinca tinca	Tench	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	▪	●	●	●	●	●	●	▪	●	●		●	●	●	●	●	●	●			30	32
	Cobit.	*Cobitis bilineata*	Italian spined loach								🟧				🟠	🟠	🟠										🟧		●		●	●		●	●	●			9	11
		Sabanejewia larvata	Italian loach																													○				●			1	2
	Nemach.	*Barbatula quignardi*	Languedoc stone loach					●			●																												2	2
		Barbatula sp. "Lineage II"	Stone loach lineage II			▪					●													●			●	●											4	5
		Barbatula sp. "Lineage I"	Stone loach lineage I												●	●	●	▪	▪	●	●	▪	▪	●	●	●													8	12

Order	Family	Scientific name	Common name	Annecy	Bourget	Bret	Bonlieu	Chalain	Saint-Point	Remoray	Geneva	Rousses	Joux	Brenet	Neuchatel	Morat	Biel	Thun	Brienz	Zug	Lucerne	Sarnen	Hallwil	ZurichObersee	ZurichUntersee	Walen	ConstanceObersee	ConstanceUntersee	Garda	Idro	Iseo	Maggiore	Lugano	Varese	Como	Mezzola	Poschiavo	Sils	Projet Lac records	Total records
Salmoniformes	Coregonidae	*Coregonus lavaretus*	Lavaret		🟢																																		1	1
		Coregonus palaea	Palée						🟠	🟠	🟠				🟢	🟢	🟢																						6	6
		Coregonus candidus	Bondelle												🟢																								1	1
		Coregonus confusus	Pfärrit														🟢																						1	1
		Coregonus albellus	Brienzlig														🟠	🟢	🟢																				3	3
		Coregonus fatioi	Felchen															🟢	🟢																				2	2
		Coregonus alpinus	Balchen															🟢	🟢																				2	2
		Coregonus profundus	Kropfer															🟢																					1	1
		Coregonus acrinasus	Albock															🟠																					1	1
		Coregonus steinmanni	Steinmann's Balchen															🟢																					1	1
		Coregonus brienzii	Brienzer Balchen																🟢																				1	1
		Coregonus helveticus	Zugerbalchen / Lavarello																	🟢												🟠	🟠		🟠	🟠			5	5
		Coregonus muelleri	Albeli																		🟢																		1	1
		Coregonus intermundia	Schwebbalchen																		🟢																		1	1
		Coregonus suspensus	Pelagic Schwebbalchen																		○ (orange)																		0	1
		Coregonus nobilis	Edelfisch																		🟢																		1	1
		Coregonus litoralis	Bodenbalchen																		🟢	🟢																	2	2
		Coregonus sarnensis	Sarnerfelchen / Bondella																			🟢										🟠			🟠	🟠			4	4
		Coregonus suidteri	Suidter's Balchen																				🟢																1	1
		Coregonus zuerichensis	Schweber / Blaalig																					🟢	🟢	🟢													3	3
		Coregonus duplex	Grunder / Sandfelchen																					🟢	🟢	🟢													3	3
		Coregonus heglingus	Hägling / Albeli																					🟢	○ (green)	🟢													2	3
		Coregonus wartmanni	Blaufelchen																								🟢												1	1
		Coregonus arenicolus	Sandfelchen																								🟢	🟢											2	2
		Coregonus macrophthalmus	Gangfisch																								🟢	🟢											2	2
		Coregonus sp.	Whitefish	🟠			🟠	🟠				🟠	🟠	🟠															🟠		🟠								8	8
Salmoniformes	Salmonidae	*Salmo trutta*	Atlantic trout	🟠	🟠	▪ (orange)		🟠	🟠		⚫	▪	⚫	⚫	⚫	⚫	▪	⚫	⚫	⚫	⚫	⚫	⚫	▪	⚫	⚫	⚫	⚫	🟠	🟠	🟠	🟠	🟠		🟠	🟠	🟠	⚫	28	32
		Salmo carpio	Carpione del Garda																										🟢										1	1
		Salmo marmoratus	Marble trout																													⚫	⚫				⚫		3	3
		Salmo cenerinus	Northern Italian brook trout																																		⚫		1	1
		Salmo labrax	Danube trout																																		🟠	⚫	2	2
		Salmo sp. "Blackspot"	Poschiavo lake trout																																		⚫		1	1
		Salvelinus umbla	Lake char	⚫							⚫				○	▪	▪		⚫	⚫	⚫	🟠	▪	⚫	▪	⚫	⚫	▪			🟠	▪ (orange)	🟠		🟠	🟠	🟠	🟠	15	22
		Salvelinus sp. "Limnetic Thun/Brienz"	Orange-bellied char															🟢	○ (green)																				1	2
		Salvelinus sp. "Benthic Thun/Brienz"	Benthic char Thun / Brienz															○ (green)	○ (green)																				0	2
		Salvelinus sp. "Profundal-dwarf Thun"	Profundal dwarf char Thun															🟢																					1	1
		Salvelinus sp. "Profundal extreme Thun"	Profundal extreme char Thun															🟢																					1	1
		Salvelinus sp. "Giant Thun"	Giant piscivorous char Thun															○ (green)																					0	1
		Salvelinus sp. "Limnetic Lucerne"	Limnetic lake char																		🟢																		1	1
		Salvelinus sp. "Profundal-dwarf Lucerne"	Profundal dwarf char Lucerne																		🟢																		1	1
		Salvelinus sp. "Giant Lucerne"	Giant piscivorous char Lucerne																		○ (green)																		0	1
		Salvelinus sp. "Profundal Walen I"	Profundal char Walen I																							🟢													1	1
		Salvelinus sp. "Profundal Walen II"	Profundal char Walen II																							🟢													1	1
		Salvelinus profundus	Profundal char																								🟢												1	1
		Salvelinus namaycush	Canadian lake trout															▪ (yellow)	▪ (yellow)		▪ (yellow)				▪ (yellow)												🟡	🟡	2	6
		Oncorhynchus mykiss	Rainbow trout										▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)	▪ (yellow)		▪ (yellow)	▪ (yellow)	🟡	▪ (yellow)				🟡	▪ (yellow)			🟡			3	18
		Thymallus thymallus	European grayling								⚫	▪	⚫	▪	▪		▪	⚫	▪		▪	▪	▪	▪	▪	▪	▪	▪				▪						⚫	4	18

Order	Family	Scientific name	Common name	Annecy	Bourget	Bret	Bonlieu	Chalain	Saint-Point	Remoray	Geneva	Rousses	Joux	Brenet	Neuchatel	Morat	Biel	Thun	Brienz	Zug	Lucerne	Sarnen	Hallwil	ZurichObersee	ZurichUntersee	Walen	ConstanceObersee	ConstanceUntersee	Garda	Idro	Iseo	Maggiore	Lugano	Varese	Como	Mezzola	Poschiavo	Sils	Projet Lac records	Total records
Perciformes	Percidae	*Perca fluviatilis* "Yellow-orange form"	Alpine lake perch	●	●			●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			●	●	●						25	25
		Perca fluviatilis "Red form"	European river perch	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			33	33
		Gymnocephalus cernua	Eurasian ruffe		🟠						🟧					🟧				🟠	🟠	🟠	🟠	🟠	🟠		🟠	🟠				🟠							10	12
		Sander lucioperca	Pike-perch		🟠	🟠		🟠					🟧		🟠	🟠	🟠			🟧	🟠	🟠	🟠				🟠	🟠				🟠	🟠	🟠	🟠	🟠			16	18
	Blenn.	*Salaria fluviatilis* "French lineage"	Freshwater blenny	🟠							🟠																												2	2
		Salaria fluviatilis "Italian lineage"	Freshwater blenny																										●			●	●		●				4	4
	Centr.	*Lepomis gibbosus*	Pumpkinseed		🟡			🟡			🟨				🟡		🟡			🟡	🟨		🟡		🟡		🟡	🟡	🟡	🟡	🟡	🟡	🟡	🟡	🟡	🟡			17	19
		Micropterus salmoides	Largemouth bass / Blackbass								🟨				🟨	🟨	🟨												🟡	🟡	🟡	🟡	🟡	🟡					6	10
	Go.	*Padogobius bonelli*	Padanian goby																										●	●	●	●	●	●	●	●			8	8
Scorpaeniformes	Cottidae	*Cottus* sp. "Rhone lineage"	Rhone sculpin	●				●																															2	2
		Cottus gobio "Rhine lineage"	Rhine river sculpin								●																●	▪											2	3
		Cottus gobio "Aare lineage littoral"	Littoral lake sculpin												●		▪	●	●	▪	●	▪	▪	●	●	●													7	11
		Cottus gobio "Profundal Thun"	Profundal sculpin Thun															🟢																					1	1
		Cottus gobio "Profundal Lucerne"	Profundal sculpin Lucerne																		🟢																		1	1
		Cottus gobio "Profundal Walen"	Profundal sculpin Walen																							🟢													1	1
		Cottus gobio "Unknown lineage"	Sculpin														●					●	●																3	3
		Cottus sp. "Po lineage"	Po littoral / stream sculpin																													●	▪		●	●	●		4	5
		Cottus sp. "Profundal Po"	Profundal Po lake sculpin																										●			●							2	2
Esocif.	Esocid.	*Esox lucius*	Northern pike	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●				🟠	🟠						27	27
		Esox cisalpinus	Southern pike																										●	●	●	●	●	●	●	●			8	8
Gaster.	Gaster.	*Gasterosteus gymnurus*	Three-spined stickleback (naked)								🟠				○																	●							2	3
		Gasterosteus aculeatus	Three-spined stickleback (armoured)												○		🟠				🟠				○		🟠	🟠											4	6
Silurif.	Si.	*Silurus glanis*	Wels catfish								▪				●	●	●	▪							▪		●	●				🟠	🟧	🟠					7	11
	Ict.	*Ameiurus melas*	Black bullhead		🟡						🟡														🟨		🟨		🟡			🟡	🟨	🟡	🟡				6	9
Clupei.	Clupei.	*Alosa agone*	Agone																										●		●	●	●		●				5	5
		Alosa fallax	Twaite shad																													●							1	1
Cy.	Po.	*Gambusia holbrooki*	Mosquitofish																															🟡					1	1
Ga.	Lo.	*Lota lota*	Burbot	●	●						🟠		●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●			25	25
An.	An.	*Anguilla anguilla*	European eel								▪				▪	▪	▪	▪		▪	▪	▪	▪	▪	▪	▪	●	●		●	●	▪	●	●	●	●			8	21
Petrom.	Petrom.	*Lampetra planeri*	Brook lamprey												▪		●	▪			▪				▪		▪	▪											1	7
		Lampetra zanandreai	Lombardy lamprey																													▪	▪						0	2
		Lake total		14	18	10	8	18	10	8	25	10	11	12	26	23	28	27	16	19	27	22	20	20	21	20	31	25	26	14	22	36	24	15	26	26	10	8		

Museum collection

Table 17: List of preserved whole fish deposited in the Eawag collection at the Natural History Museum of Bern.

Order	Family	Scientific name	Annecy	Bourget	Bret	Chalain	Saint-Point	Remoray	Geneva	Joux	Brenet	Neuchatel	Morat	Thun	Brienz	Zug	Lucerne	Hallwil	ZurichObersee	ZurichUntersee	Walen	ConstanceObersee	ConstanceUntersee	Garda	Idro	Iseo	Maggiore	Lugano	Como	Mezzola	Poschiavo	Sils	Specimen total
Cypriniformes	Cyprinidae	*Abramis brama*		2	3				28			9	40					11	5	14		9	11										135
		Alburnoides bipunctatus				1												6															7
		Alburnus alburnus							55			22	42	15	44	31	34		8	27	33	24	9										344
		Alburnus arborella																						26		1	31	2	3	2			65
		Barbus barbus							10					11				3	4				1										29
		Barbus plebejus																						6			2						8
		Blicca bjoerkna		6	21							1	27									20	4										79
		Carassius gibelio											1									2		21	1		6	1					33
		Carassius auratus																						2									2
		Chondrostoma soetta																									2			2			4
		Cyprinus carpio							7			3	1			15		1		2		3	12	8	6			2					60
		Gobio gobio	7						59			31	1	31		14	3	27	6	27	8	4											218
		Gobio obtusirostris																				4											4
		Leuciscus leuciscus							24	24	15	4	9	30	24	29	6	18	10	8	29	29	5										264
		Phoxinus septimaniae				6																									1	2	9
		Phoxinus csikii										16		44			31				28										2	1	122
		Phoxinus lumaireul																						24									24
		Phoxinus sp.																													29	32	61
		Pseudorasbora parva																						23									23
		Rhodeus amarus										5												35	9		8						57
		Rutilus rutilus	36	33	20	29	30	32	92	74	48	390	46	31	214	31	29	29	5	32	29	23	7				34	66		1			1368
		Rutilus aula																						34	17		3			10			64
		Rutilus pigus																									2		10	13			25
		Rutilus sp.																										1					1
		Scardinius erythrophthalmus		12	22	17	22	24	18		35	18	124			21		20		12		9	21										383
		Scardinius hesperidicus				12	8	6	7		13		3	2						1				48	15		39	6		10		24	191
		Scardinius sp.											1																				1
Cypriniformes	Cyprinidae	*Squalius cephalus*	10	3		9	6		32	1	14	17	12	14	1	30	3	30	19	11	7	18	10										247
		Squalius squalus																						28		1	12	15	1	2			59
		Telestes souffia				6																											6
		Telestes muticellus																						45		1	11	19	8				84
		Tinca tinca	3	4	9	23	25	19	20	3	9	5	8	1		17	7	5	3	8		8	23				1	6					219
	Cobit.	*Cobitis bilineata*										9	1											1			2						13
		Sabanejewia larvata																												1			1
	Nemach.	*Barbatula quignardi*				2			1																								3
		Barbatula sp. "Lineage I"										26	2			4	3		18	10	3												64
		Barbatula sp. "Lineage I"							2										2			23	8										35
Salmoniformes	Coregonidae	*Coregonus lavaretus*		14																													14
		Coregonus palaea					30	31				19	19																				97
		Coregonus candidus										26																					26
		Coregonus albellus												78	379																		457
		Coregonus fatioi												20	84																		104
		Coregonus alpinus												3	7																		10
		Coregonus profundus												33																			33
		Coregonus acrinasus												23																			23
		Coregonus steinmanni												7																			7
		Coregonus brienzii													13																		13
		Coregonus helveticus																										5					5
		Coregonus muelleri															5																5
		Coregonus intermundia															2																2
		Coregonus sarnensis																									2						2
		Coregonus suidteri																31															31
		Coregonus zuerichensis																	1														1
		Coregonus duplex																	1	5	2												8
		Coregonus heglingus																	4														4
		Coregonus wartmanni																				3											3
		Coregonus arenicolus																					2										2
		Coregonus macrophthalmus																				1	3										4
		Coregonus sp.	19	10		29			43	34	39	133	42	4	12	13	32		6	12	54	20	6	41			44		5	6			604

Order	Family	Scientific name	Annecy	Bourget	Bret	Chalain	Saint-Point	Remoray	Geneva	Joux	Brenet	Neuchatel	Morat	Thun	Brienz	Zug	Lucerne	Hallwil	ZurichObersee	ZurichUntersee	Walen	ConstanceObersee	ConstanceUntersee	Garda	Idro	Iseo	Maggiore	Lugano	Como	Mezzola	Poschiavo	Sils	Specimen total
Salmoniformes	Salmonidae	*Salmo trutta*	1	1		1	8		30	4	1	5	3	26	5	14	17	17		5	29	6	4	11		3	5	10			316	29	551
		Salmo carpio																						1									1
		Salmo marmoratus																									1	2			3		6
		Salmo cenerinus																													1		1
		Salmo labrax																													3	1	4
		Salmo sp. "Blackspot"																													23		23
		Salmo sp.																													40		40
		Salvelinus umbla	8						3						1	4	39		1	2	9	14						1		1	99	30	228
		Salvelinus sp. "unassigned"												16																			228
		Salvelinus sp. "Limnetic Thun/Brienz"												4																			4
		Salvelinus sp. "Profundal-dwarf Thun"												9																			9
		Salvelinus sp. "Limnetic Lucerne"															1																1
		Salvelinus sp. "Profundal-dwarf Lucerne"															6																6
		Salvelinus sp. "Profundal Walen I"																			13												13
		Salvelinus sp. "Profundal Walen II"																			2												2
		Salvelinus profundus																				7											7
		Salvelinus namaycush																													2	28	30
		Oncorhynchus mykiss																				1					2						3
		Thymallus thymallus							11	2				5																		9	27
Perciformes	Percidae	*Perca fluviatilis* "red + yellow morph"	36	32	14	27	31	30	77	61	68	31	37	49	45	154	32	30	7	26	40	23	7	54	25	4	46	59	16				1062
		Gymnocephalus cernua		31												31	30	20	9	24		25	8				33						211
		Sander lucioperca		3	20	3						3	35				4	1				15	2				26	29					141
	Blen.	*Salaria fluviatilis* "French lineage"	3						13																								14
		Salaria fluviatilis "Italian lineage"																						59			53	15					127
	Centr.	*Lepomis gibbosus*		14		3						1				31		19		17		1	3	41			30	16					179
		Micropterus salmoides																						2			6	25					33
	Gc	*Padogobius bonelli*																						6		6	31	4					47
Scorpaeniformes	Cottidae	*Cottus* sp. "Rhone lineage"	1			1																											2
		Cottus gobio "Rhine lineage"							27													8											35
		Cottus gobio "Aare lineage littoral"										9		6	11		15		21	10	18												90
		Cottus gobio "Profundal Lucerne"															16																16
		Cottus gobio "Profundal Walen"																			12												12
		Cottus gobio "Unknown lineage"																6															6
		Cottus sp. "Po lineage"																									1			10	72		83
		Cottus sp. "Profundal Po"																						4			11						15
Esoc.	Esoc.	*Esox lucius*	10	20	2	24	12	15	24	7	3	37	6	4	2	5	11	6	3	9	11	17	12				3	3					252
		Esox cisalpinus																						2				3	1	1			7
Gast.	Gast.	*Gasterosteus gymnurus*							24																		1						25
		Gasterosteus aculeatus															2					23	7										32
Siluri.	Si.	*Silurus glanis*										2	4									1	3				11						21
	Ic.	*Ameiurus melas*		23					7															1			14						45
Clupeif.	Clupeid.	*Alosa agone*																						54			17	1	1				73
		Alosa fallax																									15						15
		Alosa sp.																									4						4
Ga.	Lo.	*Lota lota*	1	1					31		11	18		30	11	14	22	4	20	5	30	34	1	8	1		30	12					284
An.	A.	*Anguilla anguilla*																				6	1			5		1	1				14
Lake total			135	209	111	193	172	157	645	210	256	840	464	496	853	458	350	284	153	267	357	381	170	585	74	21	539	304	46	59	591	156	

Common names

Scientific name	Common name	German name	Italian name	French name
Abramis brama	Common bream	Brachsmen	abramide	Brême franche
Alburnoides bipunctatus	Spirlin	Schneider	alburno di fiume	Spirlin
Alburnus alburnus	Common bleak	Laube	alburna	
Alburnus arborella	Alborella	Alborella	alborella	Alborella
Alosa agone	Agone	Agone	agone	Agone
Alosa fallax	Twaite shad			
Ameiurus melas	Black bullhead	Katzenwels	pesce gatto	Poisson chat
Anguilla anguilla	European eel	Aal	anguilla	Anguille
Barbatula quignardi	Languedoc stone loach	Bartgrundel	cobite barbatello	Loche franche
Barbatula sp. "Lineage I"	Stone loach lineage I	Bartgrundel	cobite barbatello	Loche franche
Barbatula sp. "Lineage II"	Stone loach lineage II	Bartgrundel	cobite barbatello	Loche franche
Barbus barbus	Common barbel	Barbe	barbo	Barbeau commun
Barbus plebejus	Padanian barbel	Südliche Barbe	barbo	Barbeau italien
Blicca bjoerkna	White bream	Blicke	blicca	Brême bordelière
Carassius auratus	Goldfish	Goldfisch	carassio dorato	Carassin doré
Carassius gibelio	Prussian carp	Giebel	carpa di Prussia	Carpe prussienne
Chondrostoma nasus	Common nase	Nase		
Chondrostoma soetta	Italian nase	Savetta	savetta	
Cobitis bilineata	Italian spined loach	Südlicher Steinbeisser	cobite italiano	Cobite italiano
Coregonus acrinasus	Albock	Albock		
Coregonus albellus	Brienzlig	Brienzlig		
Coregonus alpinus	Balchen	Balchen		
Coregonus arenicolus	Sandfelchen	Sandfelchen		
Coregonus candidus	Bondelle	Bondelle		
Coregonus confusus	Pfärrit	Pfärrit		
Coregonus duplex	Grunder / Sand-felchen	Grunder / Sandfelchen		

Scientific name	Common name	German name	Italian name	French name
Coregonus fatioi	Felchen	Felchen	Felchen	
Coregonus heglingus	Hägling / Albeli	Hägling / Albeli		
Coregonus lavaretus	Lavaret	Lavaret	lavarello	Lavaret
Coregonus macrophthalmus	Gangfisch	Gangfisch	bondella	
Coregonus nobilis	Edelfisch	Edelfisch		
Coregonus palaea	Palée	Palée		Palée
Coregonus profundus	Kropfer	Kropfer		
Coregonus sp.	Whitefish	Felchen	coregone	
Coregonus litoralis	Bodenbalchen	Bodenbalchen		
Coregonus suspensus	Pelagic Schwebba-lchen	Pelagisches Schweb-balchen		
Coregonus sarnensis	Sarnerfelchen / Bon-della	Sarnerfelchen	bondella	
Coregonus intermundia	Schwebbalchen	Schwebbalchen		
Coregonus helveticus	Zugerbalchen / Lavarello	Zugerbalchen	lavarello	
Coregonus brienzii	Brienzer Balchen	Brienzer Balchen		
Coregonus steinmanni	Steinmann's Balchen	Steinmanns Balchen		
Coregonus suidteri	Suidter's Balchen	Balchen		
Coregonus wartmanni	Blaufelchen	Blaufelchen		
Coregonus zuerichensis	Schweber / Blaalig	Schweber / Blaalig		
Coregonus muelleri	Albeli	Albeli		
Cottus gobio "Aare lineage littoral"	Littoral lake sculpin	See-Groppe Aare		
Cottus gobio "Profundal Lucerne"	Profundal Lake Lu-cerne sculpin	Tiefsee-Groppe VWS		
Cottus gobio "Profundal Thun"	Profundal lake Thun sculpin	Tiefsee-Groppe Thun		
Cottus gobio "Profundal Walen"	Profundal Lake Walen sculpin	Tiefsee-Groppe Walen		

Scientific name	Common name	German name	Italian name	French name
Cottus gobio "Rhine lineage"	Rhine river sculpin	Groppe Rhein		
Cottus gobio "Unknown lineage"	Sculpin	Groppe		
Cottus sp. "Po lineage"	Po littoral / stream sculpin	Groppe Po		
Cottus sp. "Profundal Po"	Profundal Po lake sculpin	Tiefsee-Groppe Po		
Cottus sp. "Rhone lineage"	Rhone sculpin	Groppe Rhone		
Cyprinus carpio	Common carp	Karpfen	carpa	Carpe
Esox cisalpinus	Southern pike	Südlicher Hecht	luccio	
Esox lucius	Northern pike	Hecht	luccio	Brochet
Gambusia holbrooki	Mosquitofish	Silberkärpfling		
Gasterosteus aculeatus	Three-spined stickle-back (armoured)	Stichling	spinarello	
Gasterosteus gymnurus	Three-spined stickle-back (naked)	Stichling	spinarello	Epinoche
Gobio gobio	Gudgeon	Gründling	gobione	Goujon
Gobio obtusirostris	Blunt-snout gudgeon	Gründling		
Gymnocephalus cernua	Eurasian ruffe	Kaulbarsch	accerina	Grémille
Lampetra planeri	Brook lamprey	Bachneunauge		
Lepomis gibbosus	Pumpkinseed	Sonnenbarsch	persico Sole	Perche soleil
Leuciscus leuciscus	Common dace	Hasel	leucisco	Vandoise
Lota lota	Burbot	Trüsche	bottatrice	Lotte
Micropterus salmoides	Largemouth bass / Blackbass	Forellenbarsch	persico trota	Black bass à grande bouche
Oncorhynchus mykiss	Rainbow trout	Regenbogenforelle	trota iridea	Truite arc-en-ciel
Padogobius bonelli	Padanian goby	Padanische Grundel	ghiozzo padano	
Perca fluviatilis "Red form"	European river perch	Flussbarsch	persico	Perche
Perca fluviatilis "Yellow-orange form"	Alpine lake perch	Egli	persico	Perche
Phoxinus csikii	Danube minnow	Elritze	sanguinerola	Vairon

Scientific name	Common name	German name	Italian name	French name
Phoxinus lumaireul	Italian minnow	Südliches Elritze	sanguinerola italiana	Sanguinerola italiana
Phoxinus septimaniae	Mediterranean minnow	Elritze	sanguinerola	Vairon
Pseudorasbora parva	Stone moroko	Blaubandbärbling	pseudorasbora	Pseudorasbora
Rhodeus amarus	Bitterling	Bitterling	rodeo amaro	Bouvière
Rutilus aula	Triotto	Triotto	triotto	Triotto
Rutilus pigus	Pigo	Pigo	pigo	Pigo
Rutilus rutilus	Common roach	Rotauge	gardone	Gardon
Sabanejewia larvata	Italian loach	Italienischer Steinbeisser	Cobite mascherato	Loche italien
Salaria fluviatilis "French lineage"	Freshwater blenny	Cagnetta	cagnetta	Blennie
Salaria fluviatilis "Italian lineage"	Freshwater blenny	Cagnetta	cagnetta	Blennie
Salmo carpio	Carpione del Garda	Carpione	Carpione	Carpione
Salmo cenerinus	Northern Italian brook trout	Trota Fario	trota fario	
Salmo labrax	Danube trout	Donauforelle		
Salmo marmoratus	Marble trout	Marmorataforelle	trota marmorata	
Salmo sp. "Blackspot"	Poschiavo lake trout	Seeforelle Poschiavo		
Salmo trutta	Atlantic trout	Forelle	trotta	Truites
Salvelinus namaycush	Canadian lake trout	Kanadische Seeforelle	trota canadese	Truite des lacs canadiens
Salvelinus profundus	Profundal char	Tiefseesaibling		
Salvelinus sp. "Benthic Thun/Brienz"	Benthic char Thun / Brienz			
Salvelinus sp. "Giant Lucerne"	Giant piscivorous char Lucerne			
Salvelinus sp. "Giant Thun"	Giant piscivorous char Thun			
Salvelinus sp. "Limnetic Lucerne"	Limnetic lake char			
Salvelinus sp. "Limnetic Thun/Brienz"	Orange-bellied char			

Scientific name	Common name	German name	Italian name	French name
Salvelinus sp. "Profundal extreme *Thun*"	Profundal extreme char Thun			
Salvelinus sp. "Profundal Walen I"	Profundal char Walen I			
Salvelinus sp. "Profundal Walen II"	Profundal char Walen II			
Salvelinus sp. "Profundal-dwarf Lucerne"	Profundal dwarf char Lucerne			
Salvelinus sp. "Profundal-dwarf Thun"	Profundal dwarf char Thun			
Salvelinus umbla	Lake char	Seesaibling	salmerino	Omble chevalier
Sander lucioperca	Pike-perch	Zander	lucioperca/sandra	Sandre
Scardinius erythrophthalmus	Common rudd	Rotfeder	scardola	Rotengle
Scardinius hesperidicus	Southern rudd	Schwarzfeder	scardola Italiana	
Silurus glanis	Wels catfish	Wels	siluro	Silure glâne
Squalius cephalus	European Chub	Alet	cavedano	Chevaine
Squalius squalus	Italian chub	Südlicher Alet	cavedano	
Telestes muticellus	Italian riffle dace	Südlicher Strömer	strigone	
Telestes souffia	Riffle dace	Strömer		
Thymallus thymallus	European grayling	Äsche	temolo	Ombre de rivière
Tinca tinca	Tench	Schleie	tinca	Tanche

Taxonomy

Order	Family	Scientific name	Author, date
Cypriniformes	Cyprinidae	*Abramis brama*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Alburnoides bipunctatus*	Bloch, 1728
Cypriniformes	Cyprinidae	*Alburnus alburnus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Alburnus arborella*	De Filippi, 1844
Cypriniformes	Cyprinidae	*Barbus barbus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Barbus plebejus*	Bonaparte, 1839
Cypriniformes	Cyprinidae	*Blicca bjoerkna*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Carassius gibelio*	Bloch, 1782
Cypriniformes	Cyprinidae	*Carassius auratus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Chondrostoma nasus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Chondrostoma soetta*	Bonaparte, 1940
Cypriniformes	Cyprinidae	*Cyprinus carpio*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Gobio gobio*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Gobio obtusirostris*	Valenciennes, 1842
Cypriniformes	Cyprinidae	*Leuciscus leuciscus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Phoxinus septimaniae*	Kottelat, 2007
Cypriniformes	Cyprinidae	*Phoxinus csikii*	Hankó, 1922
Cypriniformes	Cyprinidae	*Phoxinus lumaireul*	Schinz, 1840
Cypriniformes	Cyprinidae	*Pseudorasbora parva*	Temminck & Schlegel, 1842
Cypriniformes	Cyprinidae	*Rhodeus amarus*	Bloch, 1782
Cypriniformes	Cyprinidae	*Rutilus rutilus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Rutilus aula*	Bonaparte, 1841
Cypriniformes	Cyprinidae	*Rutilus pigus*	Lac, 1804
Cypriniformes	Cyprinidae	*Scardinius erythrophthalmus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Scardinius hesperidicus*	Bonaparte, 1845
Cypriniformes	Cyprinidae	*Squalius cephalus*	Linnaeus, 1758
Cypriniformes	Cyprinidae	*Squalius squalus*	Bonaparte, 1837
Cypriniformes	Cyprinidae	*Telestes souffia*	Risso, 1827

Order	Family	Scientific name	Author, date
Cypriniformes	Cyprinidae	*Telestes muticellus*	Risso, 1826
Cypriniformes	Cyprinidae	*Tinca tinca*	Linnaeus, 1758
Cypriniformes	Cobitidae	*Cobitis bilineata*	Canestrini, 1866
Cypriniformes	Cobitidae	*Sabanejewia larvata*	De Filippi, 1859
Cypriniformes	Nemacheilidae	*Barbatula quignardi*	Băcescu-Meşter, 1967
Cypriniformes	Nemacheilidae	*Barbatula* sp. "Lineage II"	Undescribed
Cypriniformes	Nemacheilidae	*Barbatula* sp. "Lineage I"	Undescribed
Salmoniformes	Coregonidae	*Coregonus lavaretus*	Linnaeus, 1758
Salmoniformes	Coregonidae	*Coregonus palaea*	Cuvier, 1829
Salmoniformes	Coregonidae	*Coregonus candidus*	Goll, 1883
Salmoniformes	Coregonidae	*Coregonus confusus*	Fatio, 1885
Salmoniformes	Coregonidae	*Coregonus albellus*	Fatio, 1890
Salmoniformes	Coregonidae	*Coregonus fatioi*	Kottelat, 1997
Salmoniformes	Coregonidae	*Coregonus alpinus*	Fatio 1885
Salmoniformes	Coregonidae	*Coregonus profundus*	Selz et al., 2020
Salmoniformes	Coregonidae	*Coregonus acrinasus*	Selz et al., 2020
Salmoniformes	Coregonidae	*Coregonus steinmanni*	Selz et al., 2020
Salmoniformes	Coregonidae	*Coregonus brienzii*	Selz et al., 2020
Salmoniformes	Coregonidae	*Coregonus helveticus*	Selz & Seehausen, in press
Salmoniformes	Coregonidae	*Coregonus muelleri*	Nüsslin, 1882
Salmoniformes	Coregonidae	*Coregonus intermundia*	Selz & Seehausen, in press
Salmoniformes	Coregonidae	*Coregonus suspensus*	Selz & Seehausen, in press
Salmoniformes	Coregonidae	*Coregonus nobilis*	Haack, 1882
Salmoniformes	Coregonidae	*Coregonus litoralis*	Selz & Seehausen, in press
Salmoniformes	Coregonidae	*Coregonus sarnensis*	Selz & Seehausen, in press
Salmoniformes	Coregonidae	*Coregonus suidteri*	Fatio, 1885
Salmoniformes	Coregonidae	*Coregonus zuerichensis*	Nüsslin, 1882

Order	Family	Scientific name	Author, date
Salmoniformes	Coregonidae	*Coregonus duplex*	Fatio, 1890
Salmoniformes	Coregonidae	*Coregonus heglingus*	Schinz, 1822
Salmoniformes	Coregonidae	*Coregonus wartmanni*	Bloch, 1784
Salmoniformes	Coregonidae	*Coregonus arenicolus*	Kottelat, 1997
Salmoniformes	Coregonidae	*Coregonus macrophthalmus*	Nüsslin, 1882
Salmoniformes	Coregonidae	*Coregonus* sp.	unidentified species
Salmoniformes	Salmonidae	*Salmo trutta*	Linnaeus, 1758
Salmoniformes	Salmonidae	*Salmo carpio*	Linnaeus, 1758
Salmoniformes	Salmonidae	*Salmo marmoratus*	Cuvier, 1829
Salmoniformes	Salmonidae	*Salmo cenerinus*	Kottelat, 1997
Salmoniformes	Salmonidae	*Salmo labrax*	Pallas, 1814
Salmoniformes	Salmonidae	*Salmo* sp. "Blackspot"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus umbla*	Linnaeus, 1758
Salmoniformes	Salmonidae	*Salvelinus* sp. "Limnetic Thun / Brienz"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Benthic Thun / Brienz"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Profundal-dwarf Thun"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Profundal extreme Thun"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Giant Thun"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Limnetic Lucerne"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Profundal-dwarf Lucerne"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Giant Lucerne"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Profundal Walen I"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus* sp. "Profundal Walen II"	Undescribed
Salmoniformes	Salmonidae	*Salvelinus profundus*	Schillinger, 1901
Salmoniformes	Salmonidae	*Salvelinus namaycush*	Walbaum, 1792
Salmoniformes	Salmonidae	*Oncorhynchus mykiss*	Walbaum, 1792
Salmoniformes	Salmonidae	*Thymallus thymallus*	Linnaeus, 1758

Order	Family	Scientific name	Author, date
Perciformes	Percidae	*Perca fluviatilis* "Yellow-orange form"	Linnaeus, 1758
Perciformes	Percidae	*Perca fluviatilis* "Red form"	Linnaeus, 1758
Perciformes	Percidae	*Gymnocephalus cernua*	Linnaeus, 1758
Perciformes	Percidae	*Sander lucioperca*	Linnaeus, 1758
Perciformes	Blenniidae	*Salaria fluviatilis* "French lineage"	Asso, 1801
Perciformes	Blenniidae	*Salaria fluviatilis* "Italian lineage"	Asso, 1801
Perciformes	Centrarchidae	*Lepomis gibbosus*	Linnaeus, 1758
Perciformes	Centrarchidae	*Micropterus salmoides*	Lac, 1802
Perciformes	Gobiidae	*Padogobius bonelli*	Bonaparte, 1846
Scorpaeniformes	Cottidae	*Cottus* sp. "Rhone lineage"	Undescribed
Scorpaeniformes	Cottidae	*Cottus gobio* "Rhine lineage"	Linnaeus, 1758
Scorpaeniformes	Cottidae	*Cottus gobio* "Aare lineage littoral"	Undescribed
Scorpaeniformes	Cottidae	*Cottus gobio* "Profundal Thun"	Undescribed
Scorpaeniformes	Cottidae	*Cottus gobio* "Profundal Lucerne"	Undescribed
Scorpaeniformes	Cottidae	*Cottus gobio* "Profundal Walen"	Undescribed
Scorpaeniformes	Cottidae	*Cottus gobio* "Unknown lineage"	Unidentified
Scorpaeniformes	Cottidae	*Cottus* sp. "Po lineage"	Undescribed
Scorpaeniformes	Cottidae	*Cottus* sp. "Profundal Po"	Undescribed
Esociformes	Esocidae	*Esox lucius*	Linnaeus, 1758
Esociformes	Esocidae	*Esox cisalpinus*	Bianco & Delmastro, 2011
Gasterosteiformes	Gasterosteidae	*Gasterosteus gymnurus*	Cuvier, 1829
Gasterosteiformes	Gasterosteidae	*Gasterosteus aculeatus*	Linnaeus, 1758
Siluriformes	Siluridae	*Silurus glanis*	Linnaeus, 1758
Siluriformes	Ictaluridae	*Ameiurus melas*	Rafinesque, 1820
Clupeiformes	Clupeidae	*Alosa agone*	Scopoli, 1786
Clupeiformes	Clupeidae	*Alosa fallax*	Lacepède, 1803
Cyprinodontiformes	Poeciliidae	*Gambusia holbrooki*	Girard, 1859
Gadiformes	Lotidae	*Lota lota*	Linnaeus, 1758
Anguilliformes	Anguillidae	*Anguilla anguilla*	Linnaeus, 1758

Taxonomic richness

Table 18: Number of fish species by family and distribution type category. Some species count as native in some lakes and non-native in others. See also Figure 4.

Order	Family	Endemic	Native (excl. endemic)	Non-native (excl. exotic)	Exotic	Total
Anguilliformes	Anguillidae		1			**1**
Clupeiformes	Clupeidae		2			**2**
Cypriniformes	Cobitidae		2	1		**2**
	Cyprinidae		27	6	2	**30**
	Nemacheilidae		3			**3**
Cyprinodontiformes	Poeciliidae				1	**1**
Esociformes	Esocidae		2	1		**2**
Gadiformes	Lotidae		1			**1**
Gasterosteiformes	Gasterosteidae		1	2		**2**
Perciformes	Blenniidae		1	1		**2**
	Centrarchidae				2	**2**
	Gobiidae		1			**1**
	Percidae		2	2		**4**
Petromyzonti-formes	Petromyzontidae		1			**1**
Salmoniformes	Coregonidae	25	0	6		**26**
	Salmonidae	13	6	3	2	**21**
Scorpaeniformes	Cottidae	3	5			**9**
Siluriformes	Ictaluridae				1	**1**
	Siluridae		1	1		**1**
Total		**41**	**54**	**23**	**8**	**112**

Table 19: Congeneric species with geographically exclusive native ranges.
Cyprinid species native to river catchments on different sides of the Alps. Note that these are most often not sister species but only rather distantly related species

Genus	Native to Rhine/Rhone	Native to Po
Alburnus	*A. alburnus*	*A. arborella*
Barbus	*B. barbus*	*B. plebejus*
Chondrostoma	*C. nasus* (non-native in Rhone)	*C. soetta*
Phoxinus	*P. csikii, P. septimaniae*	*P. lumaireul*
Rutilus	*R. rutilus*	*R. pigus, R.aula*
Scardinius	*S. erythrophthalmus*	*S. hesperidicus*
Squalius	*S. cephalus*	*S. squalus*
Telestes	*T. souffia aggassizi / T. souffia souffia*	*T. muticellus*

Other (non-cyprinid) congeneric species native to river catchments on different sides of the Alps.

Genus	Native to Rhine/Rhone	Native to Po
Esox	*E. lucius*	*E. cisalpinus*
Salmo †	*S. trutta / S. rhodanensis*	*S. carpio, S. cenerinus, S. marmoratus*
Cottus	*Cottus gobio* "Rhine lineage", *Cottus gobio* "Aare littoral", *Cottus gobio* "Thun profundal", *Cottus gobio* "Lucerne profundal", *Cottus gobio* "Walen profundal" / *Cottus* sp. "Rhone lineage"	*Cottus* sp. "Po lineage", *Cottus* sp. "Po lineage profundal"

† Also *Salmo labrax* native to Danube river catchment.

Table 20: Non-native and exotic species.
Non-native salmonid species

Translocated within the region:	From where to where …
Coregonus palaea	Neuchatel to Geneva
Coregonus acrinasus (partial)	Constance to Thun (genetic contribution)
Coregonus sarnensis	Sarnen to Maggiore, Como, Mezzola (Bondella)
Coregonus helveticus	Zug to Maggiore, Lugano, Como, Mezzola (Lavarello)
Coregonus suspensus (partial)	Constance to Lucerne (genetic contribution)
Coregonus spp	Species and source lake undetermined. Many lakes e.g. Annecy, Chalain
Salmo trutta	North to south of Alps
Salmo labrax	Sils to Poschiavo
Salvelinus umbla species complex	Many lakes (e.g. Figure 51)

Translocated from North America:	To …
Salvelinus namaycush	Sils, Poschiavo
Oncorhynchus mykiss	Upper Constance, Maggiore, Mezzola

Non-native cyprinid species

Translocated within the region:	From where to where …
Carassius gibelio	Either central European lowlands or Asia to many lakes
Phoxinus csikii	North to south of Alps
Phoxinus septimaniae	North to south of Alps
Rhodeus amarus	North to south of Alps
Rutilus rutilus	North to south of Alps
Scardinius hesperidicus	South to north of Alps
Translocated from Asia:	**To …**
Carassius auratus	Garda (previously recorded in other lakes)
Pseudorasbora parva	Garda (previously recorded in other lakes)

Other non-native species

Translocated within the region:	From where to where …	Family
Gymnocephalus cernua	N & W of Switzerland to many lakes	Percidae
Sander lucioperca	N & E of Switzerland to many lakes	Percidae
Salaria fluviatilis "French lineage"	Southern Rhone to Annecy, Geneva	Blenniidae
Gasterosteus aculeatus	NE Europe to Constance	Gaster-osteidae
Gasterosteus gymnurus	Middle Rhone to Geneva	Gaster-osteidae
Silurus glanis	North to south of Alps	Siluridae
Translocated from North America:	**To …**	
Lepomis gibbosus	Many lakes	Centrarchidae
Micropterus salmoides	Southern perialpine lakes	Centrarchidae
Ameiurus melas	Many lakes in Rhone and Po catch-ments	Ictaluridae
Gambusia holbrooki	Varese	Poeciliidae

Figure 69 a): Species-abundance distributions (SADs) for each of 35 perialpine lakes and 1 lowland lake. **a)** The partial SADs obtained by sampling with the CEN netting protocol (lake plots in same order as in Fig. 6). **b)** The same but with the VERT netting protocol. **c)** The same but with the electrofishing protocol. Abundances are log2-transformed. Colours are the same as in Fig 6 and indicate drainage systems: green = Rhone, red = Rhine, orange = Po, blue = Danube. Lake Aulnes is a lowland lake in the southern Rhone drainage that we sampled but did not otherwise consider in this report.

b) + c) see following page.

Figure 69 b)

Figure 69 c)

Community composition in major habitats

Littoral zone

In the littoral zone, *Perca fluviatilis* was the most abundant fish in many lakes, particularly by gillnetting. Electrofishing catches in the littoral zone also contained many *Perca fluviatilis,* however they were less dominant as abundance and biomass were more evenly distributed among species within a lake according to this method compared to gillnetting (Figure 70). Community composition in the littoral zone by electrofishing also differed more strongly among the lakes compared to gillnet catches.

Some general patterns in littoral community composition by electrofishing were evident across the lakes. *Esox lucius* contributed a large portion of the littoral biomass in many of the Jura lakes (Chalain, St-Point, Remoray, Rousses, Joux), as well as in Bonlieu, Neuchatel, Upper Constance and Walen. *Leuciscus leuciscus* formed an important part of the littoral fish catches in Joux, Zug and Hallwil and *Lota lota* contributed a high proportion of the littoral biomass by electrofishing in Joux and Brenet, and many lakes on the northern edge of the Alps (Thun, Brienz, Zurich Upper, Walen). *Salaria fluviatilis* dominated littoral abundance in Garda, Maggiore and Lugano and *Phoxinus* spp were particularly abundant in Sils, Thun and Walen. Finally, Projet Lac recorded a particularly high biomass of *Tinca tinca* in, Neuchatel, Bret and Remoray (three large individuals contributed more than 30% of total biomass by electrofishing in the latter). Interestingly, the capture of 20 individuals of *Anguilla anguilla* caused this species to dominate the littoral biomass by electrofishing in Upper Constance.

Perca fluviatilis, Rutilus rutilus and *Scardinius* spp were very abundant in the littoral zone across the lakes according to catches in the shallow-set vertical nets (Figure 71). Indeed, these taxa formed almost all the fish caught in the littoral zone by gillnetting in all lakes of the Rhone catchment and Jura (Rousses, Joux, Brenet), as well as Neuchatel, Biel and Morat. In terms of biomass, large cyprinids (*Scardinius* spp, *Squalius cephalus, Rutilus rutilus* and *Tinca tinca*) dominated the littoral catches by gillnetting in these lakes. Ten *Cyprinus carpio*, seven of which weighed more than 5 kg each, made a strong contribution to the littoral biomass by gillnets in Lake Geneva. One large *Barbus barbus* (3 kg) also formed around 30% of the fish biomass caught by shallow-set vertical nets in Lower Constance and eight large *Barbus barbus* contributed almost 50% of the catch in Lake Thun. Interesting exceptions included a high abundance and biomass of *Leuciscus leuciscus* in Lake Walen and a high abundance of *Barbatula barbatula* in Lower Constance, which was caused by one action with 36 fish. Gillnet catches in the littoral zone of the alpine lakes Sils and Poschiavo were dominated by *Salmo* spp, with *Phoxinus* spp also abundant in Sils.

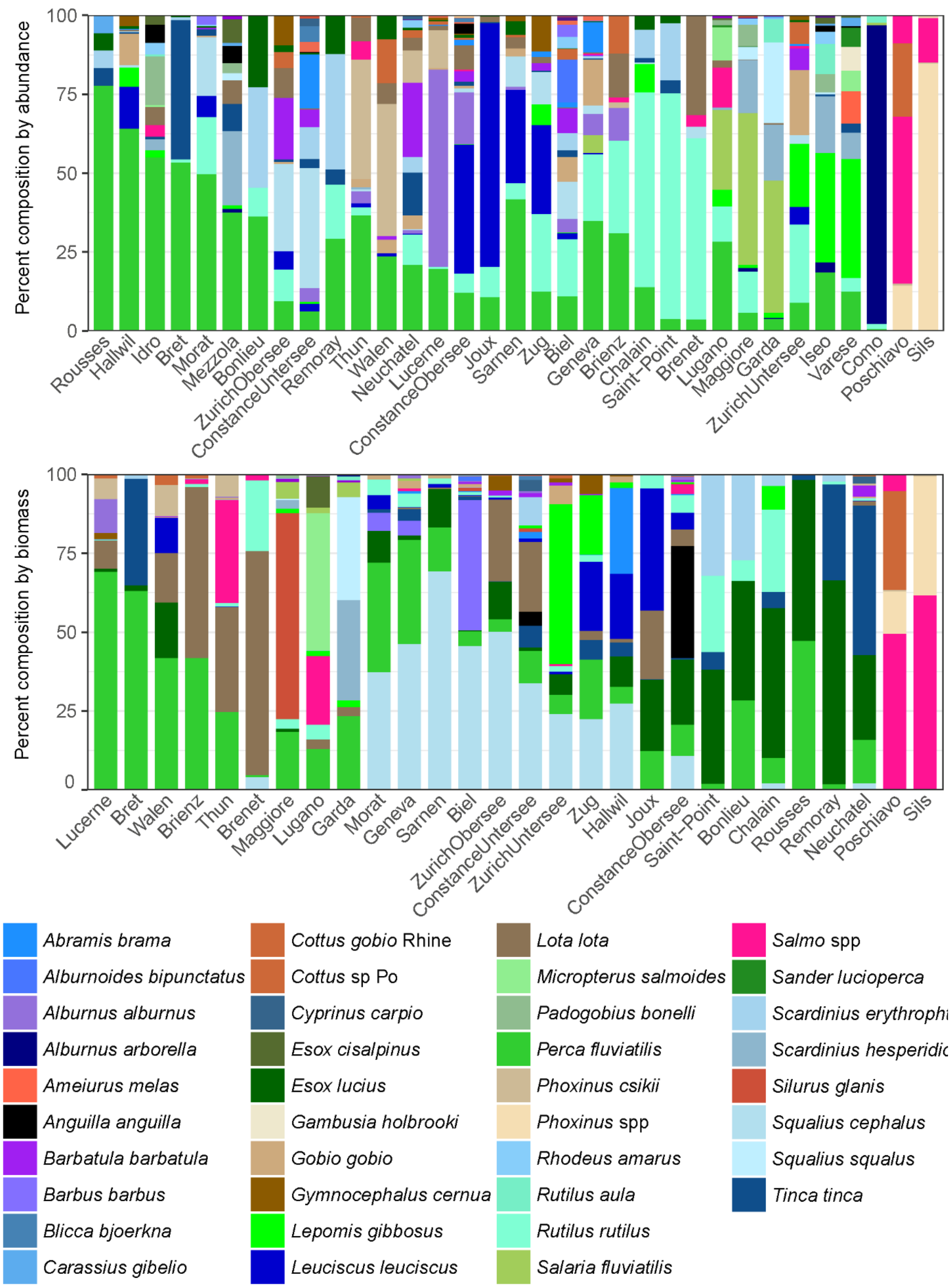


Figure 70: Composition of fish catches among lakes in the littoral zone by electrofishing (excluding streams and rivers). Note that the high relative biomass of *Esox lucius* in Rousses was caused by one large fish. The high biomass of *Tinca tinca* in Remoray was also caused by only three large individuals. Finally, the high abundance of *Alburnus alburnus* in Lucerne was caused by one action with 171 individuals.

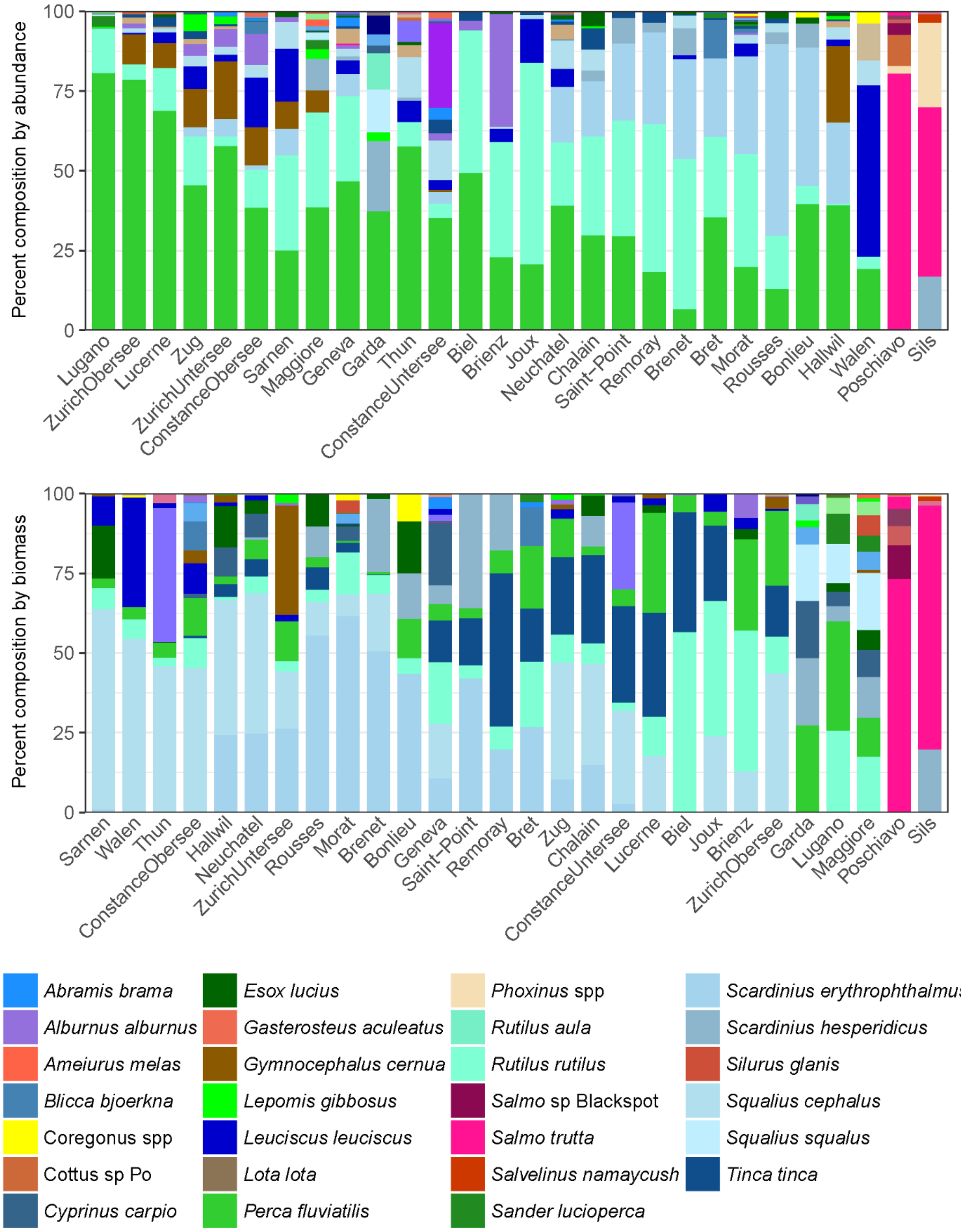


Figure 71: Species composition in the littoral zone by shallow-set vertical nets. Composition of fish catches among lakes in the littoral zone according to shallow-set (< 3 m) vertical gillnets (excluding streams and rivers). Note that the high abundance of *Barbatula barbatula* in Lower Constance was caused by one action with 36 fish. The high biomass of *Barbus barbus* in Thun and Lower Constance was caused by eight and one fish respectively. The high biomass of *Squalius cephalus* was also caused by one fish in Joux and three fish in Walen.

Benthic zone

Perca fluviatilis heavily dominated the abundance of fish in the benthic habitat according to CEN gillnets (Figure 72). The benthic biomass was dominated by *Perca fluviatilis* and *Rutilus* spp in almost all lakes according to this sampling method, with *Scardinius* spp also making strong contributions in many lakes. *Coregonus* spp was abundant and contributed a substantial amount of fish abundance and biomass in the benthic zone of Thun, Brienz and Walen. *Coregonus* spp also formed around 20% of the benthic biomass in the Jura lakes Chalain, Saint-Point and Remoray. The low relative abundance, yet high biomass reflects the particularly large average size of the whitefish in these lakes. In the alpine lakes Sils and Poschiavo, abundance and biomass of catches in the benthic CEN nets were heavily dominated by *Salmo* spp and *Salvelinus* spp, with many *Phoxinus* spp also caught in Sils.

Pelagic zone

Deep-set vertical nets and pelagic CEN nets provided a similar picture of fish community composition in the open water, pelagic habitat (Figure 73, Figure 74). *Coregonus* spp dominated the biomass in the pelagic habitat in most lakes, while abundance was mostly dominated by one of either *Coregonus* spp, *Rutilus rutilus* or *Perca fluviatilis*. *Coregonus* spp formed more than 90% of the number and weight of fish caught by both gillnetting methods in Thun, Brienz and Walen (75% of biomass in Walen in deep vertical nets; reduced by several large *Salmo trutta*). *Coregonus* spp were also the dominant species by abundance and biomass in Annecy and Chalain. *Coregonus* spp further dominated the pelagic biomass of Saint-Point, Remoray, Upper and Lower Constance, Upper and Lower Zurich, Lucerne and Neuchatel, however other species dominated the abundance in these lakes: *Rutilus rutilus* in Saint-Point, Remoray and Morat, *Perca fluviatilis* in Neuchatel and Lucerne (pelagic CEN only), and non-native *Gasterosteus aculeatus* in Upper and Lower Constance (although *G. aculeatus* was almost absent from deep vertical nets in Lower Constance; see taxonomic profile for *Gasterosteus* spp). *Rutilus rutilus* also dominated the abundance and biomass of fish caught in open water in Bret, Hallwil, Bonlieu, Brenet and Lugano. *Perca fluviatilis* dominated the pelagic fish communities of Zug, Bourget, Geneva, Joux and Como. Finally, *Alosa agone* dominated in Garda and Iseo, *Scardinius hesperidicus* in Mezzola, and non-native *Salvelinus umbla* and *Salmo trutta* in Sils and Poschiavo.

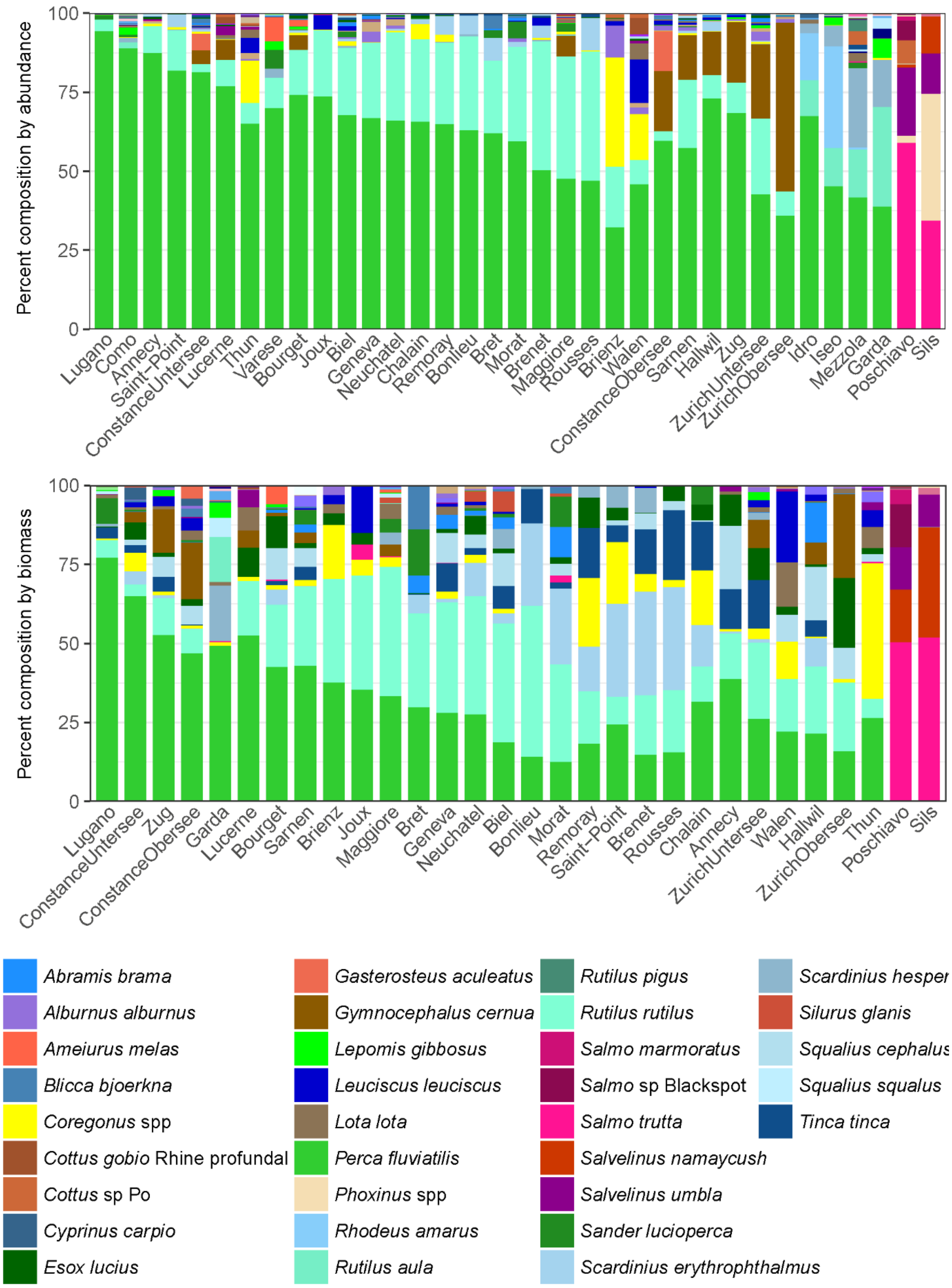


Figure 72: Composition of fish catches among lakes in benthic habitats according to benthic CEN gillnets.

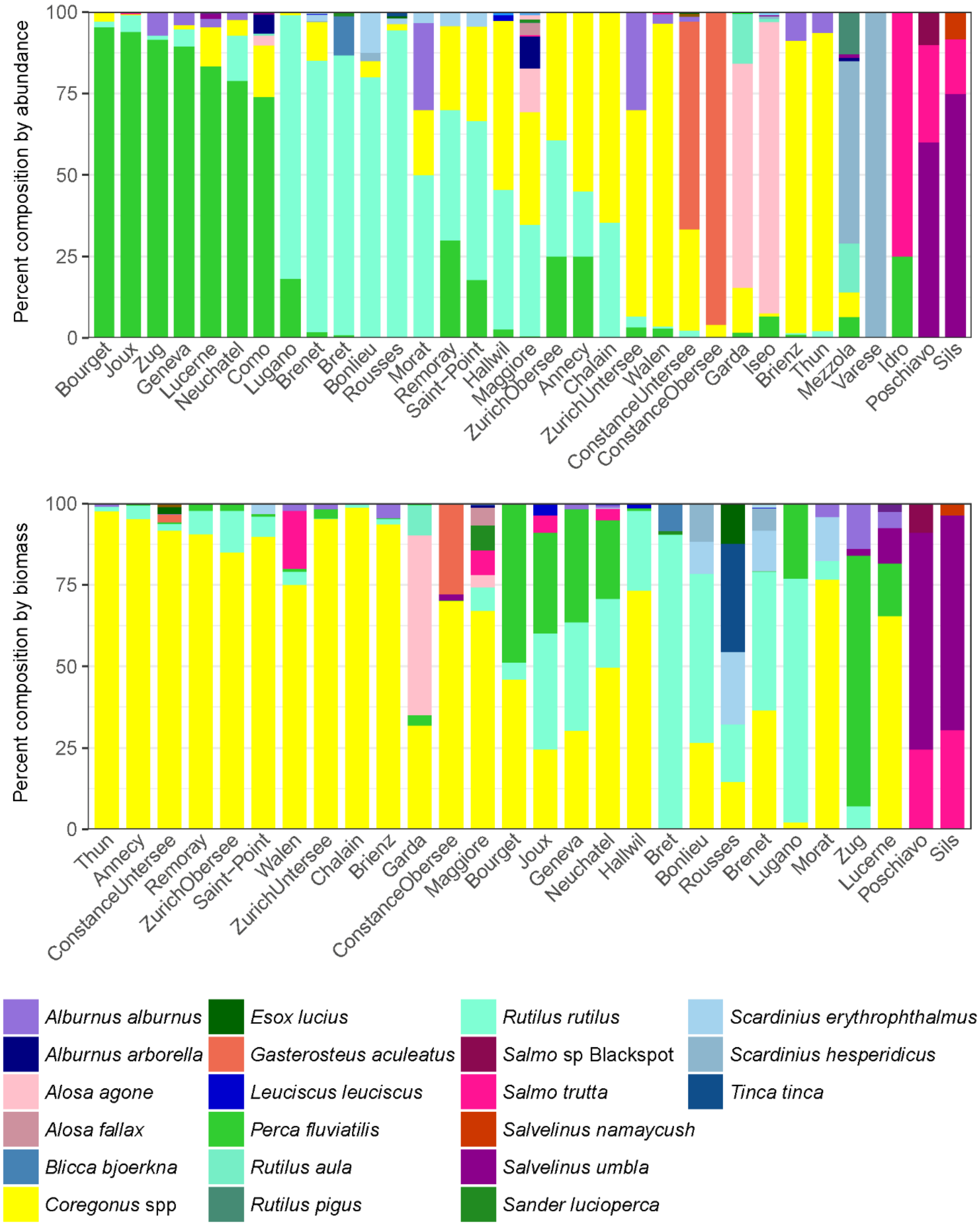


Figure 73: Composition of fish catches among lakes in open water, pelagic habitats (to 75 m deep) according to CEN pelagic gillnets. Note that only three and four fish were caught in pelagic CEN nets in Varese and Idro respectively.

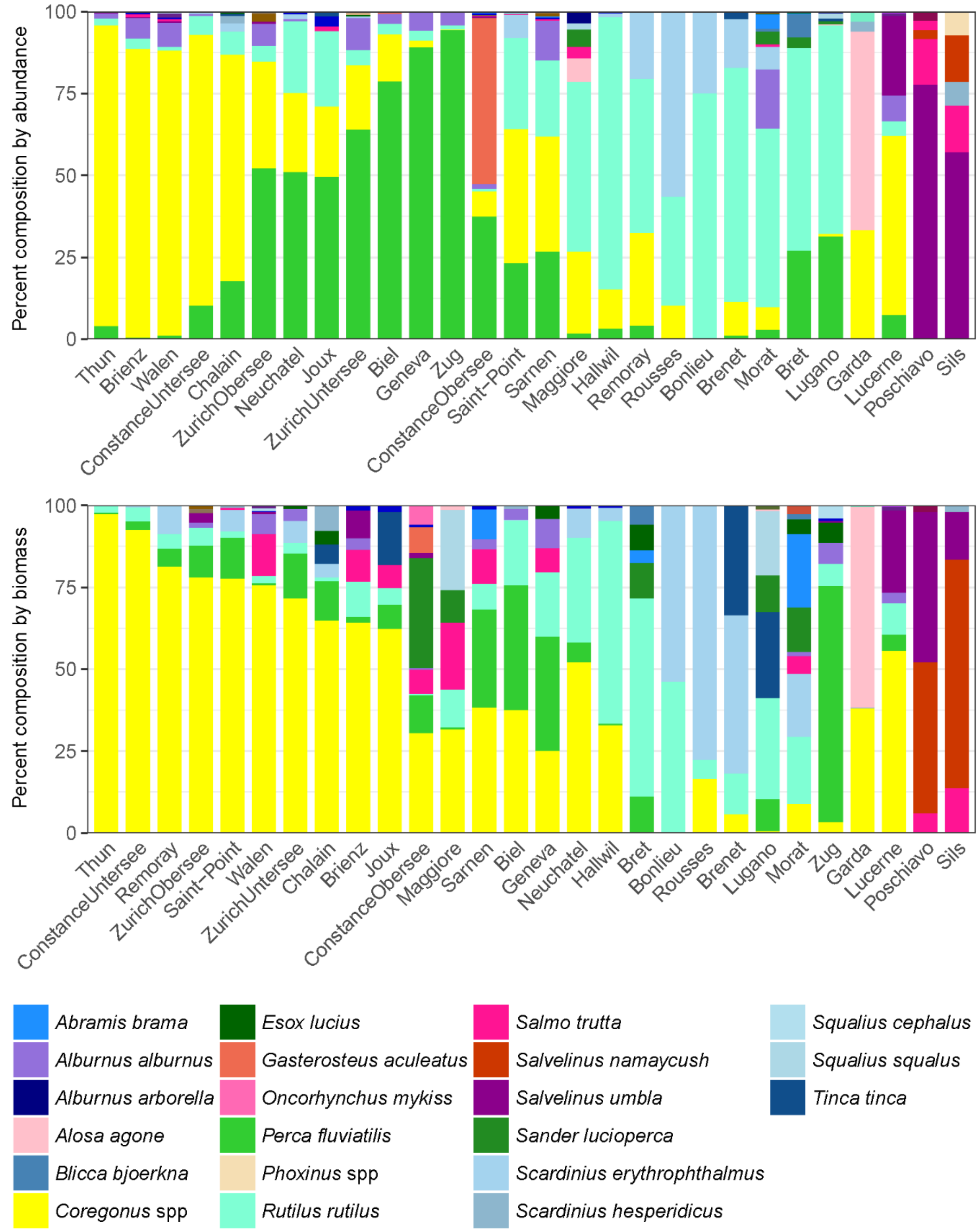


Figure 74: Composition of fish catches among lakes in open water, pelagic habitats according to deep-set (> 5 m) vertical gill-nets. Catches in the lowest 3 m of the nets were excluded to focus on fish caught in open-water. Note that the high relative biomass of *Sander lucioperca* in Upper Constance was caused by one 7.5 kg fish.

Non-native species composition by sampling method

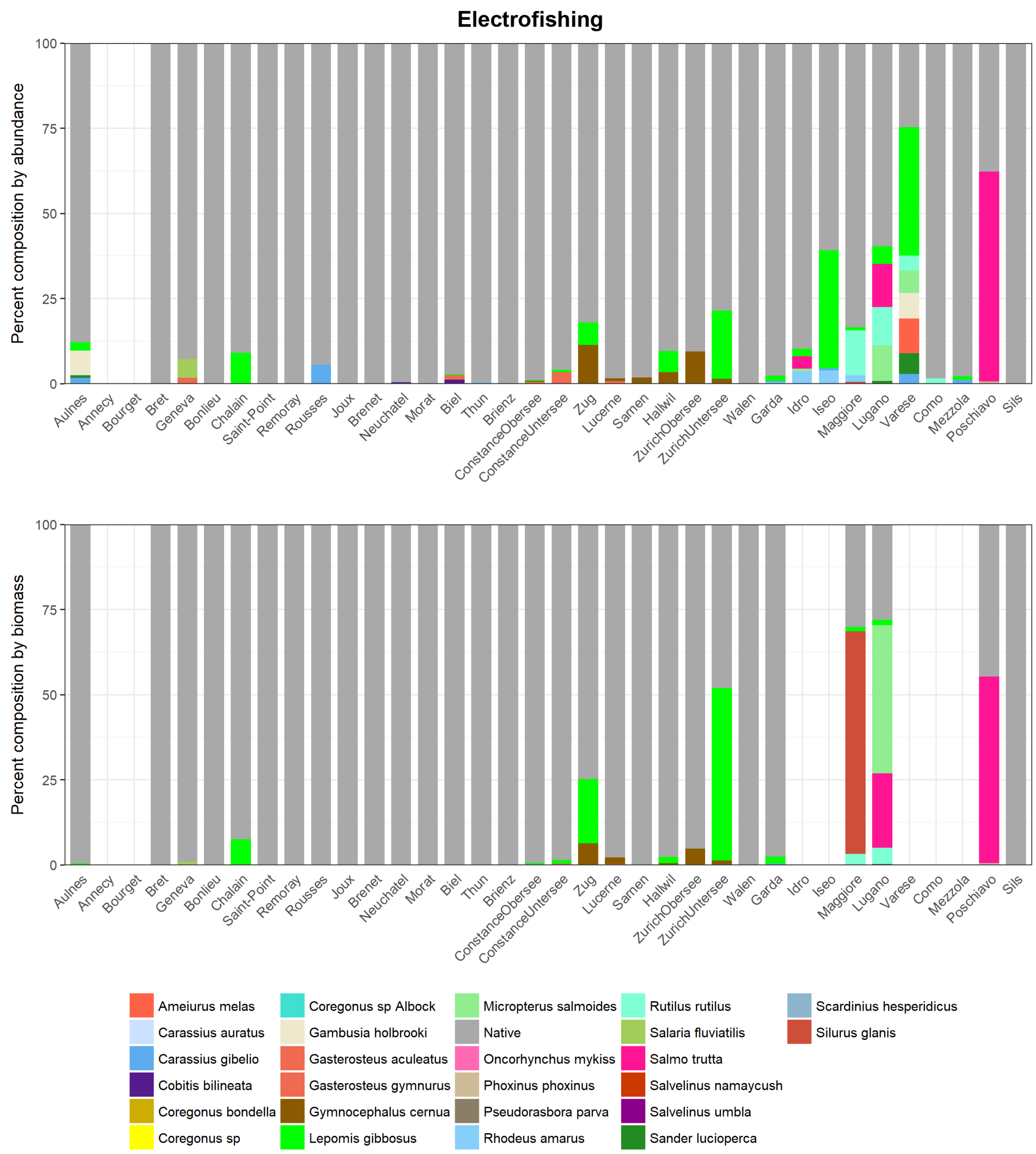


Figure 75: Proportion of non-native species in the littoral shown by electrofishing. Native species are represented in grey. Upper panel shows proportion by abundance, lower panel proportion by biomass. Note that the high relative abundance and biomass of *Salmo trutta* in Poschiavo is uncertain. These were mainly juvenile trout that could not be confidently identified to species and were assumed to be *S. trutta* for the purpose of this comparison.

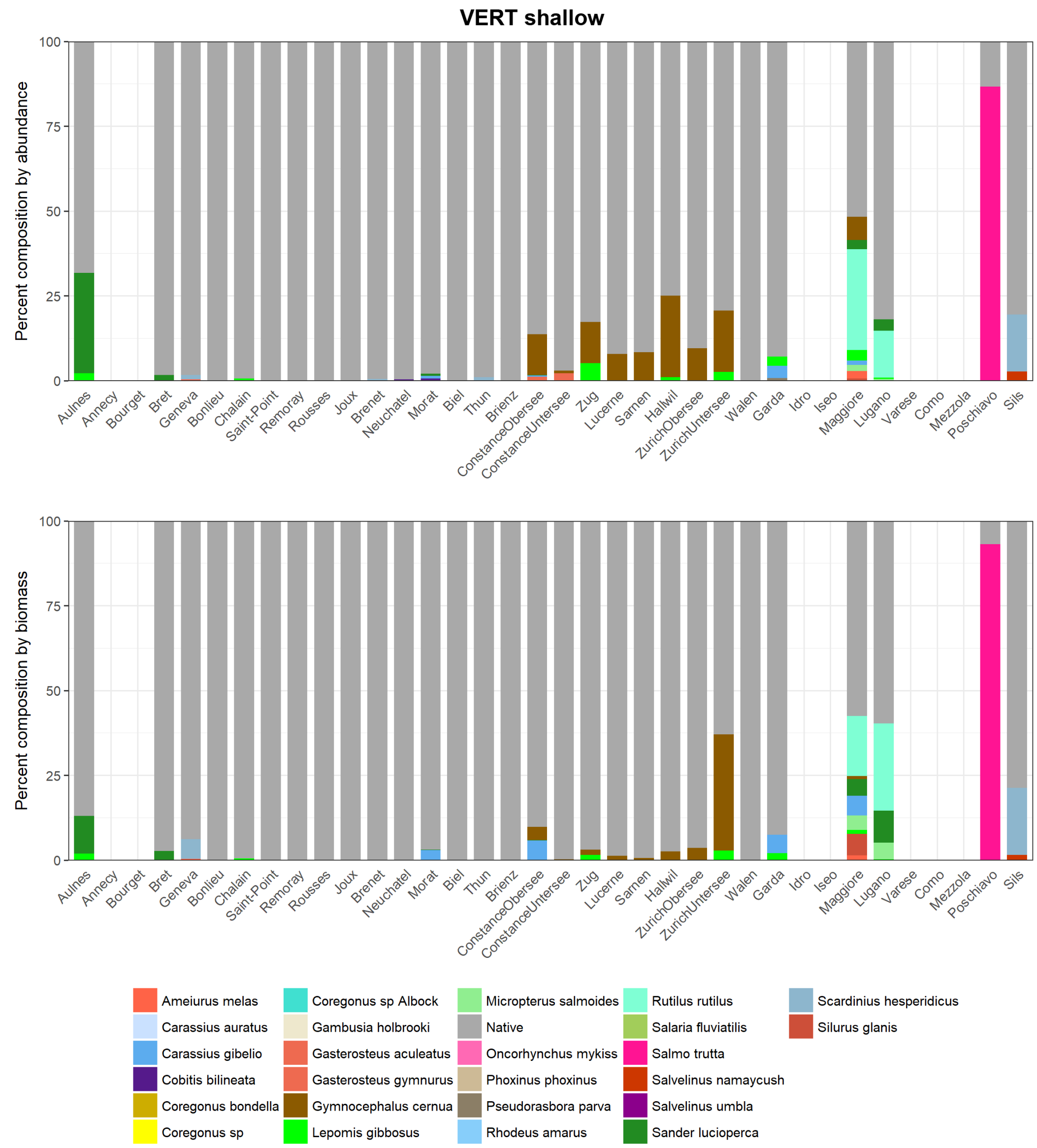


Figure 76: Proportion of non-native species in the littoral habitat shown by shallow-set vertical nets. Native species are represented in grey. Note that the very high relative abundance and biomass of *Salmo trutta* in Poschiavo is uncertain. These were mainly juvenile trout that could not be confidently identified to species and were assumed to be *S. trutta* for the purpose of this comparison.

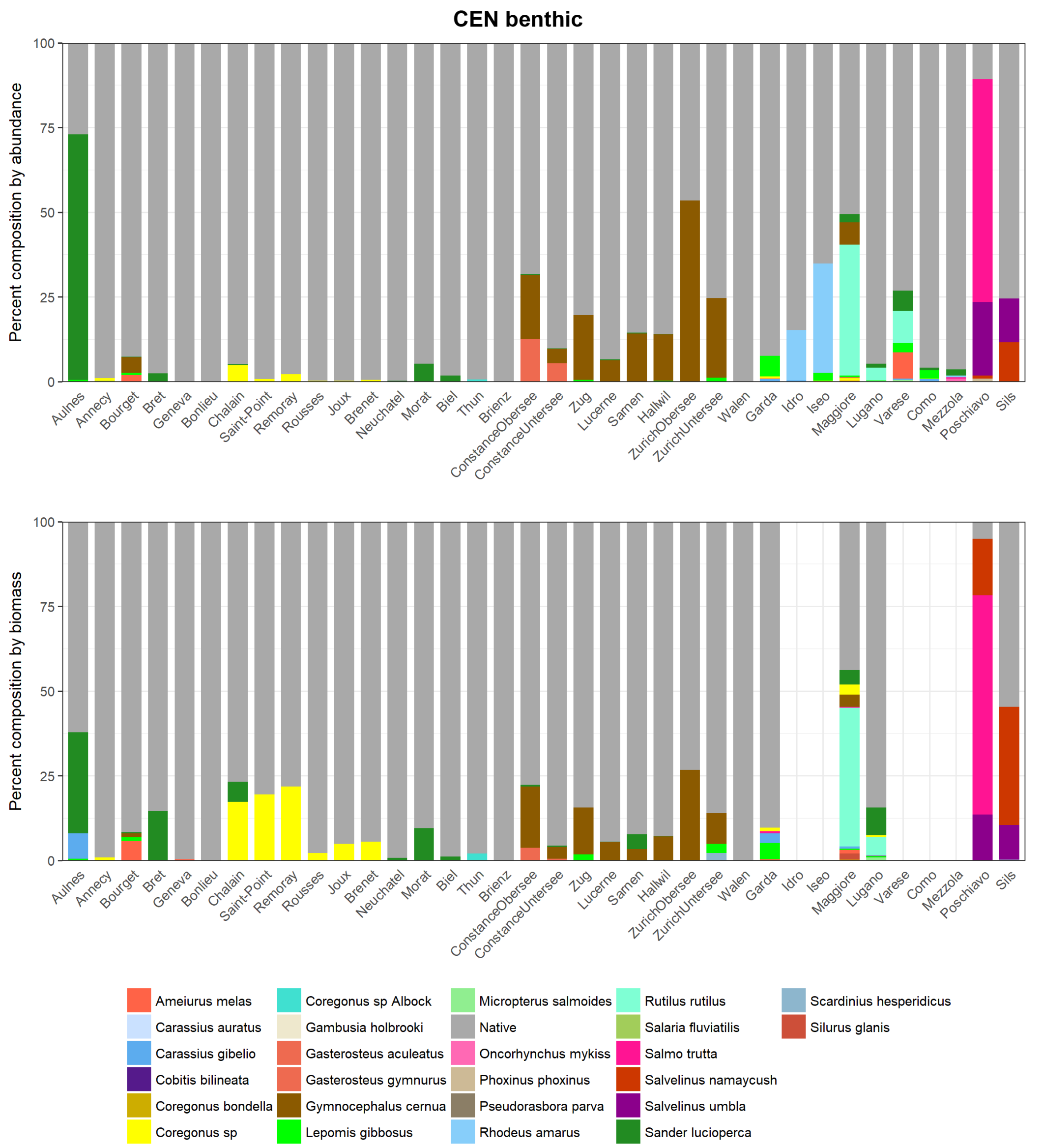


Figure 77: Proportion of non-native species in benthic habitats shown by benthic CEN nets among lakes. Native species are represented in grey. Upper panel shows proportion by abundance, lower panel proportion by biomass. Note that the high relative abundance and biomass of *Salmo trutta* in Poschiavo is uncertain. These were mainly juvenile trout that could not be confidently identified to species and were assumed to be *S. trutta* for the purpose of this comparison.

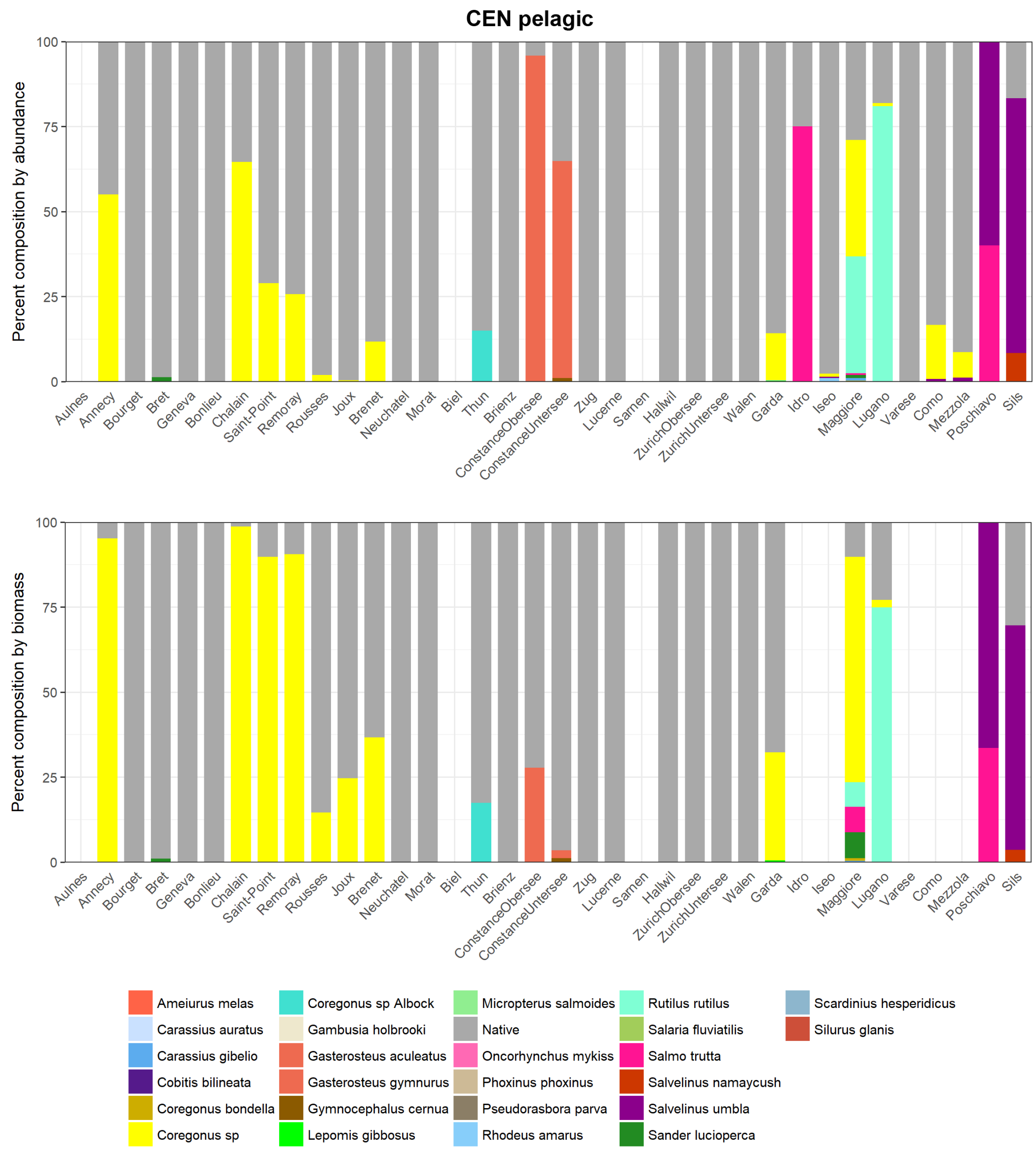


Figure 78: Proportion of non-native species in open-water habitat shown by pelagic CEN nets among lakes. Native species are represented in grey. Upper panel shows proportion by abundance, lower panel proportion by biomass. Note only four fish were caught in pelagic CEN nets in Idro (three of which were *Salmo trutta*). Note also that the high relative abundance and biomass of *Salmo trutta* in Poschiavo is uncertain. These were mainly juvenile trout that could not be confidently identified to species and were assumed to be *S. trutta* for the purpose of this comparison.

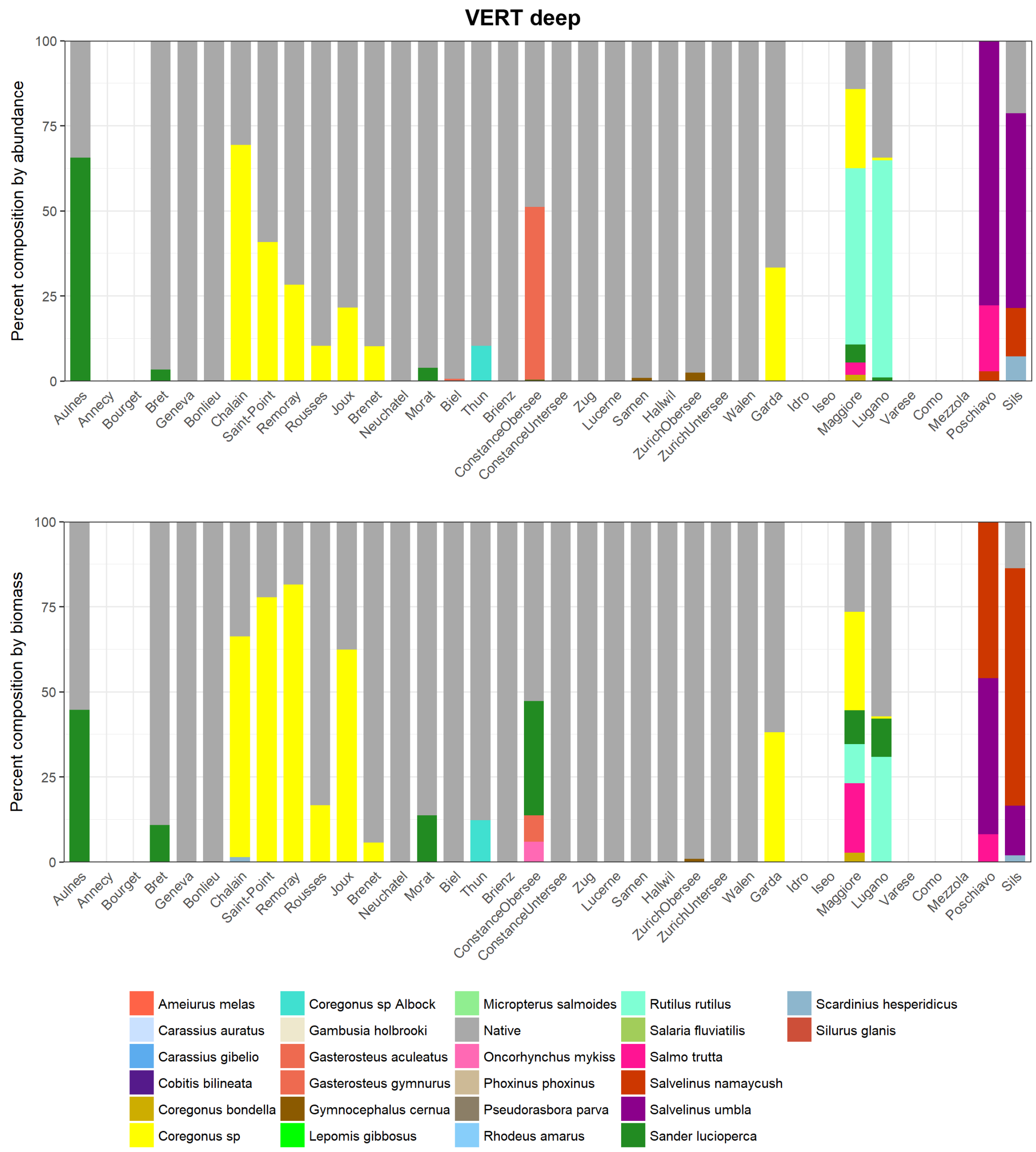


Figure 79: Proportion of non-native species by deep-set vertical nets among lakes. Native species are represented in grey. Upper panel shows proportion by abundance, lower panel proportion by biomass. The high relative biomass of this species in *Upper Upper* is one 7.5 kg fish.

Depth distribution of fishes by weight

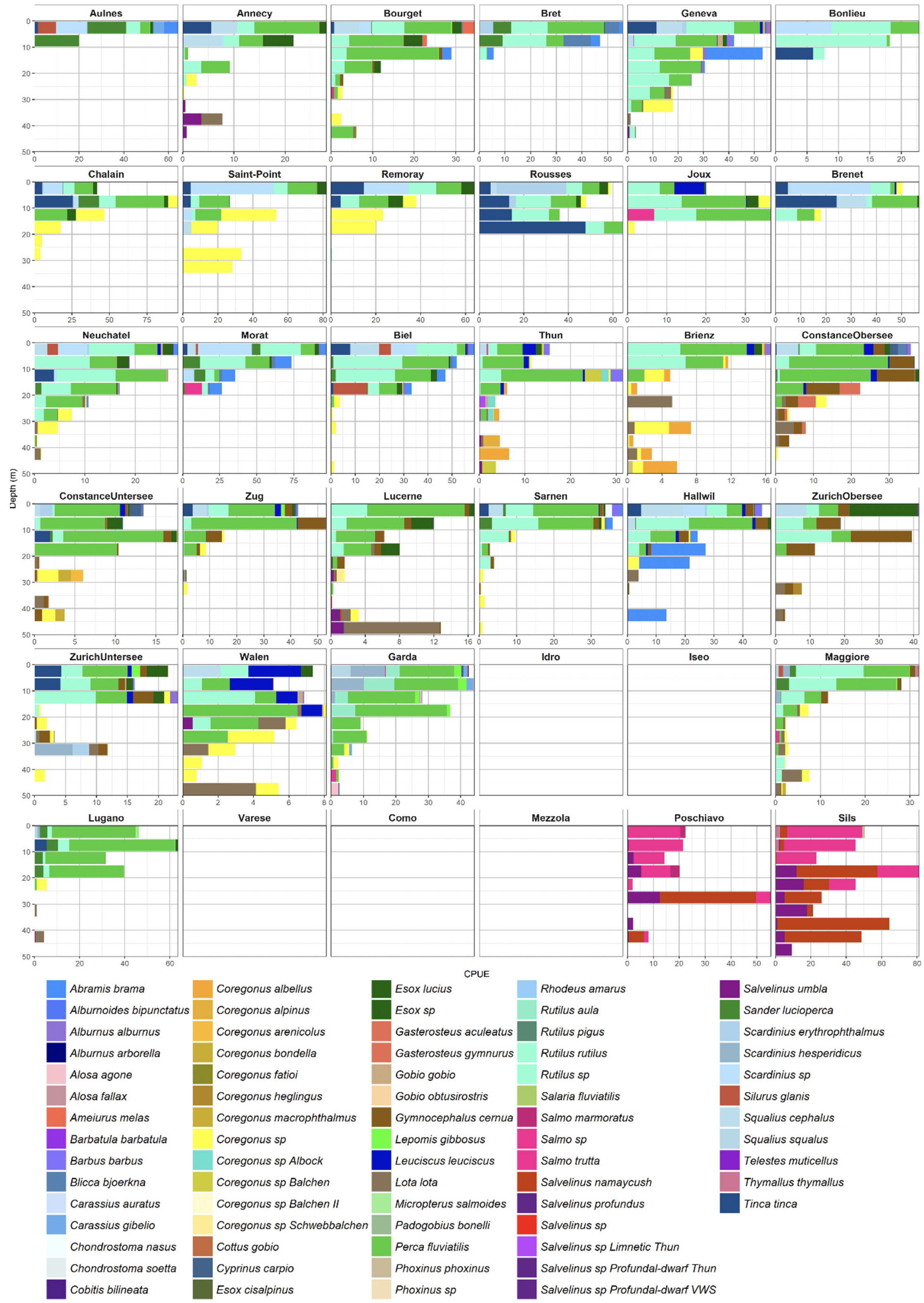


Figure 80: Depth distribution of fish weight (biomass per unit effort) in benthic habitats to 50 m deep according to CEN benthic nets.

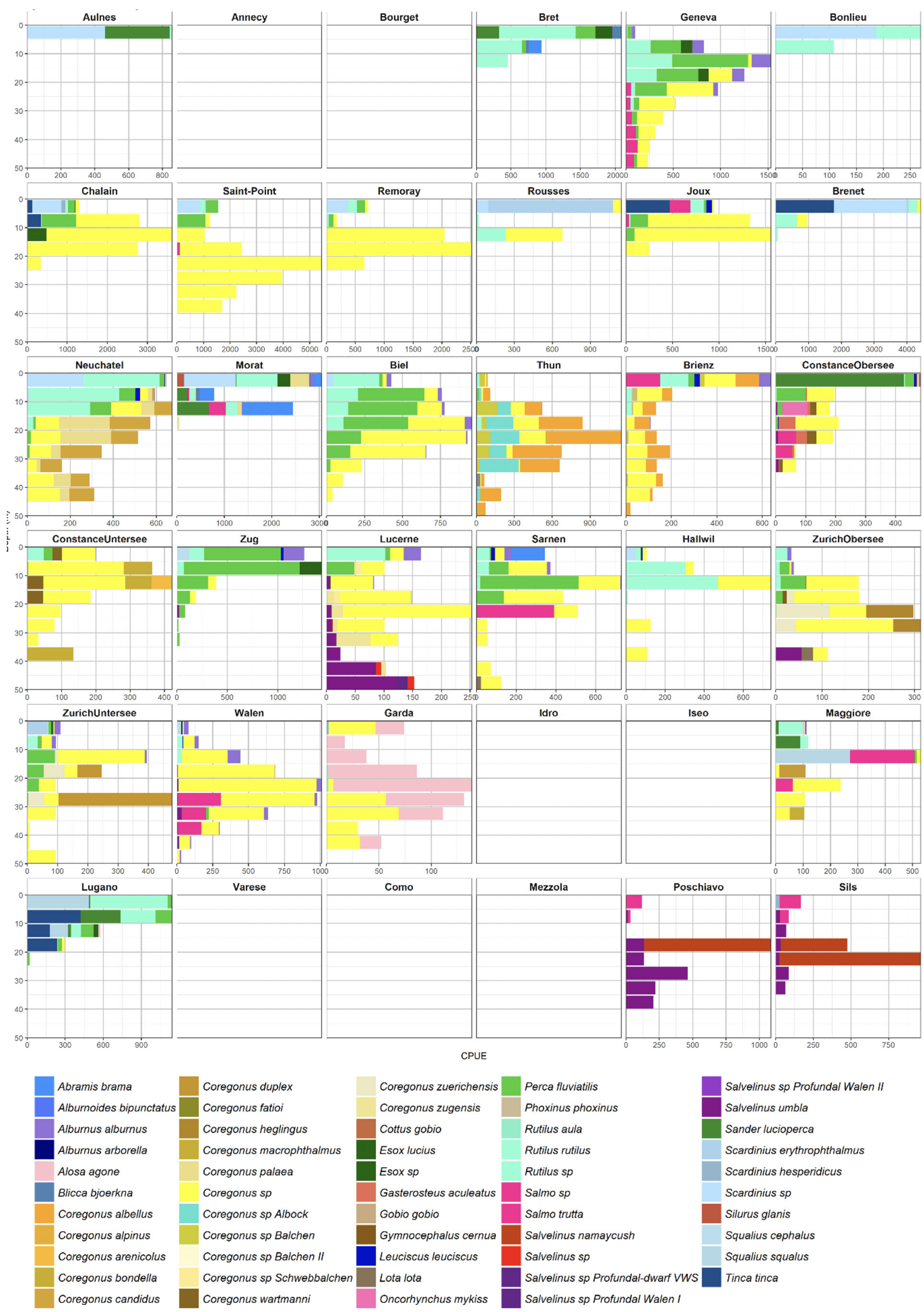


Figure 81: Depth distribution of fish weight (biomass per unit effort) in pelagic habitats to 50 m deep according to deep-set vertical nets (fish in the 3 m of net close to the lake floor were excluded).

Community composition explained

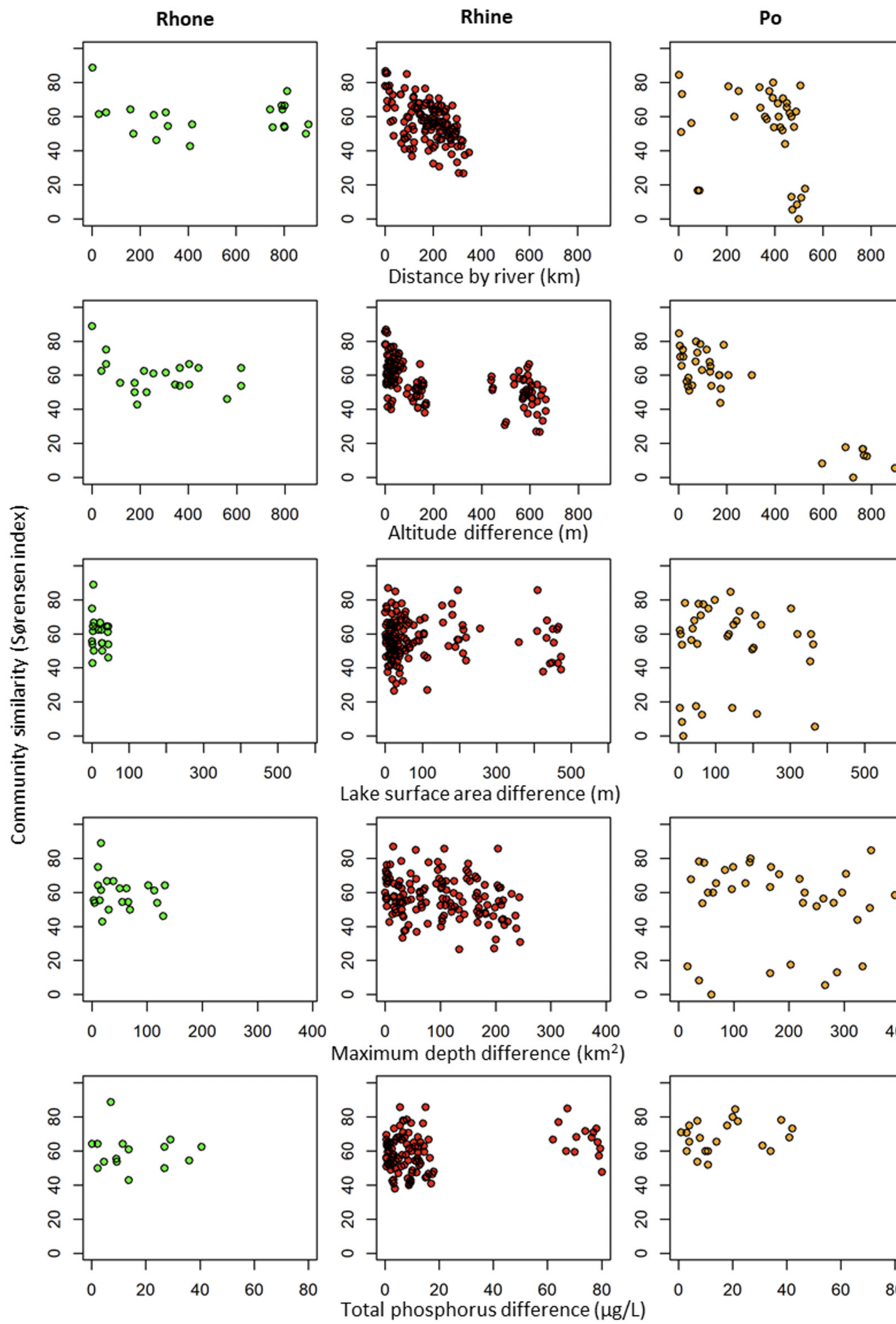


Figure 82: Factors explaining differences in the fish species composition among pairs of lakes within each catchment. No clear driver of fish community composition emerged in the Rhone catchment. In the Rhine catchment, the distance between the lakes along rivers, as well as differences in altitude, explained differences in the species composition between lakes. Altitude explained differences in fish species composition among lakes in the Po catchment (also when Poschiavo was excluded).

Uniqueness explained

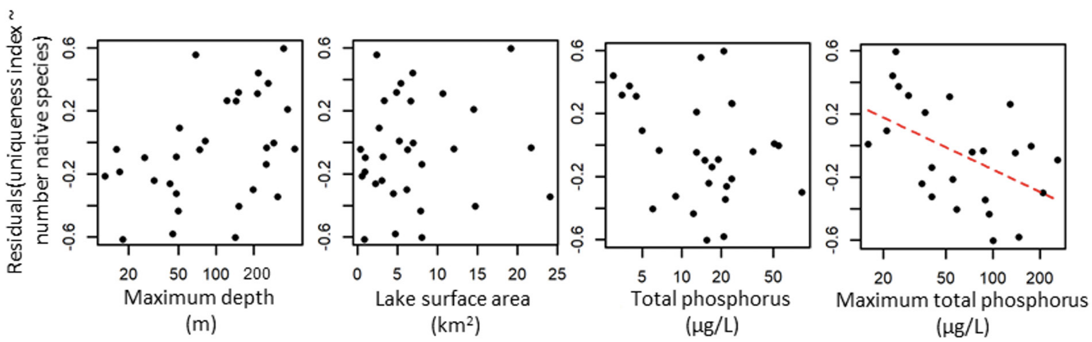


Figure 83: The uniqueness of the lake fish community relative to the number of recorded native fish species (shown in left panel of Figure 25) compared with different apects of the lakes. Only the relationship for maximum total phosphorus was significant ($R^2 = 0.248$, $p = 0.013$), and negative. Note that the horizontal axis of the plots of maximum depth, total phosphorus and maximum total phosphorus is displayed on a log scale. Lake surface area has been square-root transformed.

Perspectives on lake fish diversity

Key knowledge gaps

Ecology of the profundal zone and effects of climate change

In addition to the recommendations made above, several other important gaps in knowledge remain regarding the ecological state and functioning of perialpine lake fish communities. One of the most important is predicting the effects of climate change on lake fish and fisheries. Research to fill this gap should attempt to quantify the influence of known effects and predict their increase into the future, as well as attempting to identify and predict any hitherto unknown effects. Closely aligned with this is a need for improved understanding of the unique species and ecosystem processes of the deep, profundal zone of the perialpine lakes. This is the habitat that used to have the largest number of endemic fish species. It is also the habitat that was most strongly impacted by consequences of eutrophication, including species extinctions. It will be one of the habitats most strongly impacted by climate-induced, weaker vertical mixing, and forms a large proportion of surface area and volume of most large perialpine lakes. It would therefore be important to understand exactly what is living down there, the structure of the profundal food web, and which ecological drivers are most important, for example, dietary requirements and other key environmental requirements of the different species of fish and invertebrates. Projet Lac sampling provided an overview of the entire lake fish community and in the process, offered some insights into the unique diversity of the deep. This included the discovery of profundal forms of sculpin (*Cottus* spp) in several lakes, the rediscovery of the endemic profundal char *Salvelinus profundus* in Lake Constance and the documentation of other profundal forms of char (*Salvelinus* spp) in several other lakes. However, more targeted ecological and taxonomic research is required to properly understand this mysterious habitat and its inhabitants.

Habitat requirements of sublittoral and littoral fish species

Key knowledge deficiencies relate to the specific functions provided by different habitats for different fish species. This has been studied mostly just in the littoral zone and hardly studied at all in the sublittoral and profundal zones, yet even the littoral habitats are insufficiently understood. Largely unknown is the influence of structural complexity, particle size (i.e. silt, sand, gravel, cobbles, boulders, bedrock) and composition of the substrate (organic, mineral) on individual species and on interactions between species, and how this shapes local and regional species diversity and community composition. Such information is important to inform littoral and other habitat restoration efforts in support of biodiversity conservation, including spawning sites (e.g. salmonids) and, to some extent, management of fishery-relevant species. A further knowledge deficiency that specifically affects the littoral zone is the widespread and potentially important impact of regulation of lake water levels on littoral habitats and littoral communities of fish and macroinvertebrates, including species of fish that use the littoral only to spawn but otherwise live at greater depth or offshore. This group includes most of the large growing species of *Coregonus*.

Distinct lineages of closely related species colonized lakes and streams system

Population genetic and/or phylogenetic work conducted in the context of Projet Lac and Progetto Fiumi, on lake and stream populations of widespread taxa, has revealed that lake populations can be genetically distinct from one another, as is the case with roach [204]. In other taxa, perhaps more surprisingly, most lake populations, albeit being distinct, are more closely related to one another than they are to most stream populations, suggesting that lakes and streams were colonized by distinct lineages of even distinct species that were probably ecologically quite different. This is the case in the genus *Cottus* [41] and in *Barbatula* where different lineages occupy lakes and streams within the Aare catchment respectively. We have only just started to investigate genetic differentiation patterns at catchment scale with a few taxa. Our data and analyses on the species-area-relationship for perialpine lakes imply that lake fish communities are significantly isolated from other lake fish communities (see section 5). From this it follows that lake populations of a taxon may often not exchange genes freely with populations of the same taxon in adjacent streams. Assessing the extent of genetic distinctiveness of lake and stream populations or lineages for many more taxa will be an important task for the future in order to arrive at a more complete understanding of the biodiversity of fishes in the perialpine region.

Non-native species

In terms of non-native and exotic species, great uncertainty remains in how these taxa influence the native fauna. In particularly, the influence of invasive macroinvertebrates on fish species and on interactions among fish species could be profound in the many lakes where species such as zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*), Asian clam (*Corbicula fluminea*) and killer shrimp (*Dikerogammarus villosus*) are hyperabundant. However, their exact effects on fish species and communities are largely unknown. Particularly important would be to understand the factors that cause non-native species to become very abundant and problematic for native species and ecosystem services, as may be the case with *Gasterosteus aculeatus* in Lake Constance. These are, however, no easy questions to answer, and investigations need to be embedded in the wider context of community ecology, evolutionary ecology and invasion biology to achieve true progress in understanding. It is often uncertain, what (or whether much) can be done to control the non-native species once they are established in a lake.

Effects of stocking

A further important deficiency in knowledge of perialpine lake fish is the contribution of stocking for fisheries enhancement and its consequences for wild fish populations and native fish diversity. Experiments to quantify the contribution of stocked larvae to fisheries catches provide part of the information, but they do not show the extent to which the stocked larvae replace those from natural reproduction. Artificially increasing population density can also increase resource competition, potentially slowing growth rates of wild and stocked fish alike. Experimentally discontinuing stocking, while monitoring the fish population and fisheries yields can provide useful information in this regard. In addition to the uncertainty around the effectiveness of stocking for enhancing fisheries yields, the effects of artificial breeding and raising the young under unnatural conditions, very possibly resulting in selection for traits that are beneficial under hatchery conditions, is unlikely to be beneficial for the long-term sustainability of wild populations. While several scientists have emphasised the potential importance of these problems, e.g. [126, 128], there has been few attempts to quantitatively assess their impacts in the fish communities of perialpine lakes.

Ongoing monitoring

Finally, although all large lakes across the region were sampled in Projet Lac as well as several medium sized and a few small lakes, and streams and rivers were sampled by Progetto Fiumi, the fish communities of some medium-sized and many smaller lakes and ponds have not yet been systematically assessed. Sampling of these systems would complete the picture of fish assemblages across the region and would significantly add to a valuable reference state for future comparisons. Lakes Lauerz, Alpnach, Sempach, and Aegeri were sampled in September 2018 but fish were not identified to species level in those genera that contain closely related species, such as *Scardinius, Coregonus* and *Salvelinus* and no reference material was preserved of any species. Remaining natural lakes not yet sampled at the time of writing this report include lakes Greifen, Baldegg, Silvaplana and Pfäffiker, among many other smaller lakes. Several fish species that are known and/or expected in Switzerland, but were completely missing from Projet Lac and Progetto Fiumi might be ecologically confined to such smaller lakes or ponds. These could include *Carassius carassius, Leucaspius delineates* and perhaps also *Misgurnus fossilis* and *Cobitis taenia*. Although generally less interesting from the perspective of biodiversity conservation, the state of fish communities in the larger artificial lakes and reservoirs, such as Sihl, Gruyère, Wohlen and Schiffenen, would also help to understand the role of these waterbodies within the wider dendritic network.

Positive developments for lake fish communities

Community composition closer to near-natural state in many lakes

In several lakes, the fish community composition was similar to what would be expected under natural or weakly impacted conditions. In particular, lakes Thun, Brienz, Walen and Lucerne were strongly dominated by native salmonids, primarily *Coregonus* spp and *Salvelinus* spp. Fish were also recorded throughout the entire volume of these lakes indicating that the entire lake was habitable, although in Lake Lucerne this was true for only one of its basins (Urnersee).

Survival and recovery

Despite the many extinctions, extirpations and the many threats to surviving species, a great diversity of fish remains in the perialpine lakes. Four species that were believed to have gone extinct over the past century were rediscovered in Projet Lac. It is hoped that populations of these species will further recover as lake nutrients return to their near natural levels in many lakes, and as management starts to actively protect their habitats and populations.

Re-speciation for recovery of functional diversity

There is also some hope for recovery of functional diversity that was lost through hybridisation, with some authors suggesting that some shallow water hybrid populations or introgressed species are starting to re-colonise the deep in lakes that lost their endemic profundal species [205]. Loss of species through genetic mixing means that the resulting hybrid population may contain at least some of the genetic variation of both original species. Restoration of lakes to near-natural nutrient conditions has restored key aspects of the original regime of resource distributions and natural selection under which the ancestral *Coregonus* and *Salvelinus* stocks had diverged into distinct species. Natural selection can act again on the remaining genetic variation under the restored conditions, potentially re-establishing some of the lost ecological adaptations of deep water species. For example, there is evidence of differentiation in phenotypic (shape), trophic (gillrakers and stable isotopes) and genetic characteristics of Gangfisch (*Coregonus macrophthalmus*) populations living at different depths in Lake Constance [205]. These results support the anecdotal reports that *Coregonus macrophthalmus* in Lake Constance is beginning to extend its spawning depths deeper (and shallower) in recent years after the great loss of whitefish depth utilisation associated with the extinction of *C. gutturosus* by speciation reversal during eutrophication [42], and the recent reoligotrophication of Lake Constance. *Coregonus* may hence re-evolve the ability to occupy the deeper parts of the lake in the not-so-distant future if near-natural environmental conditions are restored and maintained. Further environmental changes and incautious stocking practices could however impede the progress of such re-speciation. Re-speciation and restoration of deepwater adaptation, however, could run out of steam if the genetic variation thatsurvived the eutrophicaction and speciation reversal phase, is insufficient, and if the continued process requires new mutations.

Fewer translocations

Translocations of stocks between lakes has become much less common in recent years with more sustainable stocking practices (Ref BAFU) due to an increasing awareness of the importance of maintaining the distinctiveness of species within lakes, as well as maintaining the differentiation between lake and stream populations or of populations from different lakes within the same species. The public has also become more aware of the dangers associated with non-native species and their negative effects.

Habitat restoration underway

The new Water Protection Act requires the cantons to plan and implement revitalization measures in rivers and lakeshores. Currently about 150 km of streams and rivers have already been restored since 2011 in Switzerland (with Federal Act on the Protection of Water Funds), until 2090 it is expected to raise up to 4’000 km. Additional near-natural restructuring of running waters and lakeshore has been realized before 2011 and in the course of ecological compensation measures and flood protection projects.

Some ecotonal habitats such as lacustrine river deltas have also been partially restored, such as the Reuss delta into the Urner basin of Lake Lucerne in 1991 or the Ticino Delta of Lake Maggiore in 2009, as well as some lake shores (e.g. Lake Murten, Vully-les-Lacs und Avenches (2012); Lake Zurich, Waedenswil (2012)). For 2022 the cantons have to strategically plan the restoration of lake shores (including littoral habitats). Moreover, awareness of the importance of sublittoral and profundal habitat variation is beginning to emerge.

Technological developments improve ecological understanding

Recent technological developments may contribute to further improving our understanding of lake ecosystems. High-resolution maps of the lake floor are now available for most large lakes, providing valuable insights into deep-water habitats [206, 207, 208]. Monitoring platforms on several lakes (Geneva, Biel, Greifen) continuously measure key properties of the lake environment which, in combination with remotely sensed data from satellites and mathematical modelling, show how the surface water changes throughout the lake and through time [209]. Continuous monitoring of phytoplankton and zooplankton on Lake Greifen provides additional insight into fine-scale temporal changes in the ecological foundations of the lake ecosystem [210, 211]. The distribution of wave energy has also been modelled throughout several Swiss lakes (Geneva, Neuchatel, Biel, Morat, Lucerne and Zurich) [212], providing information on the natural disturbance in the littoral zone. However, none of these data have yet been analysed together with fish data. Tracking of several hundred trouts and other species over several years using electronic tags in the tributaries of Lake Lucerne will reveal movement patterns of fish between lake and rivers (River Fish Ecology group of Eawag). Genetic techniques are becoming more advanced and can help to delineate species and to identify population structure within species, as well as to characterize the ecological and evolutionary processes responsible for the origination and maintenance of species diversity and functional diversity (e.g. *Coregonus* spp in Lakes Brienz/Thun, Lucerne and Walen/Zurich [24, 26, 161], sculpins [41], roach [204], stickleback [174, 213]). Finally, the inter-connectedness of these different components of the lake ecosystems and the complexity of interactions are increasingly being acknowledged in fundamental and applied research.

Physical characteristics of sampled lakes

Table 21: Lake morphology and nutrients of lakes sampled by Projet Lac.

Catchment	Local name	Short English name	Altitude (m)	Surface area (km²)	Maximum depth (m)	Average depth (m)	Volume (10^6 m³; GL)	Shoreline length (km)	Total phosphorus (µg/L)
Rhone	Lac d'Annecy	Annecy	447	27.6	82	41	1,125	?	51
Rhone	Lac de Bonlieu	Bonlieu	791	0.2	16	?	2	?	?
Rhone	Lac de Bret	Bret	674	0.4	13	7	5	4	24.1
Rhone	Lac de Chalain	Chalain	486	2.3	32	17	46	11	10.5
Rhone	Lac de Remoray	Remoray	850	1.0	27	14	14	5	15
Rhone	Lac de Saint-Point	Saint-Point	850	5.2	43	16	94	24	22
Rhone	Lac du Bourget	Bourget	232	44.5	145	85	3,600	?	24.2
Rhone	Lac Léman	Geneva	372	582.0	310	152	88,770	200	21.6
Rhine	Bodensee Obersee	Constance Obersee	395	473.0	254	101	47,678	165	6.7
Rhine	Bodensee Untersee	Constance Untersee	395	63.0	50	13	808	90	12.3
Rhine	Brienzersee	Brienz	564	29.8	261	173	5,162	35	4
Rhine	Hallwilersee	Hallwil	449	10.3	48	28	291	19	19
Rhine	Lac Brenet	Brenet	1002	0.8	18	9	6	4	?
Rhine	Lac de Bienne / Bielersee	Biel	429	39.3	74	29	1,240	?	13
Rhine	Lac de Joux	Joux	1004	8.8	32	16	128	21	16.1
Rhine	Lac de Morat / Murtensee	Morat	429	22.8	45	23	537	24	21
Rhine	Lac de Neuchâtel	Neuchatel	429	218.3	152	64	13,940	120	6
Rhine	Sarnersee	Sarnen	469	7.5	51	31	239	?	5
Rhine	Thunersee	Thun	558	48.3	217	136	6,435	54	3
Rhine	Vierwaldstättersee	Lucerne	433	114.0	214	104	11,800	144	4.5
Rhine	Walensee	Walen	419	24.2	151	105	2,468	37	3.5
Rhine	Zugersee	Zug	414	38.3	198	84	3,203	42	83
Rhine	Zürich Obersee	Zurich Obersee	406	20.3	48	23	377	29	9
Rhine	Zürich Untersee	Zurich Untersee	406	65.0	143	52	3,340	59	15.6
Po	Lago di Como (Lario)	Como	198	145.9	418	161	23,370	160	35
Po	Lago di Garda (Benaco)	Garda	65	368.0	350	133	50,350	158	21
Po	Lago di Lugano (Ceresio)	Lugano	271	48.7	288	134	5,705	98	55
Po	Lago di Poschiavo	Poschiavo	962	2.0	85	61	112	7	?
Po	Lago d'Idro (Eridio)	Idro	368	11.4	122	60	684	24	24
Po	Lago d'Iseo (Sebino)	Iseo	181	65.3	251	124	7,600	?	17
Po	Lago Maggiore (Verbano)	Maggiore	194	212.5	372	177	37,442	185	13
Danube	Silsersee / Lej da Segl	Sils	1797	4.1	71	35	130	15	?

? Data not available.

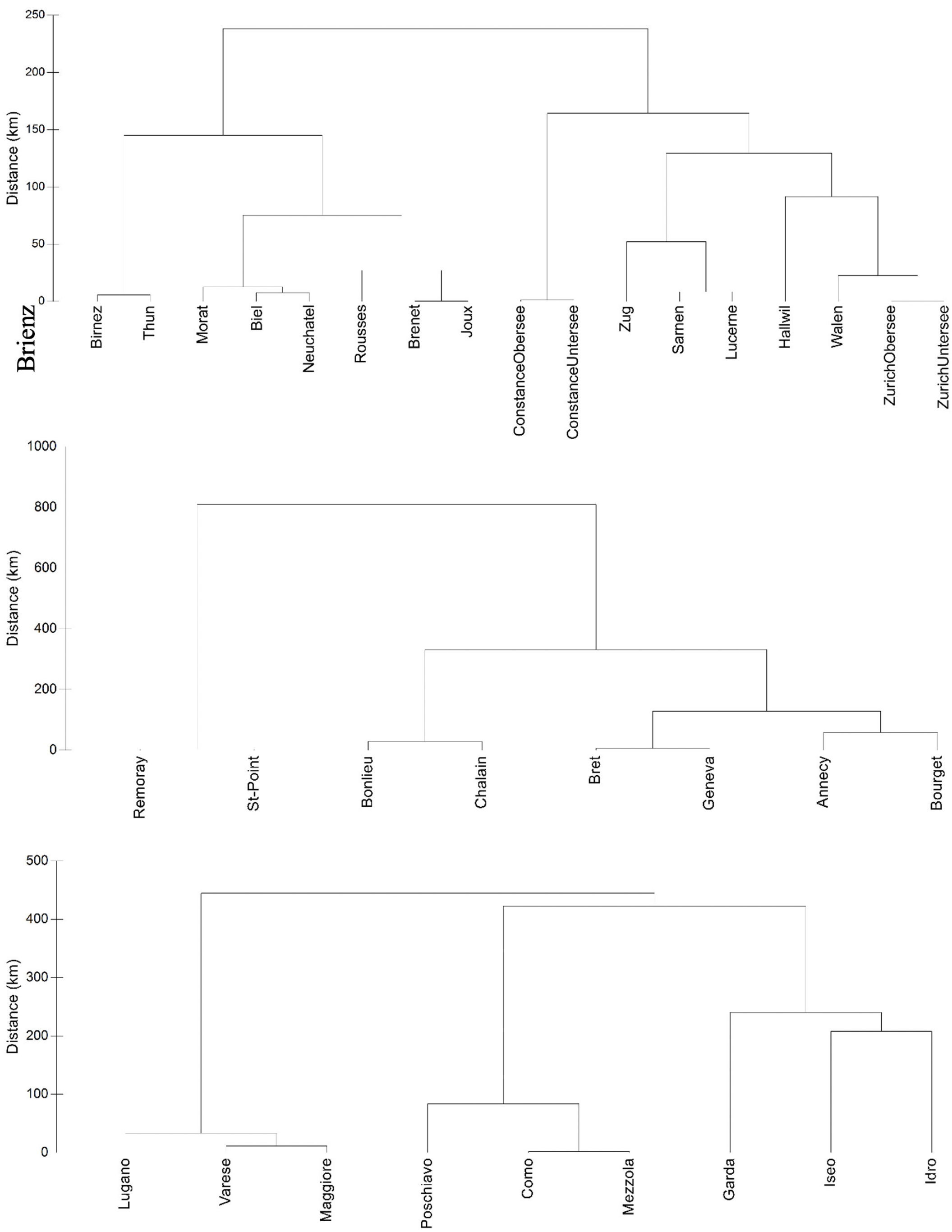


Figure 84: Distance among lakes by river in the Rhine (upper panel), Rhone (middle panel) and Po (lower panel) river catchments.

Correlations between lake morphology and other environmental variables

Lake surface area was correlated with the maximum depth of the lake (Figure 86), such that larger lakes tended to be deeper. There was however much variation in this relationship, particularly among the larger lakes. For example, Lake Brienz with a surface area around 30 km^2 and Upper Lake Constance with a surface area of around 475 km^2 have similar maximum depths (around 260 m). The largest surveyed lakes were Lake Geneva in the Rhone catchment, Upper Lake Constance in the Rhine catchment and Lake Garda in the Po catchment. A greater proportion of smaller lakes (surface area < 10 km^2) were surveyed in the Rhone (5 of 8 lakes) compared to the Rhine (4 of 17 lakes) and Po (3 of 9 lakes) catchments (Figure 85). Lakes in the Po catchment were relatively evenly distributed across the range of maximum depths, from the two deepest lakes Como (425 m) and Maggiore (372 m) to Varese with a deepest point of 26 m.

Among the lakes sampled by Projet Lac, the smallest lakes in each catchment tended to be at higher altitude e.g. Poschiavo in the Po catchment, and Rousses, Brenet and Joux in the Rhine catchment. Similarly, the largest lakes also tended to be low in the catchment e.g. Lake Garda and Upper Lake Constance. The relationship between altitude and lake size was not linear however and 12 of the 17 lakes in the Rhine catchment were at altitudes between 395 m (Lake Constance) and 470 m (Lake Sarnen). The main influence of altitude in the perialpine region is cooler air/water temperatures, and reduced connectivity to the rest of the river/lake network due to smaller connecting rivers, and natural and man-made barriers (e.g. current, waterfalls and dams). Analysis of satellite remote sensing data for the large lakes surveyed by Projet Lac [214] showed that the minimum lake surface water temperature decreased with the height of the lake above sea level (Figure 87). In other words, the surface waters of lower altitude lakes, particularly those south of the Alps, stayed warmer in the winter compared to the higher altitude and northern lakes. Among lakes at similar altitude in close proximity, e.g. Neuchatel, Biel, Morat, the surface waters of larger lakes tended to remain warmer through the colder months. All surveyed perialpine lakes in the Po catchment (i.e. excluding Poschiavo) were closer to sea level and generally warmer than even the lowest-altitude lake in the Rhine catchment and most of the lakes in the Rhone catchment.

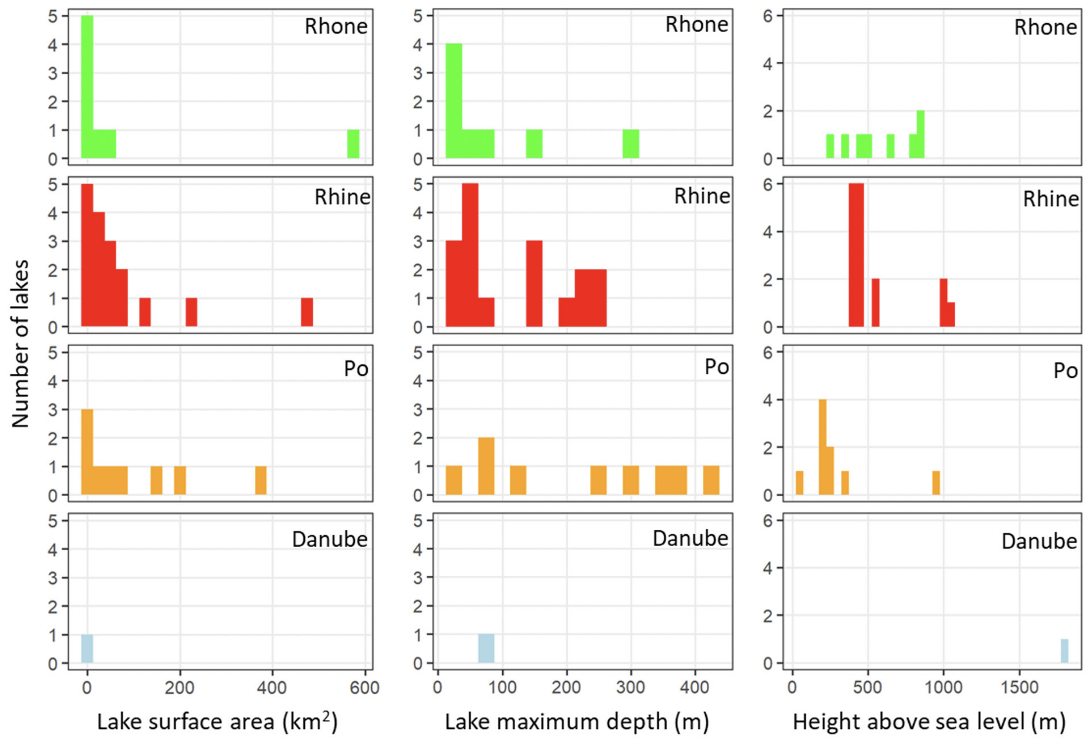


Figure 85: Histograms showing variation in lake surface area (left column), lake maximum depth (middle column) and height above sea level (altitude; right column) among the major catchments.

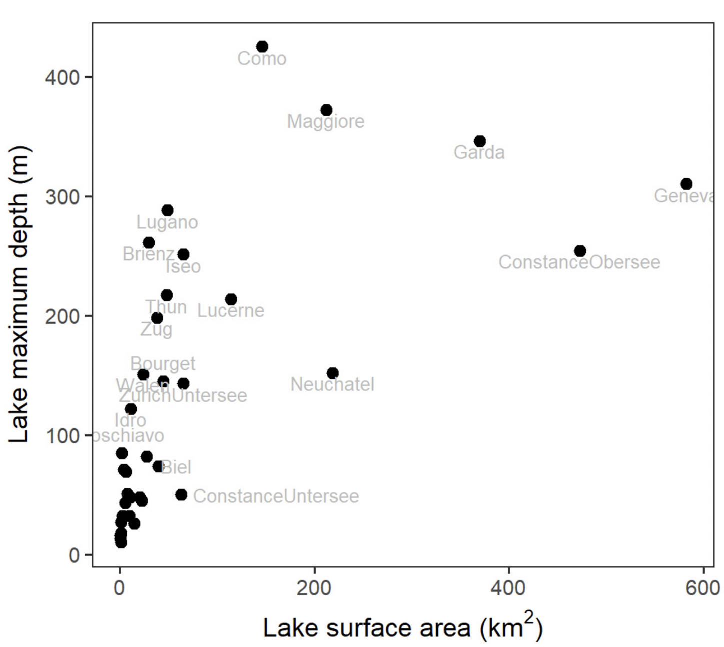


Figure 86: Correlation between the surface area and maximum depth of lakes surveyed in Projet Lac.

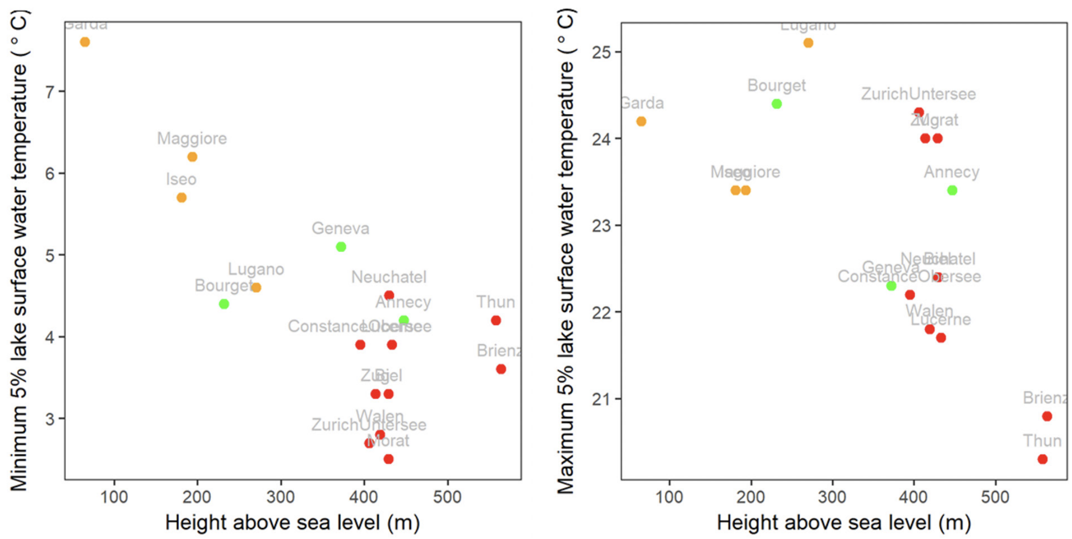


Figure 87: The surface waters of lakes closer to sea level (lower altitude) were warmer in the cooler months (left), while the surface waters of higher elevation lakes tended to be cooler in the warmer months (right). Smaller lakes also tended to be cooler in winter (data not shown). Monthly mean lake surface water temperatures based on remote sensing (Advanced Very High Resolution Radiometer; 1989 – 2014 [214]). The 5% quartiles were used to avoid the effects of outliers.

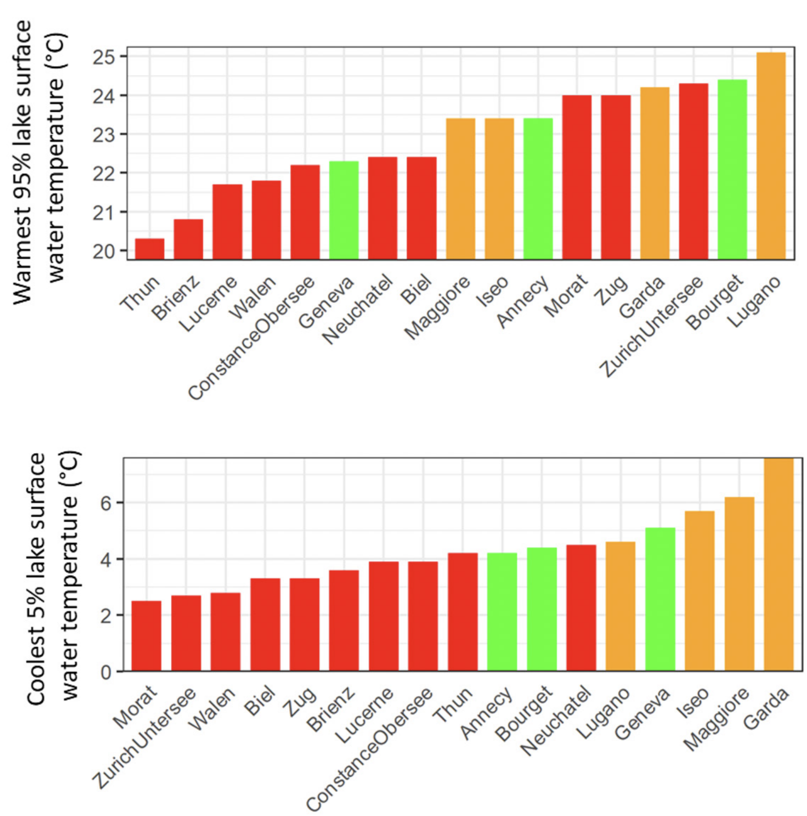


Figure 88: Water temperature in lakes of the Po river catchment (orange) were generally warmer than in lakes of the Rhone (green) and Rhine (red) catchments. The lakes on the northern edge of the Alps remain cooler in summer and the lakes in the south remain warmer in winter. Upper panel shows 95 % quartile and lower panel shows 5% quartile of monthly mean lake surface water temperatures based on remote sensing (Advanced Very High Resolution Radiometer; 1989 – 2014 [214]). Quartiles were used rather than true minimum/maximum to avoid the effects of outliers.

Additional background information

Why conserve biodiversity?

The arguments for maintaining biodiversity can be grouped into two main categories: anthropocentric (human-centred) and ethical [215].

The anthropocentric arguments for conserving biodiversity are based on the fact that biodiversity directly or indirectly provides many short and long-term benefits or services to humans. For example, biodiversity tends to be positively associated with higher productivity and increased stability of ecosystem services [216, 217]. Different species, ecotypes, populations and phenotypes within populations can have different functions and may specialise on different aspects of available food and habitats at different times of the day or year. This can increase the efficiency by which a community makes use of the available resources [90]. Biodiversity also provides security or insurance for ecosystem services, such as productivity, in the face of ecosystem fluctuations or changes [218]. The different responses among individuals, populations and species to environmental changes in a lake mean that ecosystem services, such as fisheries yields, based on diverse communities should be more stable through time [218, 219]. This is known in the perialpine lakes at the taxonomically coarsest level, for example, catches of *Perca fluviatilis* and *Rutilus rutilus* generally increased in eutrophied lakes, compensating to some extent for declining fisheries catches of salmonids such as *Coregonus* spp and *Salvelinus* spp (e.g. [220]). However similar compensation is likely to also occur among very closely related species, such as different whitefish species. Closely related species, ecotypes or different populations of the same species can respond differently to environmental fluctuations and changes [221]. This phenomenon is termed the "portfolio effect", a concept borrowed from financial stock markets, which recognises that diversified financial investment portfolios tend to produce more stable returns than simple portfolios. Homogenization of populations and assemblages, for example through incautious hatchery and stocking practices, tends to synchronise how the different populations vary through time as they respond in similar ways to environmental changes [221]. The result is higher overall variation in yield between the years [221]. In addition to buffering against fluctuations, preserving species, genetic and trait diversity increases the chance that fish assemblages will be able to adapt to future changes and that the ecosystems will continue to provide the services from which humans benefit.

Diversity in the fish community also contributes to safeguarding human cultural diversity. Different fish species may be targeted by subsistence, recreational and commercial fishers, as well as by different human cultures sharing an ecosystem. It also allows changes in targeted fish species through time with changing consumer preferences or availability of species. For example, in Lake Geneva, differences in local preferences meant that *Lota lota* was traditionally only fished in the part of the lake belonging to France [85]. In Lake Constance, *Anguilla anguilla* is commercially fished only in the part of the lake belonging to Germany and the same species is not sought after in Switzerland. Also in Lake Constance, *Perca fluviatilis* became a more desirable, and therefore fishery-targeted, species after the practice of filleting fish became popular in the 1960s [222]. These spatial, temporal and cultural differences in fisheries were possible because the diversity of the fish community provided alternatives.

The ethical argument for conserving biodiversity gives an intrinsic value to the diversity of other life forms for their own sake. This way of thinking reflects that humans are a major force on the Earth's biosphere and we have a responsibility to reduce our impact on other organisms, with extinction of a species being the ultimate form of impact. While extinction is also a natural process, the ethical argument for conserving biodiversity reflects that humans have a responsibility to prevent rates of extinction from accelerating beyond their natural or background levels [5].

In between the anthropocentric and ethical sets of arguments is the acknowledgement that many humans derive significant psychological, spiritual and cultural value from living in a world of richness and variety compared to one of monotony and uniformity. A terrestrial example is the difference between experiencing a diverse alpine meadow filled with a variety of colourful flowers and insects versus a eutrophic meadow with very few plant and insect species or a monoculture field. Being surrounded by this diversity, being able to witness it, or even just knowing that it exists, has positive effects on people's creativity, productivity and brings happiness, peace, health and well-being to many people [223]. The alternative is the negative feelings associated with being the generation of humans responsible for further losses of these natural assets [224].

Finally, much of our technological, medical, ecological and environmental knowledge is acquired by learning from nature, and by studying biodiverse systems. Based on all of these arguments, the high value of biodiversity for current and future human generations undoubtedly exceeds the short-term gains that are associated with the causes of most biodiversity loss [225].

"Desirable" and "undesirable" diversity?

The distinction between "desirable" and "undesirable" elements of biodiversity is complicated and can differ depending on the perspective of the assessor and the available knowledge. Every ecosystem has is own species composition, genetic variation and unique ecological interactions. Generally, every ecosystem needs protection and is natural state should be protected as a whole, and if necessary restored, independently from the presence of desirable species. Desirable species are indeed a plus value and every possible measure to conserve them should be implemented.

Relevant for management is the definition of "desirable" and "undesirable" fish and crayfish fauna in the Fishery ordinance (VBGF):, the different species are listed in three groups

Annexe 1: Indigenous/native species in Switzerland within their natural distribution range.
An indigenous species is considered as non native out of his natural distribution range or drainage.
Annexe 2: Non indigenous/native or exotic species not considered as invasive.
Allowed within a defined "Einsatzbereich"
Annexe 3: Exotic and invasive species.

"Desirable" species

Endemic species and other unique elements of genetic or ecological and phenotypic diversity are universally considered to be "desirable" and of high value to conservation. When endemic species occur in only one lake or a few interconnected lakes, the importance to conservation of an individual population approaches the importance of an entire species because the loss of such a population means permanent and global extinction of a species. An extinct population of a lake-endemic species cannot be replenished by immigration from elsewhere.

Native species that arrived in a lake through natural colonization processes and that have been present for many centuries are also undoubtedly considered "desirable". The immediate importance of local populations of such species to conservation depends on the size of the geographic range of the species, the temporal trends of the populations of the species across its range and the genetic and ecological distinctiveness of the local populations.

"Undesirable" species

Non-native and exotic species are often automatically considered to be "undesirable" and problematic. Indeed, non-native species can have severe negative impacts through ecological effects on populations of endemic and other native species, such as through competition, predation, the introduction of new parasites and pathogens. The arrival of non-native species can also lead to the erosion of genetic uniqueness via hybridisation, leading to genetic homogenization and associated loss of the portfolio effect [218]. As such, non-native species and populations are considered to be among the greatest threats to aquatic biodiversity [226] and can have severe negative impacts on ecosystem services [227].

However, **not every non-native species poses the same level of threat** [228]. In some cases, non-native species have only weak or no negative effects on native species. Non-native species may even be perceived as enhancing lake ecosystem services, and as such can be seen by some lake users as being positive additions to the fish community of a lake. For example, non-native species of *Coregonus* and *Rutilus,* as well as *Sander lucioperca* currently form the majority of the commercial fisheries catches in southern perialpine lakes (albeit with possibly large negative effects on some native species) [97]. Lake-foreign species of *Coregonus* and *Salvelinus* have also been introduced to replace the endemic species that had previously gone extinct in several lakes over the past century.

The automatic classification of a non-native species as "undesirable" is complicated by the fact that species ranges are not static. It is a natural process that species change their distribution ranges through time, such that some species would be expected to arrive and others to be locally lost, even without human impact, albeit at lower rates than those driven by human-facilitated translocations. Some species were also introduced to a region or specific lake by humans many decades or even centuries ago. In such cases, severe negative effects of the introduction are often considered to have been played out long ago. New problems with long-established non-native species can however arise with changing environmental conditions. It is also difficult to categorise species that arrive on their own in new areas as they expand their range with shifting environmental conditions, such as climate change, or species arriving in new areas due to increased connectivity between lakes and drainage systems caused by human engineering.

What is a species?

Defining species

There are many ways of answering the question 'what is a species?', with no universally accepted definition (e.g. [229]). In this report, **a species is defined as a group of individuals that, under natural conditions and in the absence of geographical isolation, maintains its distinctiveness from other such groups over many generations**. This definition is a practical application close to, but not identical to the **"Biological Species Concept"** [230].

Genetic differences between groups that persist over generations in the absence of geographical isolation indicate reproductive isolation between these groups, and reproductive isolation defines "Biological Species" [231]. Groups of individuals living in the same lake that are genetically distinct across much of their genomes (not just some few genes) are thus considered to be distinct species. These genetic differences between species are often correlated with differences in the appearance, i.e. sympatric species can often be phenotypically distinguished. However, species can be genetically distinct without any external differences that are immediately visible to an observer (so called "cryptic species").

On the other hand, two populations of the same taxon in separate lakes that differ in their DNA sequences and/or morphology can belong to the same species. Genetic differences inevitably arise between populations that are geographically separated for many generations, however this does not mean that these populations will function as different species should they encounter each other again in the same lake. Closely related, but genetically differentiated populations living in different lakes are, hence, not assumed in this report to represent different species. Instead, these are considered as distinct populations of the same species. This is the case for *Rutilus rutilus*, where the population in Lake Brienz differs in shape and genes from those in other perialpine lakes [232]. It is important to emphasize, however, that distinct populations of the same species also constitute important intraspecific biodiversity, very worthy of protection.

Groups of individuals of the same species interbreed and exchange genes freely when occurring together. The majority of individuals do not breed with members of other species, either by spawning at different times of the year and/or by spawning in different parts of the lake (e.g. depths), or by actively choosing mates of their own species. The combination of these factors makes hybridization sufficiently rare that the species remain distinct in the absence of geographic isolation. Individuals of different species may occasionally interbreed however. In these cases, the species can nonetheless remain distinct over generations for a number of potential reasons:

- the eggs of a pairing between different species may not develop properly (i.e. hybridization, but no gene flow; also called hybrid inviability),
- the offspring may be healthy, but unable to reproduce (often the case with hybrids between very old cyprinid species, such as bream and roach; also called hybrid infertility),
- the offspring may be healthy and capable of producing offspring, but hybrids are less well adapted to the ecological niches of the parental species, such that their chances of survival and reproduction are lower than that of individuals of the parental species in the habitats of the parents (ecological postzygotic reproductive isolation). But note that such hybrids may have excellent chances of survival and reproduction outside the habitats of the parents.

Ice age refuges and recolonization of the lakes and rivers of the perialpine region

Ice ages

Between 2.5 million and 11,700 years ago[8], the Earth experienced repeated ice ages or glaciations, with intervening periods of warmer climate. During this time, the higher-latitude (i.e. towards the earth's poles) and higher-elevation areas (e.g. mountain chains such as the Alps) were repeatedly covered and uncovered by large ice sheets or glaciers (Figure 89). These ice sheets forced most plants and animals to move their distributions towards lower elevations and the equator.

Recolonization of the perialpine lakes

With their re-emergence of the alpine region from under the ice at the end of the last glacial period around 12,000 years ago[9], species moved into the perialpine lakes from their glacial refuges. The lakes south of the Alps were probably quite quickly recolonized by a diverse array of fish species that had taken refuge during the ice age in the not so distant lower parts of the Adriatic Sea catchment (Po River and tributaries) [233, 234]. The northern perialpine lakes were colonized by species from multiple origins, reflecting their links to three major river catchments (Rhine, Rhone and Danube) and their corresponding lowland, ice-age refuges, some of which were quite distant from Switzerland [147, 235]. Some species, such as sculpins and trouts survived the ice ages north of the Alps in the rivers of the Tundra [233, 236]. Many of the anadromous fish, i.e. fish that migrate up rivers from the ocean to spawn, including many salmonids, came directly from the Atlantic Ocean shores [233]. Other species, including many of the cyprinids, colonised the northern perialpine lakes more slowly as they gradually expanded their ranges upstream along the Danube River from the warm-water glacial refugia in the Black Sea region [234, 237].

Connections between catchments

The glaciers of the ice ages clearly reshaped the landscape, including the network of rivers and lakes. However, ephemeral lakes and rivers formed at the retreating edge of the glacier, may have also created "bridges" between river catchments and provided the opportunity for cold-water fish species to colonise new areas [184]. The relative rates of retreat among different glaciers around the Alps could have further affected recolonization pathways in pioneering fish species. For example, the arm of the Rhone glacier extending over the Aare-Rhine may have retreated more quickly than the part over the lower Rhone, facilitating the colonisation of Lake Geneva by *Cottus gobio* and possibly other species from the Rhine [41, 184].

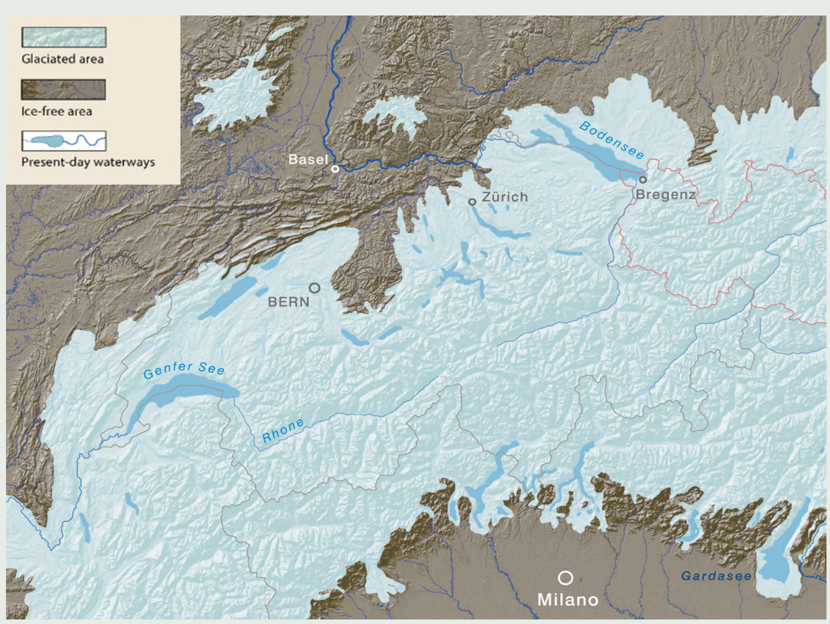


Figure 89: Reconstruction of the maximum glacial extent during the high point of the last ice-age (26 – 20 thousand years ago). Figure adapted from the publication Geologische Bundesanstalt (Hrsg.) (2013): Der Alpenraum zum Höhepunkt der letzten Eiszeit – Posterkarte. Geologische Bundesanstalt, Wien.

[8] Geological epoch known as the Pleistocene.

[9] The most recent glacial period extended from around 115,000 to 11,700 years ago. The glaciation of the alpine region during this period is known as the Würm glaciation.

Lake stratification and vertical mixing

Lake stratification is a natural process and refers to a difference in temperature between the water near the surface and in the deeper parts of the lake. This usually occurs as the surface waters warm as they accumulate heat from the atmosphere during the warmer months of the year. In the northern perialpine region, lake surface waters reach around 20 to 22 °C in summer, while the deeper water remains around 4 to 5 °C throughout the year [10]. Inverse stratification in winter is also possible, particularly in smaller and higher altitude lakes, where the surface water becomes colder than 4 °C and therefore less dense than the deeper water. In both cases, the difference in temperature and associated density acts as a barrier to mixing, and the lake is effectively divided into two separate waterbodies above (epilimnion) and below (hypolimnion) the zone of steep temperature change (thermocline). The thermocline usually forms between 15 and 25 m below the lake surface. While the lake is stratified, oxygen from the lake surface is mixed only within the epilimnion and nutrients released from organic matter decomposing on the lake floor remain in the hypolimnion.

Stratification breaks down when the water at the surface of the lake is cooled in fall/winter (or warmed in spring/summer in the case of inverse stratification) to temperatures close to those of the deeper part of the lake. When the temperature is similar between the surface and the deeper parts of the lake (i.e. a difference of less than 0.5°C), wind across the lake surface can move the water to create currents that force the surface water into the deep and vice versa, known as vertical mixing. The depth of penetration of vertical mixing depends on the length of time that the surface and deep water have similar temperature, and the strength and duration of wind over the lake surface during this period. Complete vertical mixing is critical to the functioning of lakes as it replenishes oxygen in the deeper habitats and brings nutrients into the surface waters where they can be used by primary producers such as phytoplankton and other aquatic plants.

Certain characteristics reduce the propensity of a lake for vertical mixing: small wind fetch, e.g. a small lake surface area compared to average/maximum depth (e.g. Lake Lugano), complex or "bent" lake shape (reduced longest axis and fetch length; e.g. Lower Lake Zurich), or oblique alignment of the longest axis of the lake to the dominant wind direction during the period of homothermy, and high water residence time, i.e. low discharge of river inflows/outflows (e.g. Lake Zug).

Source: National Geographic Society, Tim Gunther

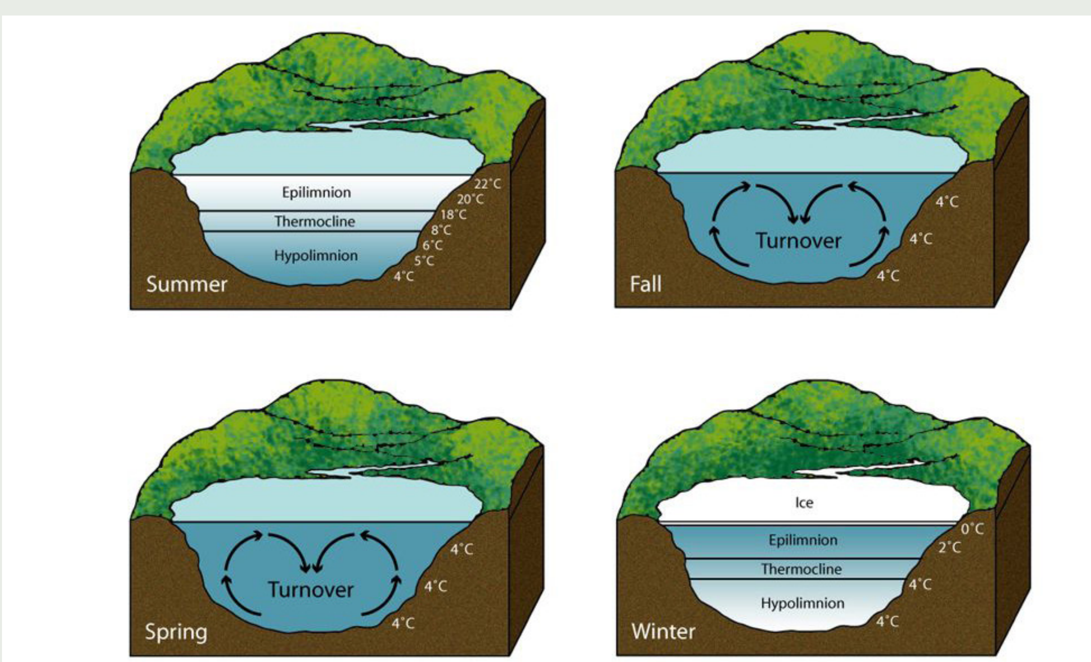


Figure 90: Representation of the seasonal cycle of stratification and mixing in a dimictic lake throughout a year.

[10] Warmer water is generally lighter and sits above cooler, heavier water. Water is most dense, and therefore most heavy, at 4°C.

Appendix C – Lake Info Sheets

Lake Info Sheets

General information
These lake info sheets aim to show key aspects of the results of the Projet Lac fish sampling in each lake, with brief mention of other relevant information on the fish community and the lake environment. This preface aims to assist with interpretation of the lake info sheets, first with general information about the figures and the fish sampling, and then specific details on the different types of figures.

Snapshot in time
The figures show the distribution of fish throughout the lake at the time of sampling (late-summer/autumn) according to the sampling methods used. The distribution of fish throughout a lake and their catchability by different sampling methods varies with the seasons. The date of the fish sampling is provided in the Projet Lac synthesis report.

Sampling bias
The figures show the fish recorded by the different sampling methods, which may differ from the actual fish community due to the biases of the sampling methods. Gillnets tend to catch deeper-bodied fish that are more active. Fish with hard spines are also more likely to be caught in nets. Electrofishing tends to catch fish that are smaller and less mobile, with longer, more slender body shapes. The sampling methods were used in the same way in all lakes however, meaning that the results are comparable among the lakes.

Fish survey methods
Not all fish survey methods were applied in all lakes. Electrofishing and vertical gillneting were not conducted in lakes Annecy and Bourget. The nets used in lakes Sarnen and Biel consisted of mesh sizes with different surface areas, and no pelagic CEN nets were used. The Italian lakes Idro, Iseo, Varese, Como and Mezzola were surveyed by GRAIA and CNR-ISE. In these lakes, point sampling was used for electrofishing and no vertical nets were deployed. Fish weight was not recorded for every fish in these lakes, so biomass patterns are not discussed. Also, in these lakes, gillnets were set within each depth range described by the CEN gillnetting protocol, with exact depths of the nets not available. For graphs showing the distribution of fish by depth, the fish are therefore assigned to the middle of the CEN depth range.

Use of colour
Different colours are used in the figures to represent different fish species. The colours assigned to each species are indicated by the coloured squares next to the fish images on the right of the page. It is difficult to assign more than 100 unique colours to make every fish species easily distinguishable from every other species. A brief description of the main trends in each figure is provided to assist interpretation.
Where multiple species of *Coregonus* occurred in a lake, an additional yellow square is shown next to the colour square for the *Coregonus* species to represent the individuals that could not be assigned to a species in the field.
Scientific names of species are coloured to reflect their status in the lake as endemic, non-native or exotic.

Conservation status
Conservation status of the fish species is based on the Swiss Red List (2021), which follows the categories used by the Red List of the International Union for the Conservation of Nature (IUCN):
† Extinct – beyond reasonable doubt that the species is no longer extant.
CR Critically endangered – in a particularly and extremely critical state.
EN Endangered – very high risk of extinction.
VU Vulnerable – at high risk of unnatural (human-caused) extinction without further human intervention.
NT Near threatened – close to being at high risk of extinction in the near future.
LC Least concern – unlikely to become extinct in the near future.
DD Data deficient.
nn Non-native.

Fish species reported to occur in the lake but not recorded in Projet Lac
The species list in this section is predominantly derived from the Swiss Fish Atlas, with additional information from recent research. This section is omitted from the info sheets for lakes outside of Switzerland and for small lakes without reliable information.

Community composition
Purpose: to show the composition of the fish community in different parts of the lake and by different sampling methods.
Data: electrofishing, shallow-set vertical gillnets (to 3 m deep), CEN benthic gillnets, CEN pelagic gillnets, deep-set vertical gillnets (excluding the 3 m closest to the lake floor). Fish caught in inflowing or outflowing streams/rivers are excluded. Catches (abundance/biomass) in each sampling action were corrected for sampling effort (area electrofished or net surface area) and then averaged across all actions in the lake.
Tips for understanding: the figure shows the fish caught by the different sampling methods, which may differ from the actual fish community due to the biases of the sampling methods. Note also that this figure does not show the total number or biomass of fish, only the proportions of the total contributed by the different species.
Ecological interpretation: heavy dominance of one species could be a sign of a disturbed ecosystem.

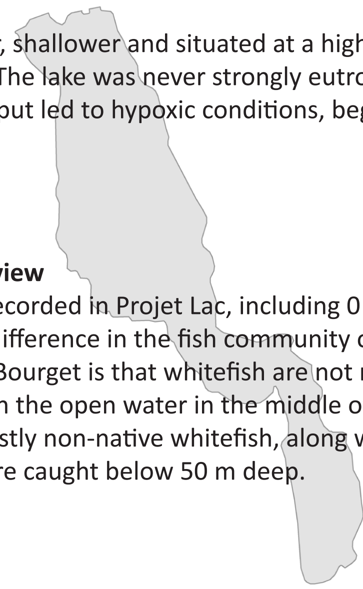
Fish lengths
Purpose: to show which species and size of fish dominated the catches.
Data: total lengths (tip of snout to tip of tail) of fish caught in the CEN benthic gillnets and CEN pelagic gillnets. More benthic nets were set in each lake than pelagic nets so the patterns tends to be dominated by benthic fish.
Tips for understanding: the scale of the vertical axis differs between the lakes, so the visibility of rarer size classes, e.g. larger fish, depends on the abundance of the most abundant size class (small perch in many lakes).
Ecological interpretation: heavy dominance of a particular size class could be a sign of a disturbed ecosystem. For example, a hyper-abundance of many small perch, but few medium-sized or larger perch, mean that very few of these small fish are surviving through to larger life-stages.

Depth distribution
Purpose: to show the vertical distribution of different fish species across the lake depth.
Data: benthic fish, i.e. fish caught near the lake floor, is based on CEN benthic gillnets. Pelagic fish, i.e. fish caught in open water, based on vertical gillnets, excluding the 3 m closest to the lake floor.
Tips for understanding: the horizontal axis of the plots show the abundance or biomass of fish corrected for the amount of net set in the depth zone i.e. catch per unit effort (CPUE). The scale of the horizontal axis differs between plots and is determined by the CPUE of the depth zone with the highest CPUE. The visibility of catches in depth zones with low CPUE therefore depends on the value of the highest CPUE in a depth zone. Note that, for the benthic fish, nets were not set in every depth zone, with sampled depth zones indicated by a small grey mark on the vertical axis. Note also that the distribution of fish throughout a lake changes with the seasons.
Ecological interpretation: concentration of most fish into a narrow depth range could be a sign of a disturbed ecosystem.

Lake cross section
Purpose: to show the vertical distribution of different fish species by depth and their horizontal distribution between the lake shore and the deepest part of the lake, i.e. usually towards the center of the lake.
Data: vertical gillnets and CEN benthic gillnets. Vertical nets are indicated by the vertical dashed line extending from the top of the water column, i.e. the lake surface to the lake floor. CEN benthic nets are shown by the shorter dashed lines near the lower end of the water column, i.e. the lake floor. CEN benthic nets are 1.5 m high. Therefore, in shallow water (less than 1.5 m deep), the CEN benthic nets extend across the water column. Moving into deeper water, the CEN benthic nets sample less and less of the water column, rather reflecting only the fish living near the lake floor.
Tips for understanding: the figure shows the water column on the vertical axis (i.e. the relative position of the fish between the lake surface and the lake floor) and the water depth (i.e. the height of the water column where the net was set) on the horizontal axis. Without manipulation, this type of lake cross-section would normally be represented by a wedge, with a low water depth meaning a short water column expanding to a high water depth and a tall water column. However, in this figure, the shallow part of the lake has been expanded vertically to also show the details of the fish community in this part of the lake. The solid, curved grey lines indicate 10 m depth bands. For example, all fish caught upwards and to the left of the grey line at 10 m were caught between the lake surface to 10 m down from the surface. Each fish is shown by a point, with colours representing different species. The points are staggered around the line of the net to improve visibility. Note that the distribution of fish throughout a lake changes with the seasons, however only one season was sampled in this project.
Ecological interpretation: an absence of fish from large parts of the lake may reflect a disturbance to the ecosystem.

Lake Annecy

Rhone catchment



Lake environment

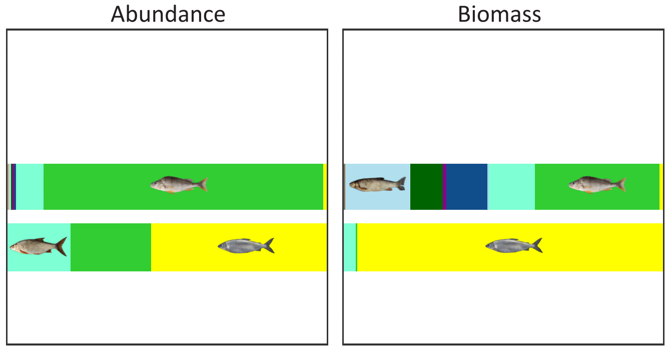
Lake Annecy is smaller, shallower and situated at a higher altitude compared to nearby Lake Bourget. The lake was never strongly eutrophied, however a slight increase in nutrient input led to hypoxic conditions, beginning around 1950.

Fish community overview

14 fish species were recorded in Projet Lac, including 0 endemic and 3 non-native species. A major difference in the fish community of Lake Annecy compared to nearby Lake Bourget is that whitefish are not native to this lake. Very few fish were caught in the open water in the middle of the lake. The few fish caught there were mostly non-native whitefish, along with some small roach and perch. No fish were caught below 50 m deep.

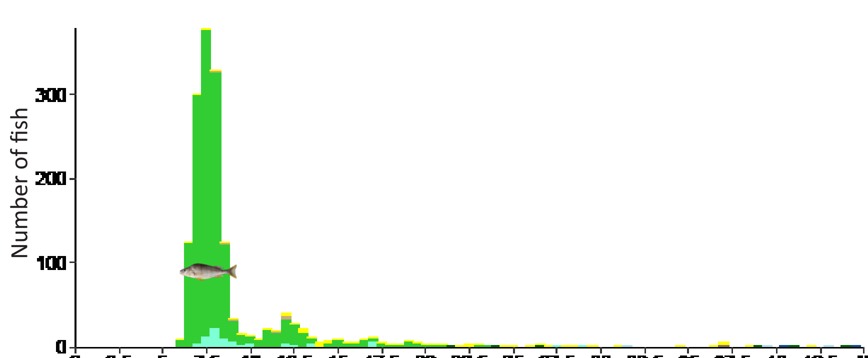
Community composition

Fish caught near the lake floor (benthic) were dominated by perch, along with rudd, tench and pike. Open water (pelagic) was dominated by whitefish, albeit in low numers, along with some small roach and perch. Electrofishing and vertical gillnetting were not conducted in this lake.



Fish lengths

Fish caught in CEN nets were heavily dominated by small perch 7-8 cm, with another peak around 12.5 cm.



Gudgeon LC
Gobio gobio

Common roach LC
Rutilus rutilus

Common rudd LC
Scardinius erythrophthalmus

European Chub LC
Squalius cephalus

Tench LC
Tinca tinca

Whitefish NT
Coregonus sp

Atlantic trout NT
Salmo trutta

Lake char VU
Salvelinus umbla

Alpine lake perch LC
Perca fluviatilis "Yellow-orange form"

European river perch DD
Perca fluviatilis "Red form"

Freshwater blenny NT
Salaria fluviatilis "French lineage"

Rhone sculpin NT
Cottus sp "Rhone lineage"

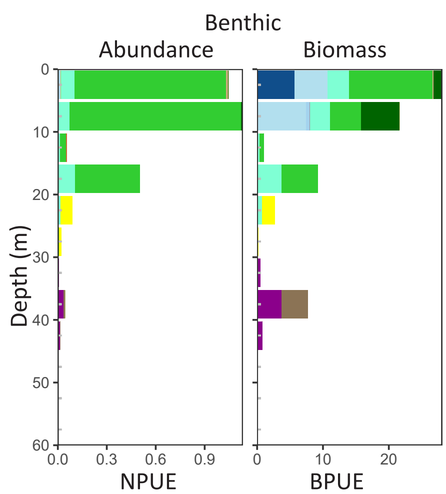
Northern pike LC
Esox lucius

Burbot LC
Lota lota

Lake Annecy

Depth distribution

Perch and roach dominated the lake floor habitat in the upper 20 m of the lake, followed by a layer of whitefish between 20-30 m, with char and burbot deeper below. Vertical nets were not used to sample the fish of Lake Annecy, so a two-dimensional depth distribution cannot be shown.

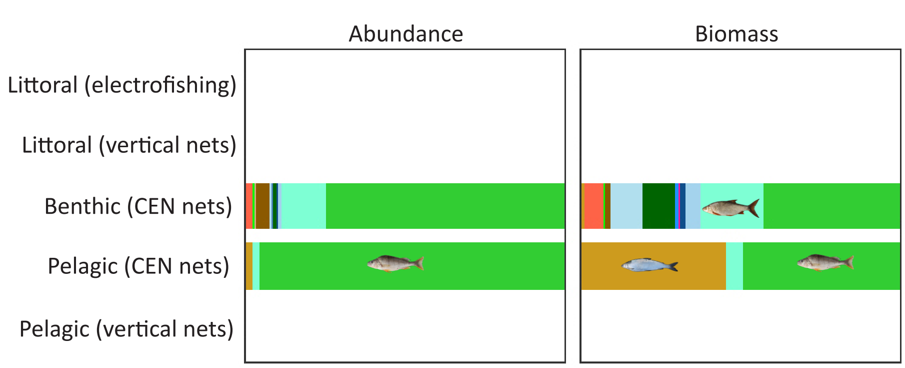


Lake Bourget
Rhone catchment

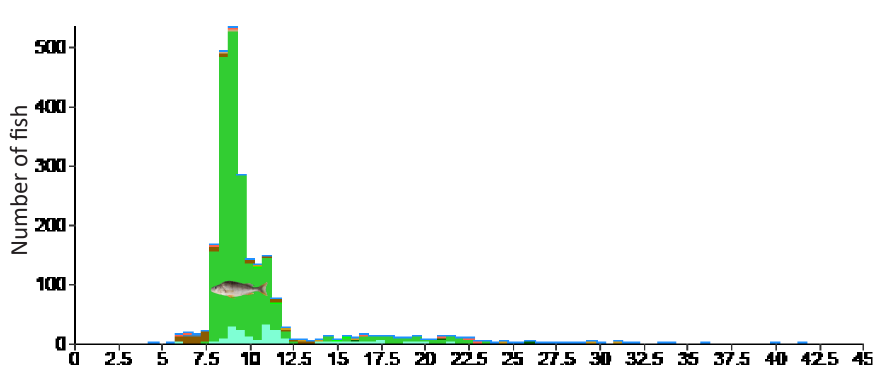
Lake environment
Lake Bourget is larger and deeper than nearby Lake Annecy and was the lake with the lowest altitude sampled in the Rhone catchment. Lake Bourget has experienced strong eutrophication, but was meso-eutrophic at the time of sampling, however the lake still frequently experiences issues with hypoxia.

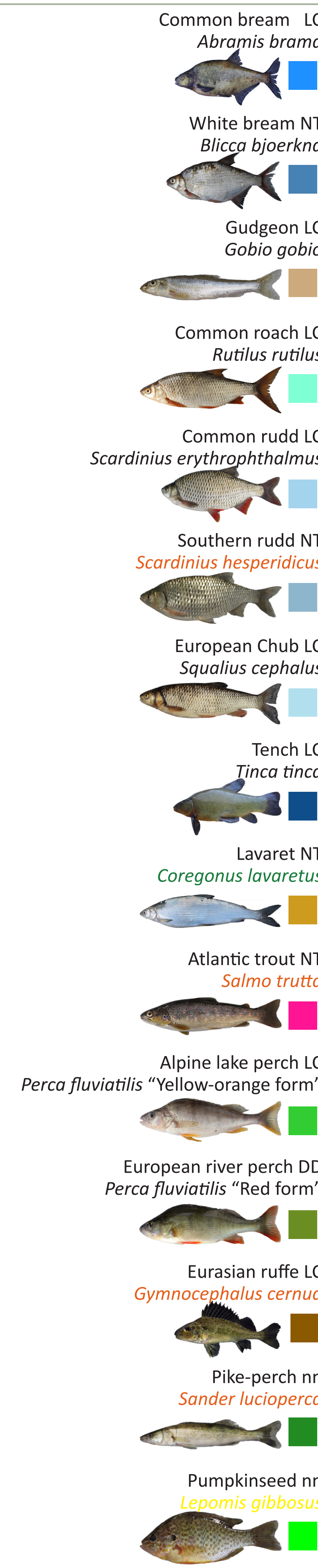
Fish community overview
18 fish species were recorded in Projet Lac, including 1 endemic and 6 non-native species. Lake Bourget contains an endemic species of whitefish Coregonus lavaretus, which dominated the biomass of the open water, along with perch. Considerably more non-native species were recorded in Lake Bourget compared to Annecy: black bullhead and ruffe were particularly common in the benthic nets. Very few fish were caught below 50 m.

Community composition
Fish caught near the lake floor (benthic) were dominated by perch, along with roach. Open water (pelagic) contained mostly perch, but with approximately half the biomass contributed by whitefish.



Fish lengths
Fish caught in CEN nets were very heavily dominated by small perch 8-12 cm long.





Lake Bourget

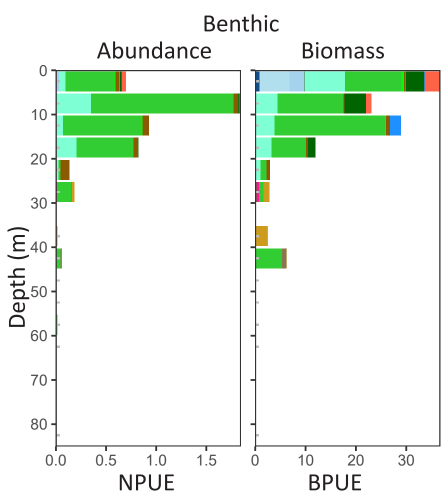
Northern pike LC
Esox lucius

Black bullhead nn
Ameiurus melas

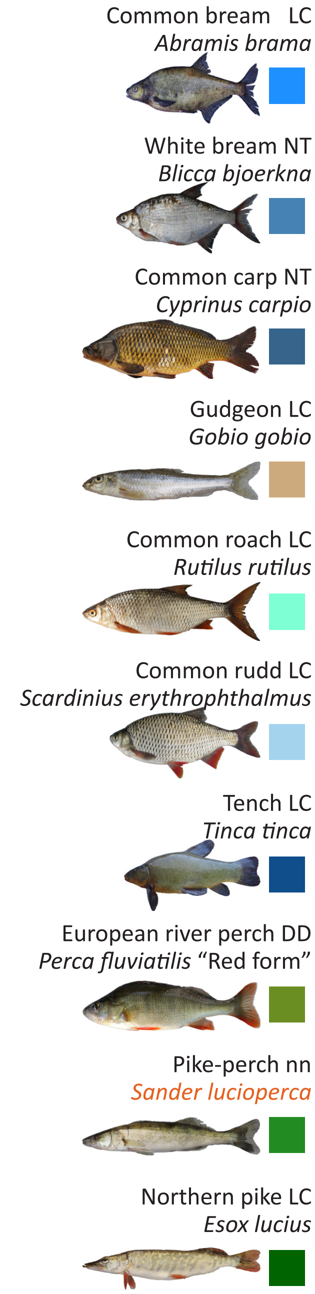
Burbot LC
Lota lota

Depth distribution

Perch were common in the nets set close to the lake floor above 20 m. Roach were also common in the upper layers, with the largest roach close to the surface. Vertical nets were not used to sample the fish of Lake Bourget, so a two-dimensional depth distribution cannot be shown.



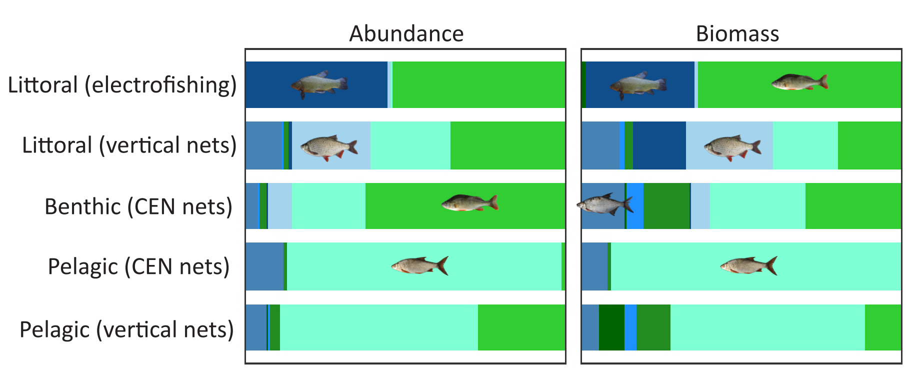
Lake Bret
Rhone catchment



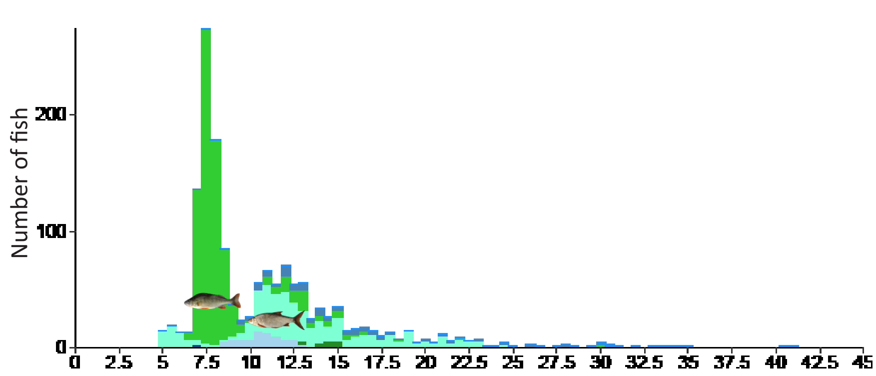
Lake environment
Lake Bret is a small, shallow, meso-eutrophic lake located in the hills to the north of Lake Geneva. There was no dissolved oxygen in the lake below 10 metres around the time of sampling.

Fish community overview
10 fish species were recorded in Projet Lac, including 0 endemic and 1 non-native species. The fish community living close to the lake floor was dominated by perch and roach. Tench and rudd were also common near the lakeshore. The open water was dominated by roach, with particularly large numbers caught close to the lake surface. No fish were caught below 13 m.

Community composition
Near the lakeshore (littoral), electofishing catches were dominated by perch and tench. Littoral nets were dominated by perch, roach, rudd and bream. Perch was the most abundant fish in nets near the lake floor (benthic), while open water (pelagic) was heavily dominated by roach.



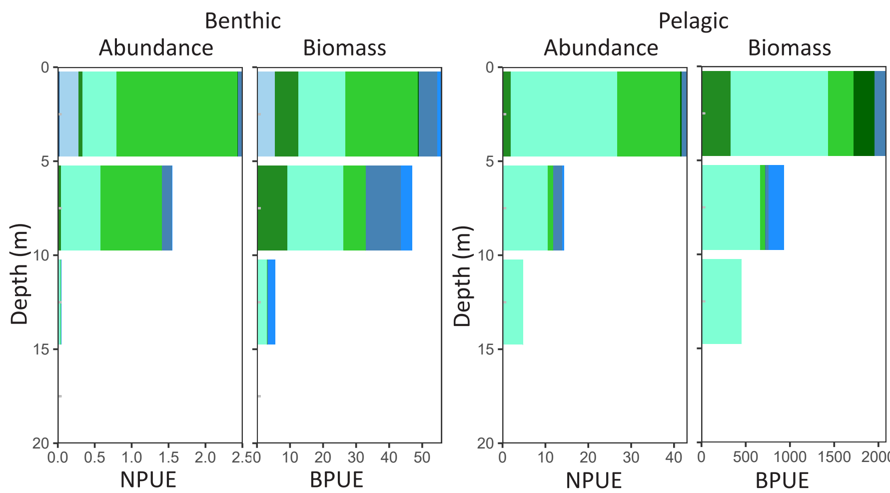
Fish lengths
Fish caught in CEN nets were dominated by a large number of small perch 7-8 cm, while most roach were around 11 cm.



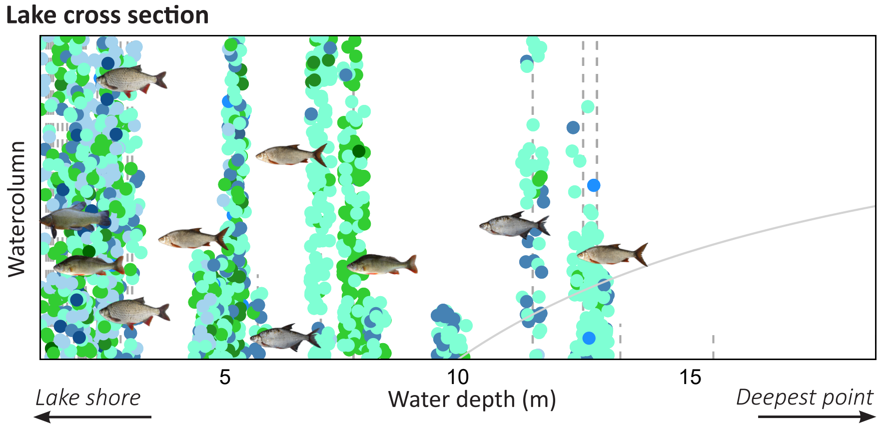
Lake Bret

Depth distribution

The highest number and biomass of fish near the lake floor and in open water were caught in the layer of water close to the surface. Abundance and biomass was very low below 10 m. Vertical nets showed a high density of fish (mostly roach and perch) throughout the watercolumn in the shallower half of the lake. The two deepest set nets on the lake floor caught no fish.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common bleak LC
Alburnus alburnus

Goldfish nn
Carassius auratus

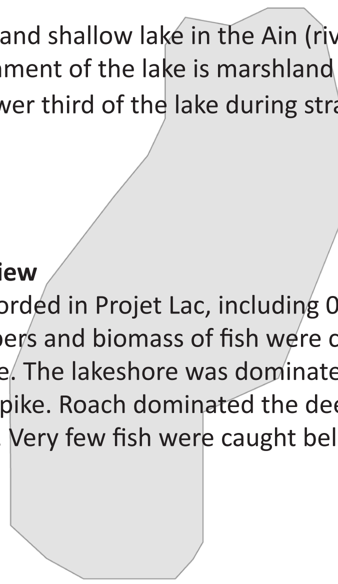
European Chub LC
Squalius cephalus

Stone loach lineage II DD
Barbatula sp "Lineage II"

Atlantic trout NT
Salmo trutta

Lake Bonlieu

Rhone catchment

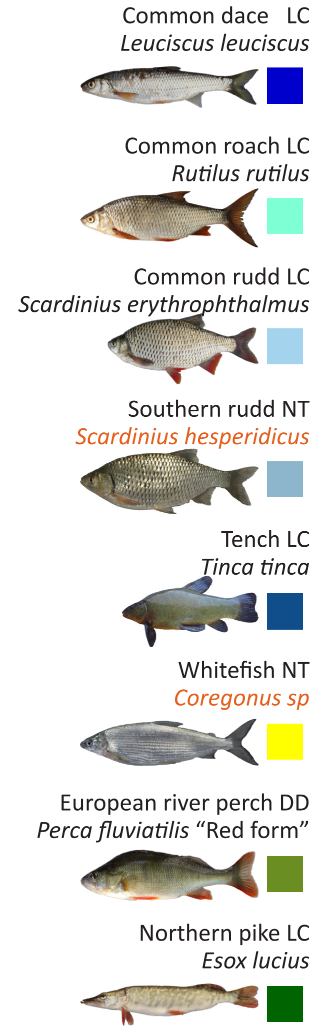


Lake environment

Lake Bonlieu is a small and shallow lake in the Ain (river) subcatchment. Most of the immediate catchment of the lake is marshland and forests. No dissolved oxygen is present in lower third of the lake during stratification.

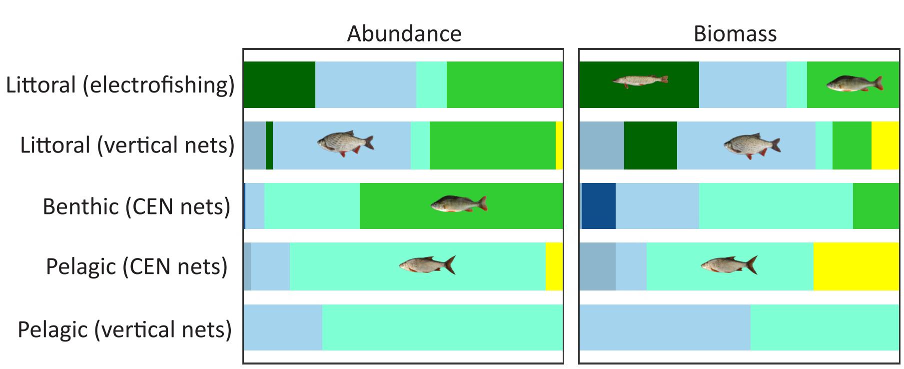
Fish community overview

8 fish species were recorded in Projet Lac, including 0 endemic and 2 non-native species. Low numbers and biomass of fish were caught in littoral and benthic habitats of this lake. The lakeshore was dominated by perch and common rudd, along with small pike. Roach dominated the deeper benthic habitats, as well as the open water. Very few fish were caught below 10 m.



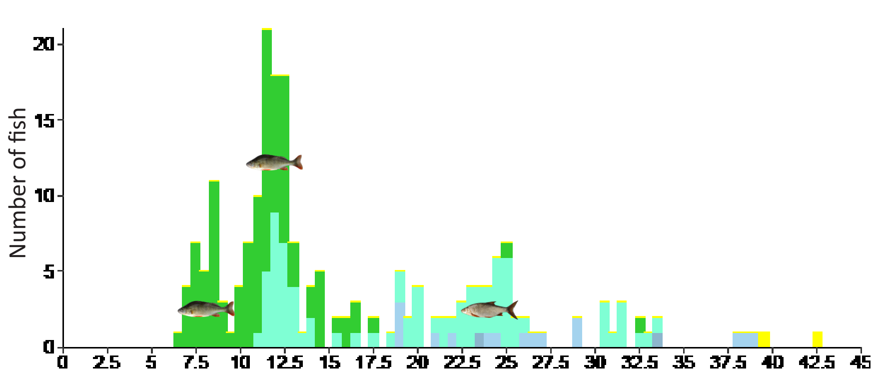
Community composition

Near the lakeshore (littoral), electrofishing and nets caught similarly high proportions of perch and rudd. Pike also formed a significant proportion of the fish caught be electrofishing. Perch and roach were common in the nets close to the lakefloor (benthic). Roach dominated the catches in open water (pelagic).



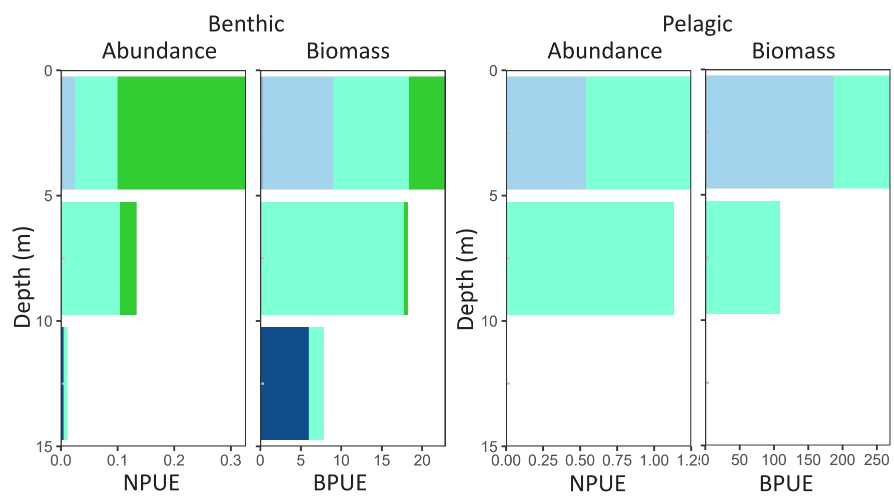
Fish lengths

Fish caught in CEN nets were mostly perch with peaks 7-9 cm and 11-12 cm, along with roach of lengths 12-13 cm and 22-25 cm.

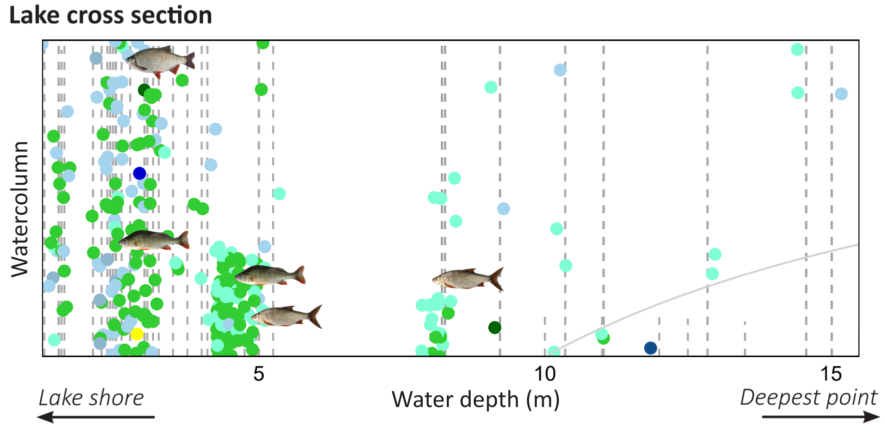


Lake Bonlieu

Depth distribution
Small perch were common in the nets near the lakeshore, while rudd and roach formed most of the biomass. Roach were more common in middle depths near the lake floor. In the open water, rudd and roach dominated the meagre catches in the upper layers, with no fish caught below 10 m from the surface. Low densitity of catches in the open water above the deeper parts of the lake.



Lake cross section



Lake Chalain

Rhone catchment

Lake environment

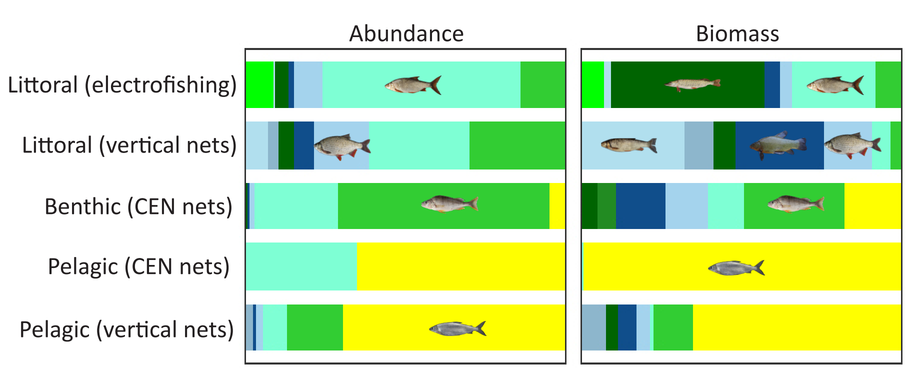
Lake Chalain lies in the Ain (river) subcatchment, a short distance downstream from Lake Bonlieu. The lake suffered from hypoxia below 20 m around the time of sampling.

Fish community overview

18 fish species were recorded in Projet Lac, including 0 endemic and 5 non-native species. Among the highest biomass catch rates of whitefish in open water were recorded in this lake, contributed by many large fish. A particularly large number of fish species were recorded considering the surface area of the lake, including the riffle dace recorded only in this lake, and the only native record of the Mediterranean minnow in Projet Lac. Despite this, almost no fish were recorded in the deepest third of the lake (i.e. below 20 m).

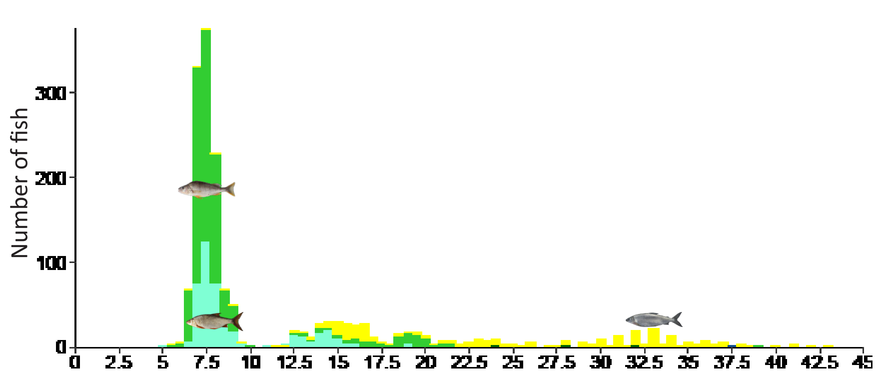
Community composition

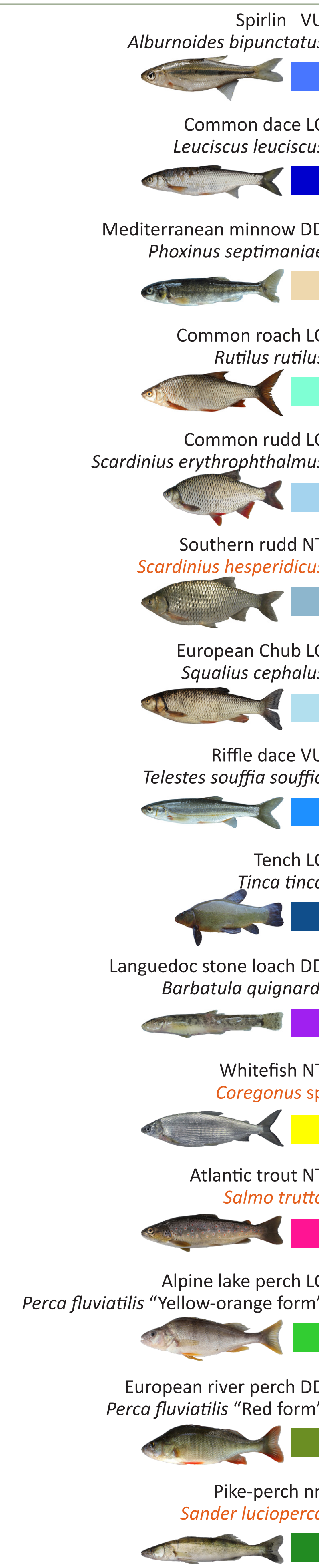
Near the lakeshore (littoral), roach formed much of the abundance by electrofishing, while pike contributed a high proportion of the biomass. Roach, perch, chub and tench formed high proportions in the littoral nets. Close to the lake floor (benthic), perch and roach dominated the abundance. Whitefish dominated in the open water (pelagic).



Fish lengths

Fish caught in CEN nets were mostly small perch and roach 7-8 cm. Many larger whitefish were caught in this lake.





Pumpkinseed nn
Lepomis gibbosus

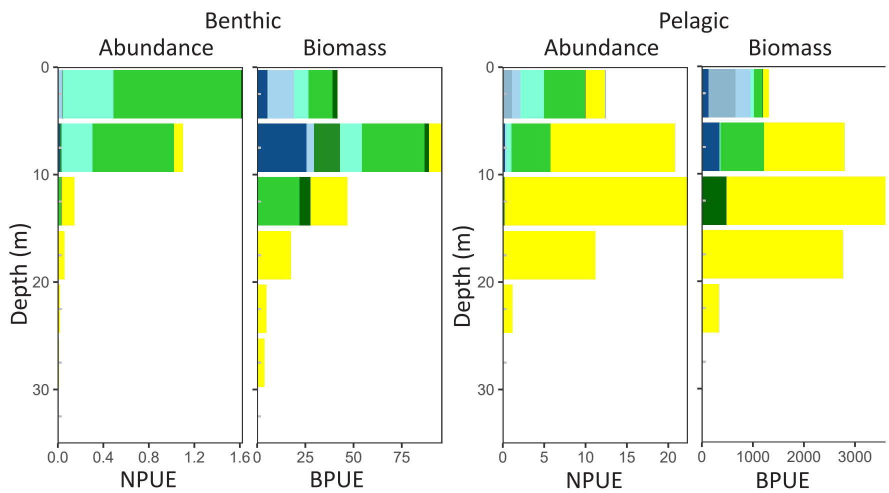
Rhone sculpin NT
Cottus sp “Rhone lineage”

Northern pike LC
Esox lucius

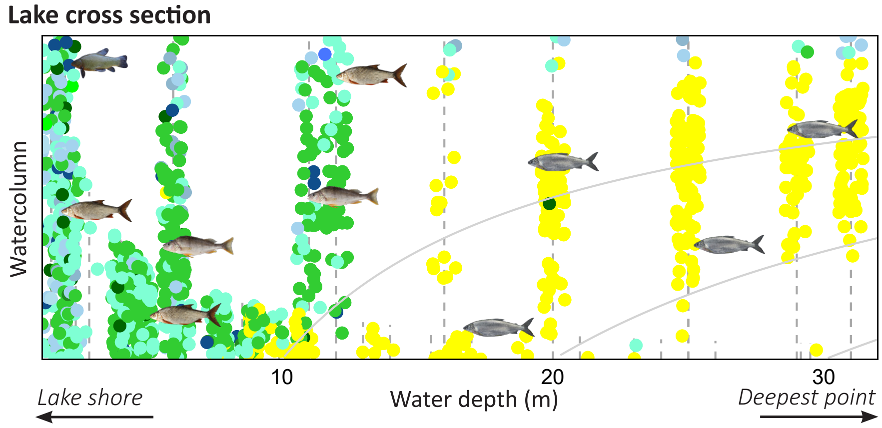
Lake Chalain

Depth distribution

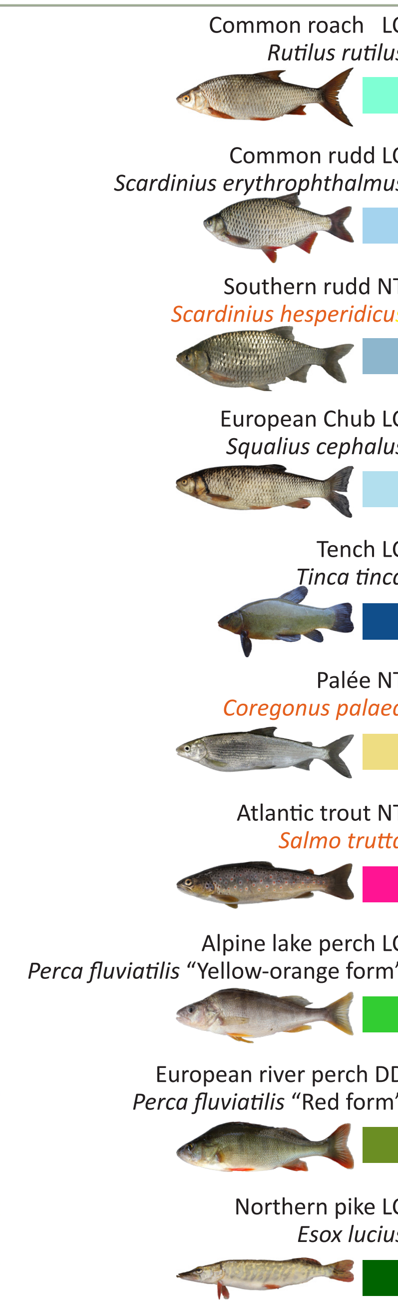
Different fish species clearly occupied different parts of the lake. Perch and roach dominated the shallow parts of the lake, with small perch and roach particularly common in nets near the lakeshore, to 10 m deep. Rudd and tench made substantial contributions to biomass in the shallow benthic zone. In the open water, whitefish dominated, with abundance and biomass peaking 10-15 m. A thin layer of roach and rudd was recorded close to the lake surface in open water. Very few fish were caught below 20 m.



Lake cross section



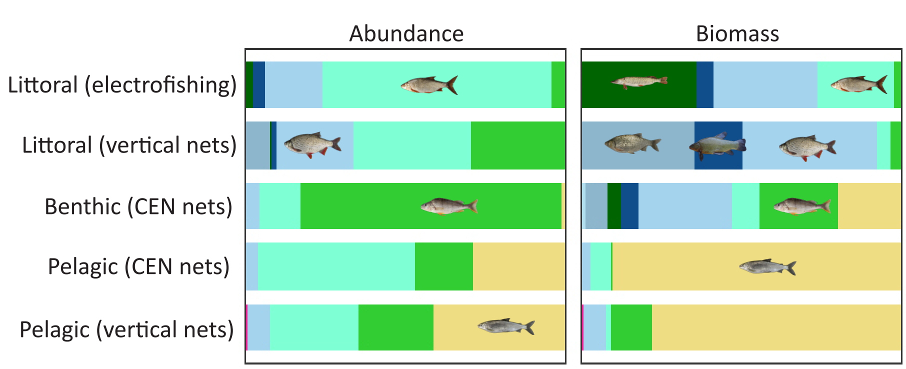
Lake Saint-Point
Rhone catchment



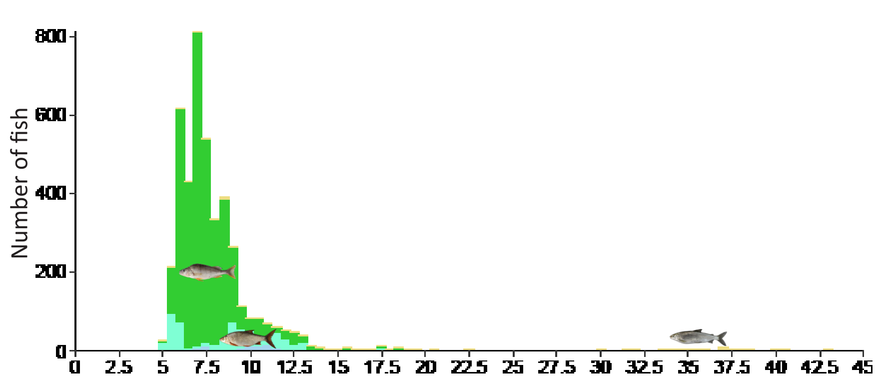
Lake environment
Lake St Point is in the Doubs (river) subcatchment and is the largest of the natural lakes within the French Jura. Lake St Point is the sister lake to the smaller Lake Remoray, separated by just over 2 km of wetland. At the time of Projet Lac sampling, the lake was mesotrophic, with problematic dissolved oxygen concentrations below 30 m towards the end of the stratification period.

Fish community overview
10 fish species were recorded in Projet Lac, including 0 endemic and 3 non-native species. The highest average catch rate of whitefish biomass of Projet Lac was recorded in Lake St Point, contributed by a large number of very large fish. The whitefish were recorded mostly in open water below 10 m deep. Perch, roach and rudd dominated the surface layer of the open water, as well as benthic habitats. No fish were caught below 35 m.

Community composition
Near the lakeshore (littoral), roach formed much of the abundance by electrofishing. Pike and rudd also contributed a significant proportion of biomass. Rudd, roach and perch were common in littoral nets. Close to the lake floor (benthic), perch dominated abundance, while rudd and whitefish also contributed to biomass. Whitefish dominated in the open water (pelagic).



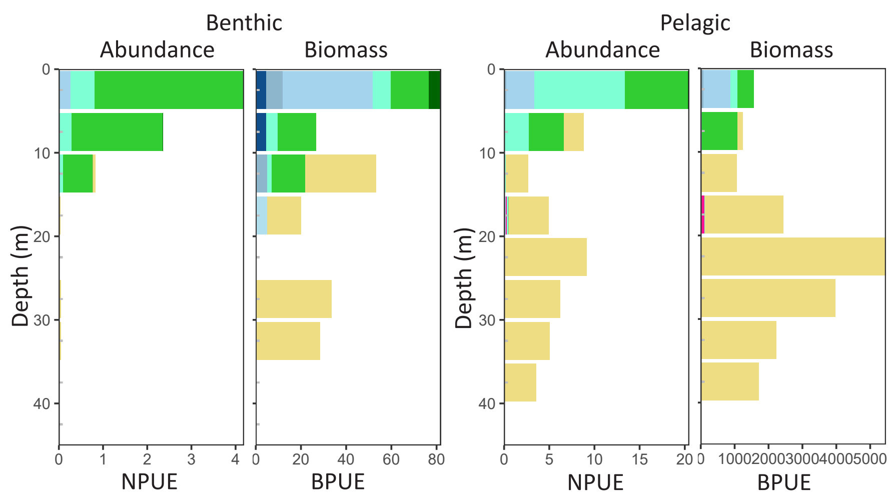
Fish lengths
Fish caught in CEN nets were heavily dominated by small perch 6-9 cm. Small roach of 5-12 cm were also common.



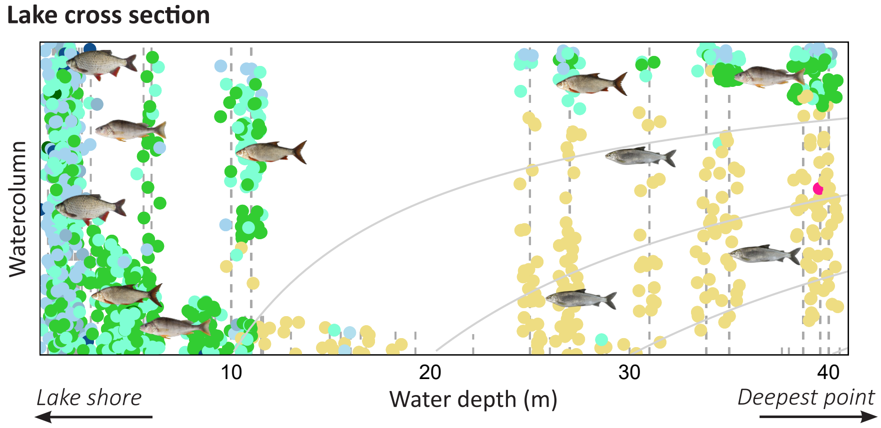
Lake Saint-Point

Depth distribution

Different fish species clearly occupied different parts of the lake. Perch, roach and rudd dominated the upper layers to 10 m deep in both benthic and pelagic habitats. Whitefish dominated the open water over the deeper parts, with biomass peaking between 20-25 m. A layer of perch, roach and rudd were recorded close to the surface above the deeper water.

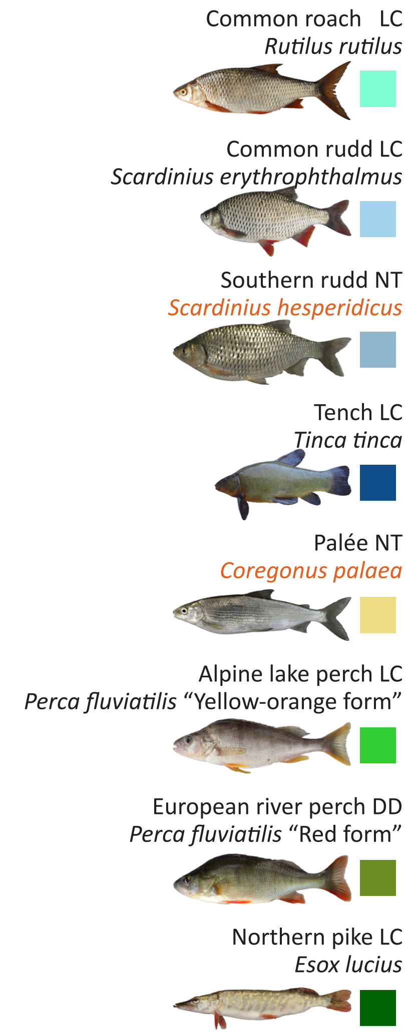


Lake cross section



Lake Remoray

Rhone catchment



Lake environment

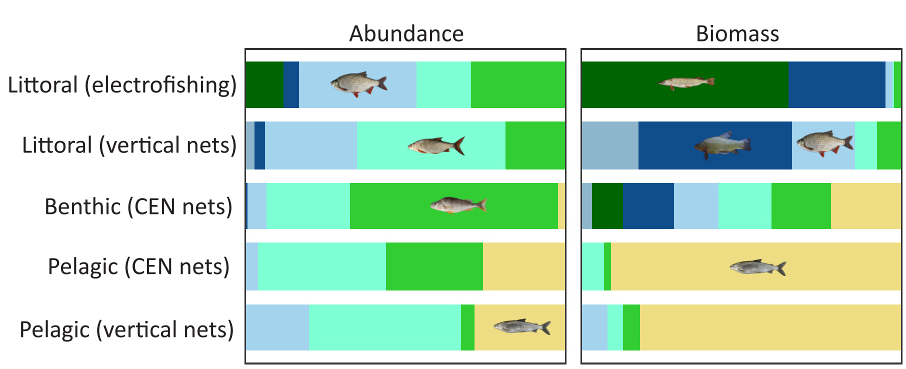
Lake Remoray is in the Doubs (river) subcatchment and is the smaller sister lake to Lake St Point, separated by just over 2 km of wetland. The lake was oligo-mesotrophic at the time of sampling and experienced very low dissolved oxygen concentrations below 20 m towards the end of the stratification period.

Fish community overview

8 fish species were recorded in Projet Lac, including 0 endemic and 2 non-native species. Rudd, along with small perch and roach dominated the littoral and benthic habitats to 10 m. Roach and rudd were also common in the surface layers of the open water. Exclusively whitefish were caught below 10 m deep, with no fish caught below 20 m. The fish species list in Lake Remoray was very similar to Lake St Point, with two species not recorded in this smaller lake. All fish species recorded in Lake Remoray were common across the perialpine region, resulting in a low uniqueness.

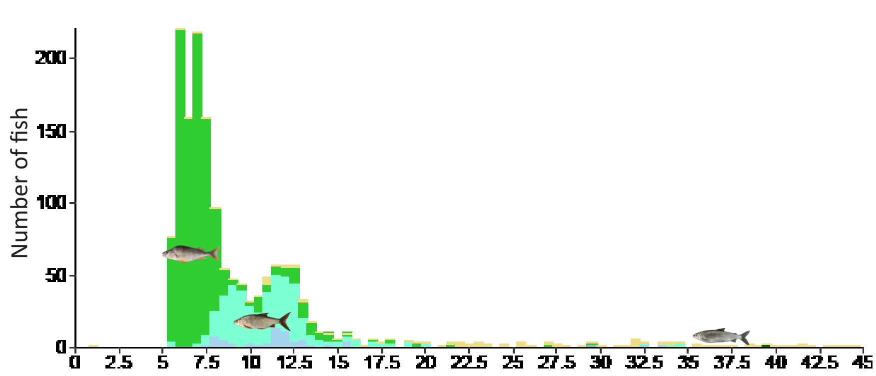
Community composition

Near the lakeshore (littoral), rudd and perch formed most of the abundance by electrofishing, while pike and tench dominated biomass. Rudd, roach and tench dominated the littoral nets. Close to the lake floor (benthic), perch and roach dominated abundance, with biomass evenly distributed across multiple species. Whitefish dominated biomass in the open water (pelagic), with roach also common.



Fish lengths

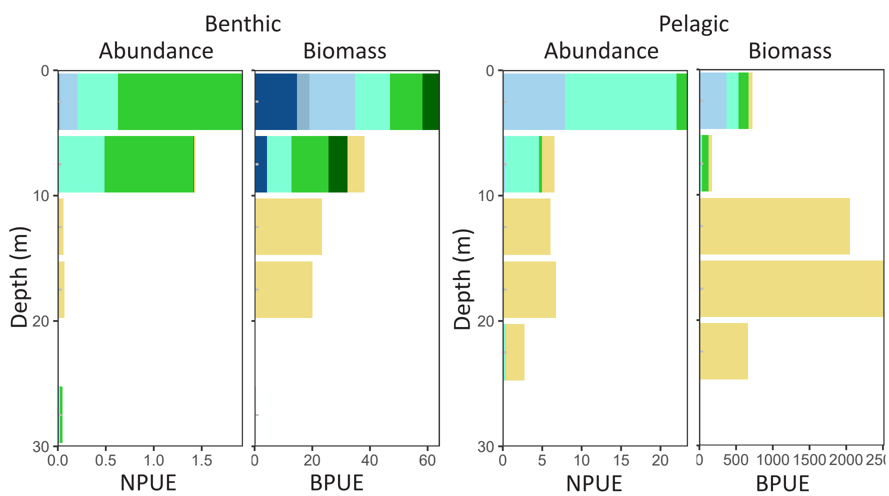
Fish caught in CEN nets were dominated by small perch 6-8 cm and roach 8-9 cm and 11-12 cm.



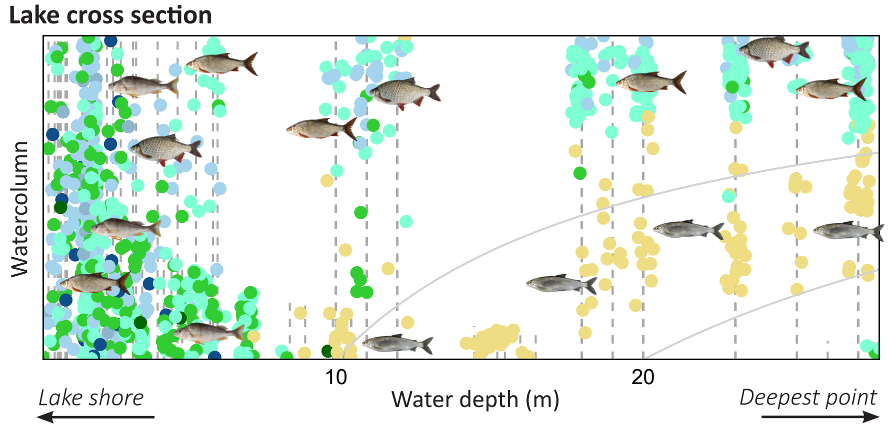
Lake Remoray

Depth distribution

Different fish species clearly occupied different parts of the lake. Perch, roach and rudd dominated the shallow benthic zone, with biomass contributed by multiple species. A layer of roach and rudd were recorded in the upper layers of the open water. Only whitefish were caught below 10 m, with biomass peaking at 15-20 m.



Lake cross section



Lake Geneva

Rhone catchment

Lake environment

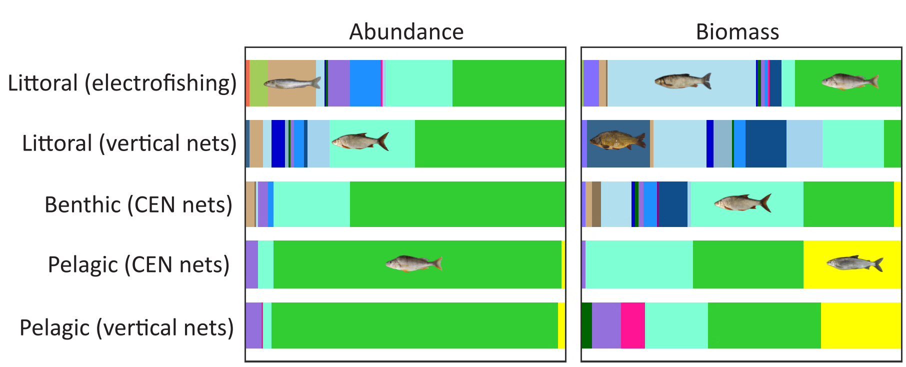
Lake Geneva is the largest perialpine lake. The lake became eutrophied in the last century, peaking in the 1970s and was mesotrophic at the time of sampling. Dissolved oxygen was present to the deepest point of the lake at the time of sampling, however vertical mixing is becoming infrequent due to climate warming. 70% of habitats around the edge of the lake are unnatural.

Fish community overview

25 fish species were recorded in Projet Lac, including 0 endemic and 6 non-native species. Despite being part of the Rhone catchment, the fish community of Lake Geneva shared many similarities with the larger lakes of the Rhine catchment. Small perch dominated the catches in littoral, benthic and pelagic habitats, followed by roach. Gudgeon and chubb formed noteworthy proportions of the electrofishing catches by weight and numbers respectively. In the open water, perch and bleak dominated the upper layers, with whitefish and Atlantic trout in the layers below. The endemic Féra (*Coregonus fera*) and Gravenche (*Coregonus hiemalis*) are presumed extinct.

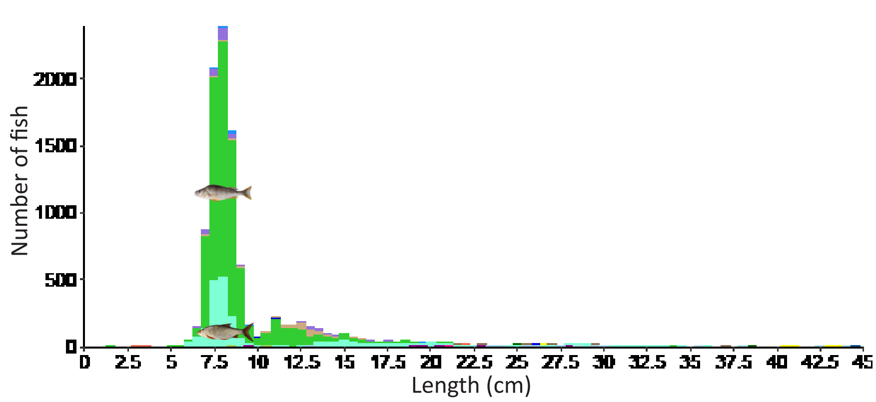
Community composition

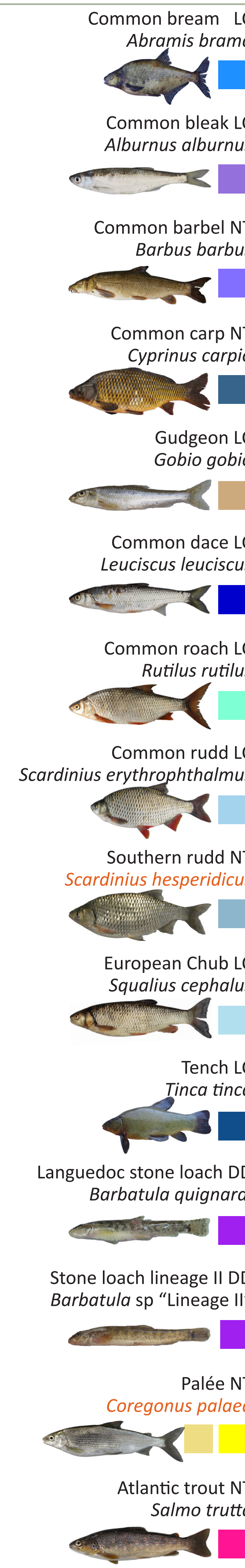
Near the lakeshore (littoral), perch, roach and gudgeon dominated the catches by electrofishing, with chubb dominating biomass. Littoral nets were also dominated by perch and roach. Close to the lake floor (benthic), perch and roach dominated abundance and biomass. Small perch were by far the most common fish caught in the open water (pelagic), while roach and whitefish made significant contributions to biomass.



Fish lengths

Fish caught in CEN nets were heavily dominated by small perch (7-8 cm, 11-12 cm) and small roach (7-8 cm).

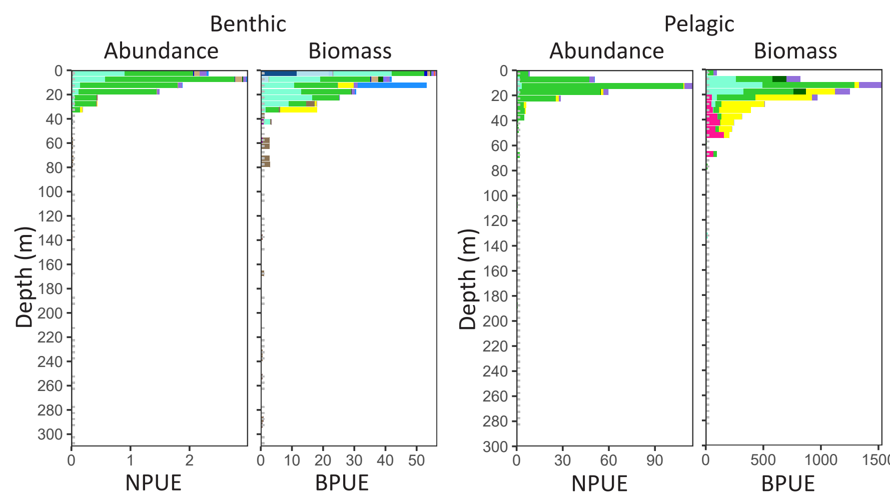




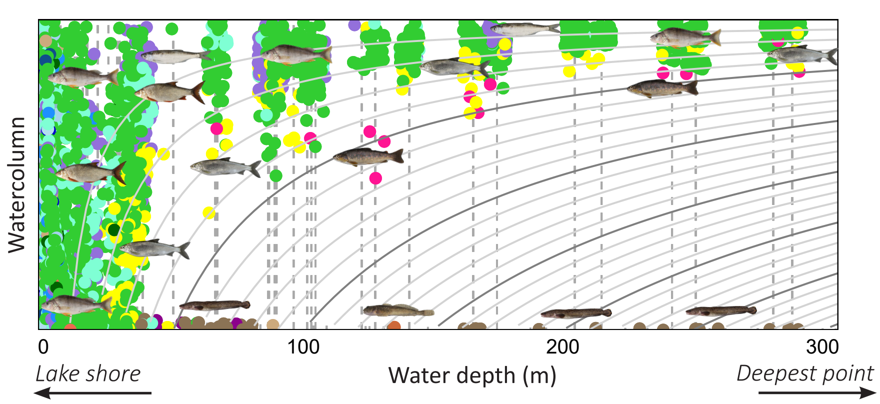
Lake Geneva

Depth distribution

Perch, roach and bleak dominated the upper 20 m near the lake floor and in open water. In open water, abundance and biomass peaked at 10-15 m. Open water biomass showed a transition with depth from perch, roach and bleak, to whitefish and Atlantic trout. Burbot were recorded in benthic nets across the depths to the deepest point of the lake.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Spirlin VU
Alburnoides bipunctatus

White bream NT
Blicca bjoerkna

Goldfish nn
Carassius auratus

Mediterranean minnow DD
Phoxinus septimaniae

Danube minnow DD
Phoxinus csikii

Spiny loach (species unknown) DD
Cobitis sp

Eurasian ruffe LC
Gymnocephalus cernua

Pumpkinseed nn
Lepomis gibbosus

Largemouth bass / Blackbass nn
Micropterus salmoides

Wels catfish LC
Silurus glanis

European eel CR
Anguilla anguilla

Féra †
Coregonus fera

Gravenche †
Coregonus hiemalis

Lake Rousses

Rhine catchment

Lake environment

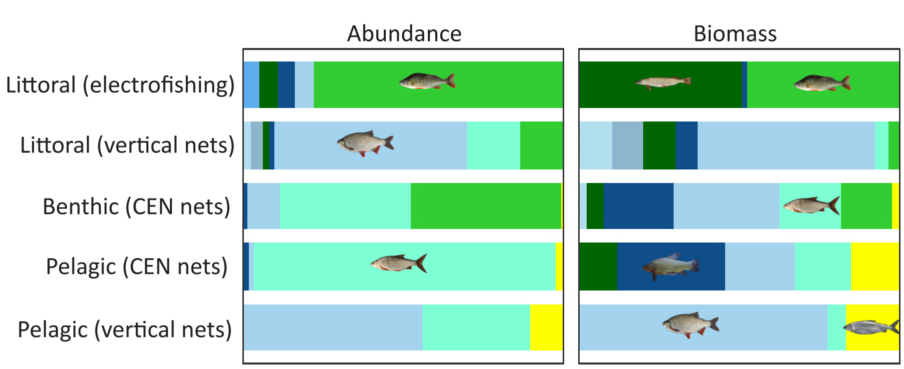
Lake Rousses is a small, shallow, relatively high-altitude lake in the Jura Mountains, within the Orbe-Aare (river) subcatchment. The lake is a short distance upstream from the paired lakes Joux and Brenet.

Fish community overview

10 fish species were recorded in Projet Lac, including 0 endemic and 3 non-native species. The lowest number of fish species of any lake in the Rhone catchment were recorded in this lake. Very low numbers of fish were recorded by electrofishing with 75% of electrofishing actions recording no fish. On the other hand, the highest catch rate of fish biomass in the open water surface layer was recorded in this lake (mostly large rudd). Roach and rudd were the most common species throughout the lake.

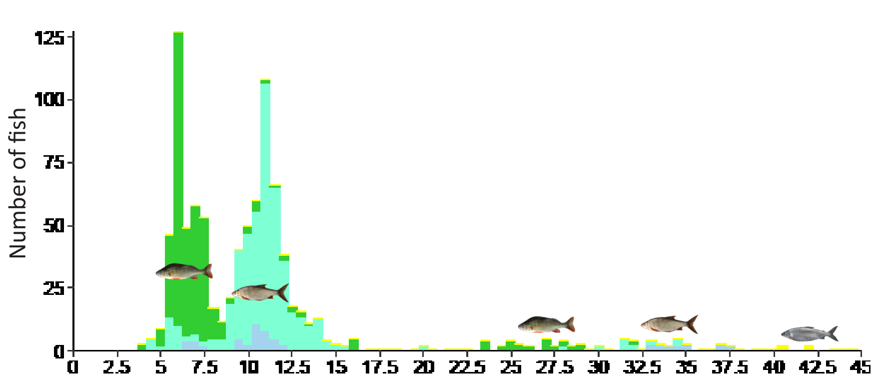
Community composition

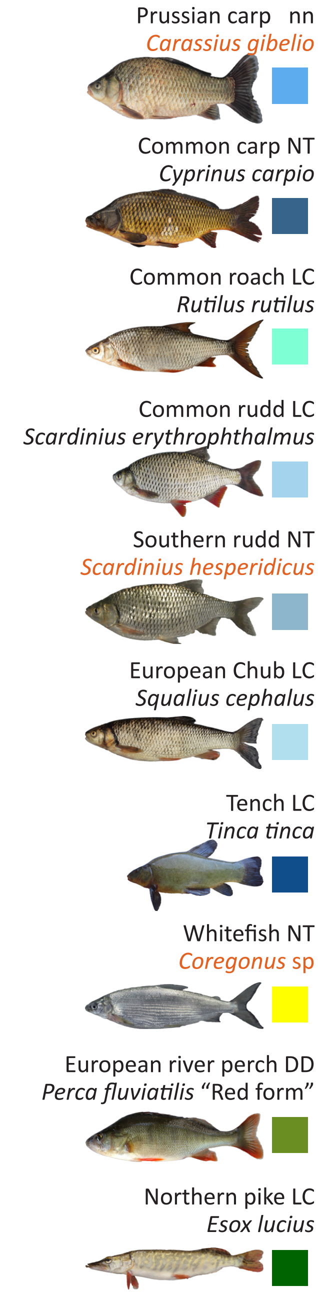
Near the lakeshore (littoral), perch dominated the meagre catches by electrofishing, while perch and pike dominated biomass. Littoral nets were dominated by rudd. Close to the lake floor (benthic), abundance was dominated by roach and perch, while tench and rudd made significant contributions to biomass. The open water (pelagic), was dominated by roach and rudd, while tench and whitefish also contributed to biomass.



Fish lengths

Fish caught in CEN nets were heavily dominated by small perch 6-8cm and roach 9-12cm. A number of large perch, roach and whitefish were also caught.

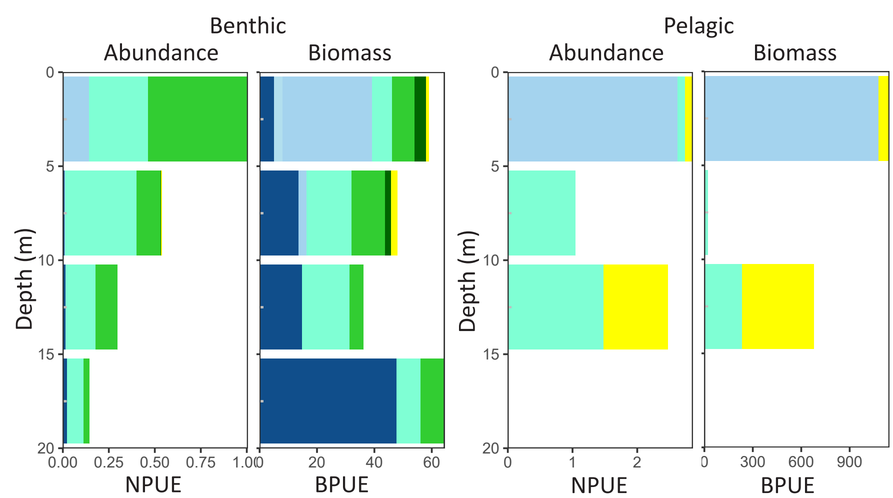




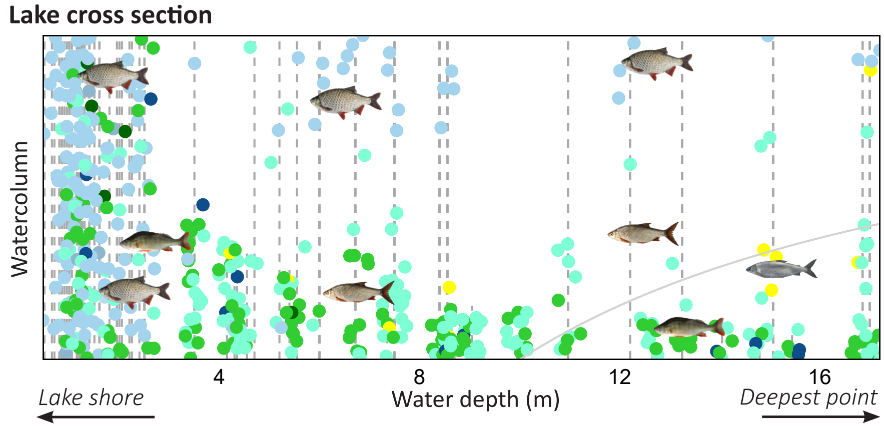
Lake Rousses

Depth distribution

Perch dominated the shallowest layer of the benthic zone, while roach was more common in the deeper layers. Tench contributed significant biomass throughout the layers. In open water, rudd dominated at the surface, with roach and whitefish below. The density of fish was low in open water.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common dace LC
Leuciscus leuciscus

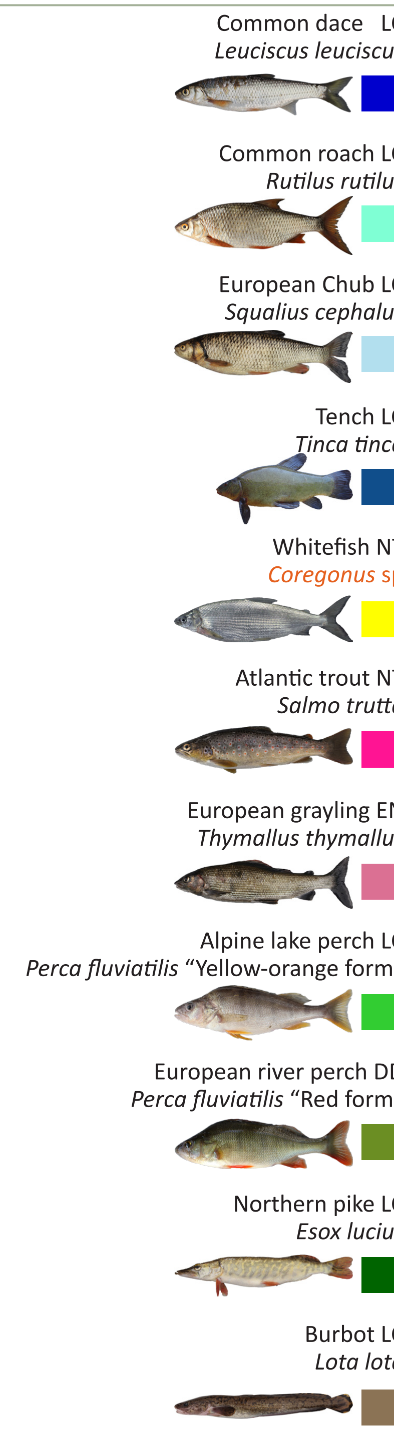
Minnow (species unknown) DD
Phoxinus sp

Atlantic trout NT
Salmo trutta

European grayling EN
Thymallus thymallus

Lake Joux

Rhine catchment



Lake environment

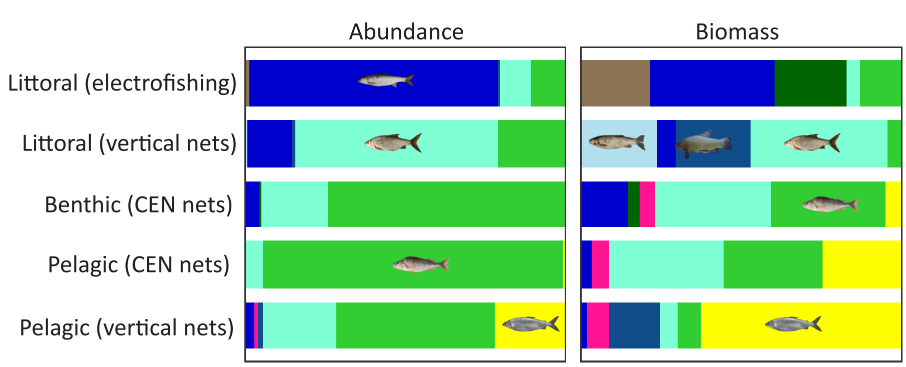
Lake Joux is a relatively high-altitude, mesotrophic lake in the Jura Mountains, within the Orbe-Aare (river) subcatchment. The lake is immediately upstream of Lake Brenet. Lake Joux has a high proportion of littoral habitats in a near-natural state, however these are affected by large, unnatural variations in water level. The lake suffers from hypoxia below 15 m during stratification.

Fish community overview

11 fish species were recorded in Projet Lac, including 0 endemic and 1 non-native species. Lake Joux was one of only two lakes in the Rhine catchment where grayling were caught, perhaps due to the cooler water temperature from the higher elevation. Perch dominated the numbers of fish caught in the benthic and open water habitats, with roach and dace common close to the lake shore. Dace were unusually abundant in this lake compared to all other surveyed lakes. Whitefish formed much of the biomass caught in open water. No fish were caught in the deeper half of the lake (i.e. below 15 m deep).

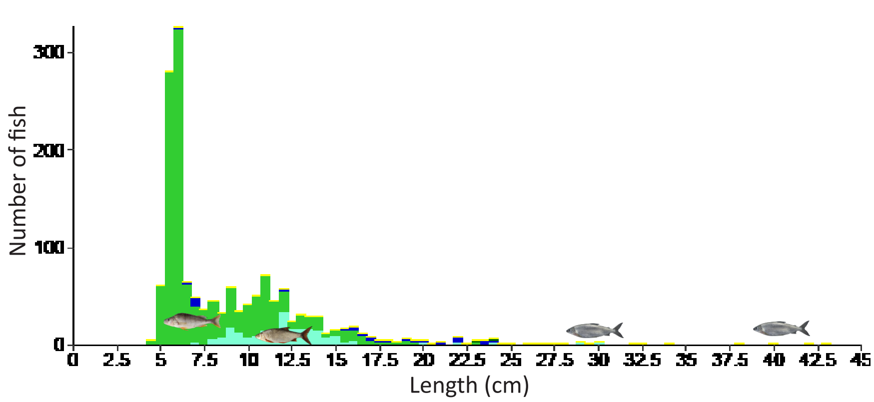
Community composition

Near the lakeshore (littoral), dace dominated the catches by electrofishing, while burbot, pike and perch significantly contributed to biomass. Littoral nets were dominated by roach, with chub and tench. Close to the lake floor (benthic), abundance was dominated by perch, while roach also formed around 30% of the biomass. The open water (pelagic) was dominated by perch, while roach and whitefish also made significant contributions.



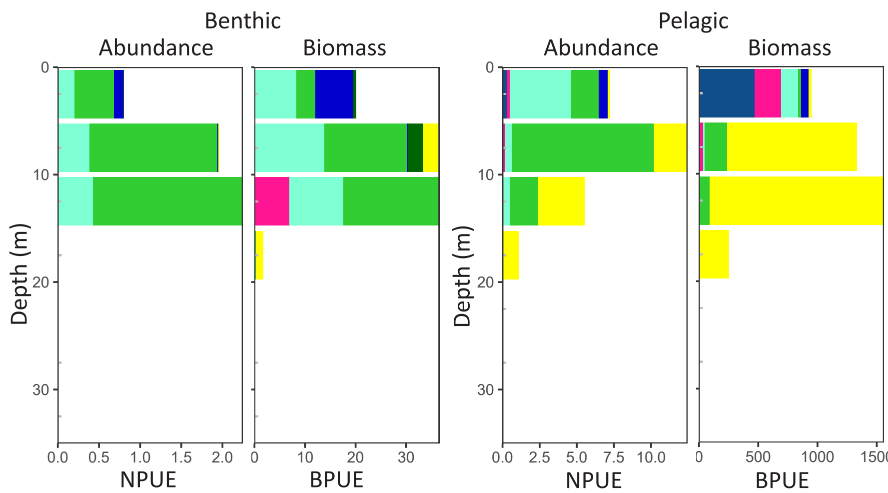
Fish lengths

Fish caught in CEN nets were dominated by small perch, with most 5-7 cm. Roach of 9-14 cm were also common.

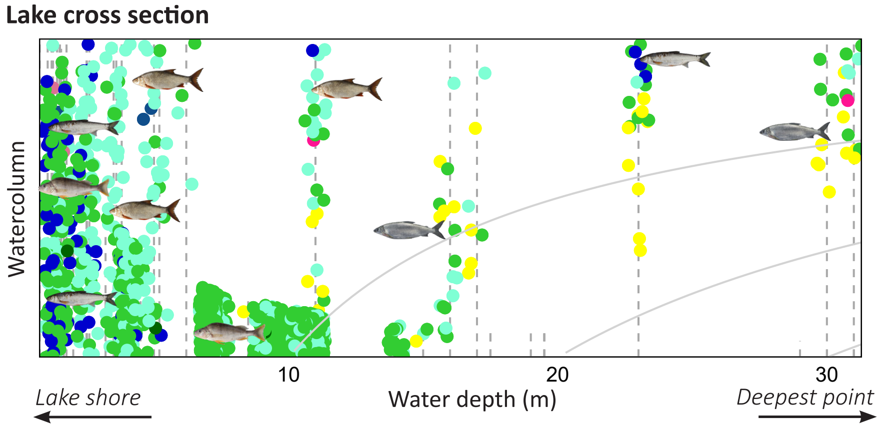


Lake Joux

Depth distribution
Surface layers dominated by perch, roach and dace, with abundance and biomass near the lake floor increasing with depth to 10-15 m. In the pelagic zone, fish were layered by depth, with roach near the surface, followed by perch, and whitefish below peaking between 5-15 m in open water. No fish recorded below 20 m from the surface.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common bleak LC
Alburnus alburnus

Common carp NT
Cyprinus carpio

Minnow (species unknown) DD
Phoxinus sp

Rainbow trout nn
Oncorhynchus mykiss

Pike-perch nn
Sander lucioperca

Lake Brenet

Rhine catchment

Lake environment

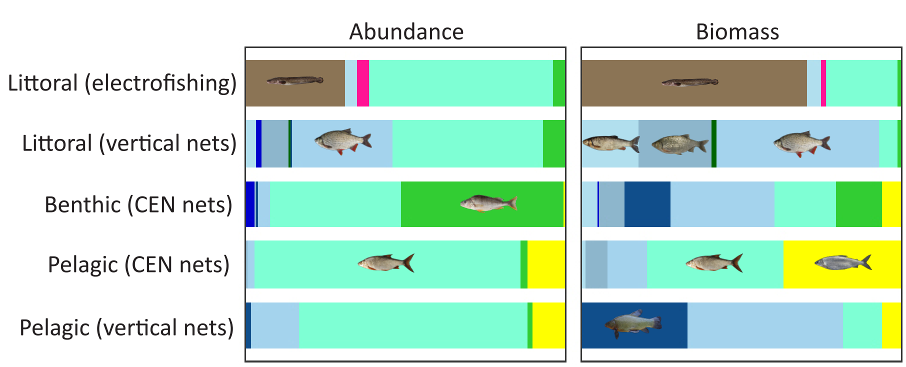
Lake Brenet is a small, shallow, relatively high-altitude, mesotrophic lake in the Jura Mountains, within the Orbe-Aare (river) subcatchment. The lake is immediately downstream of Lake Joux, with Lake Rousses a short distance upstream of the paired lakes. This lake had the highest proportion of littoral habitat in a near-natural state recorded in Projet Lac.

Fish community overview

12 fish species were recorded in Projet Lac, including 0 endemic and 2 non-native species. Fish species recorded in Lake Brenet were similar to those in neighbouring Lake Joux. Common and non-native southern rudd were recorded only in the smaller Lake Brenet, where they formed the majority of the fish biomass in the littoral and benthic nets. Roach dominated the numbers of fish caught in the littoral, benthic and pelagic habitats. Burbot also were common in the littoral zone (in electrofishing).

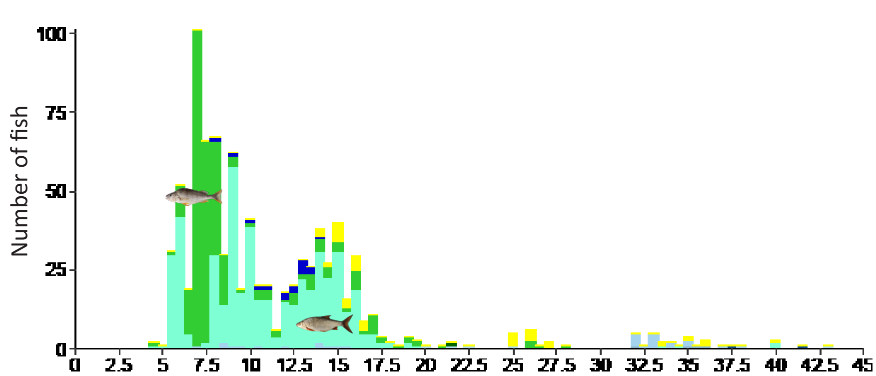
Community composition

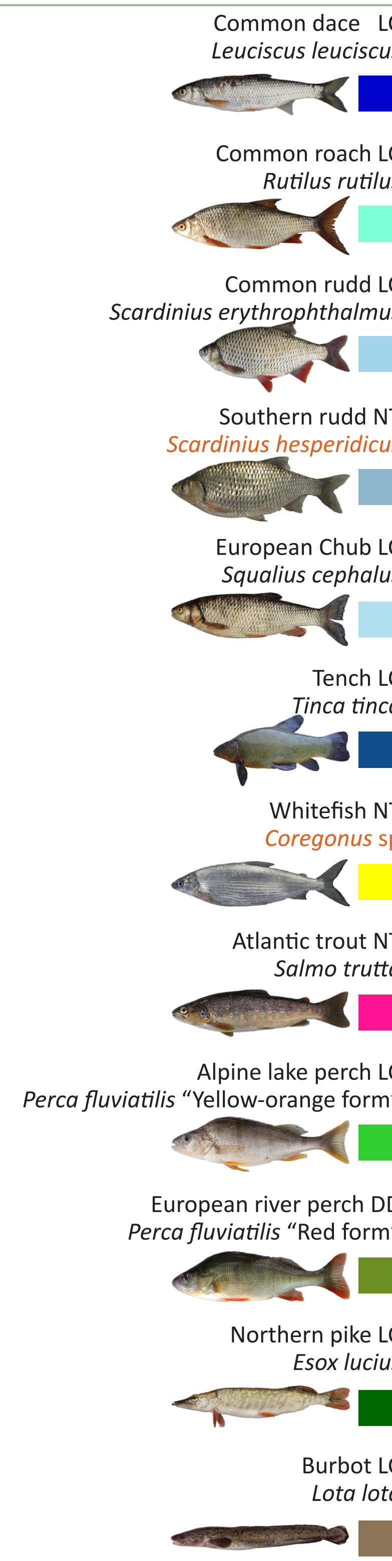
Near the lakeshore (littoral), electrofishing catches were dominated by burbot and roach. Littoral nets contained many rudd and roach, while biomass was dominated by common and non-native southern rudd. Lake floor (benthic) habitat was dominated by perch and roach, along with a high biomass contributions from common rudd and tench. Open water (pelagic) was dominated by roach, while whitefish, rudd and tench also contributed to biomass.



Fish lengths

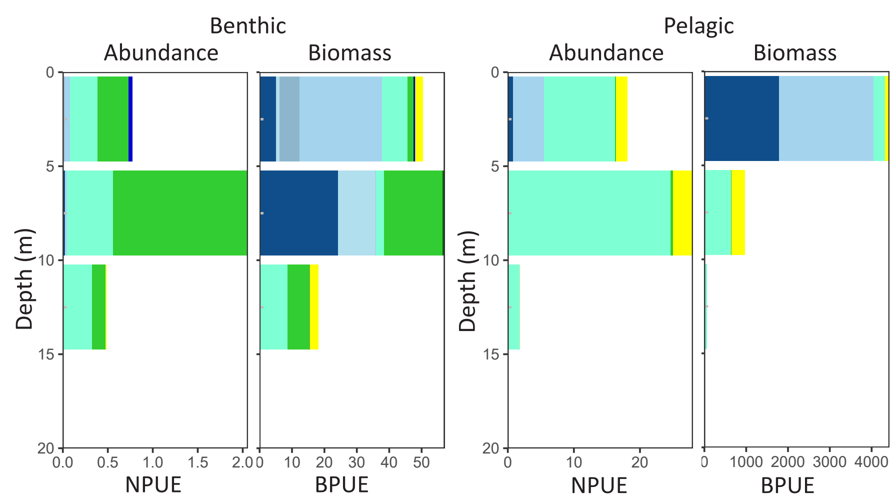
Fish caught in CEN nets were dominated by three sizes of roach: 5-6 cm, 8-11 cm, 12-16 cm. Many small perch 7-8 cm were also caught.



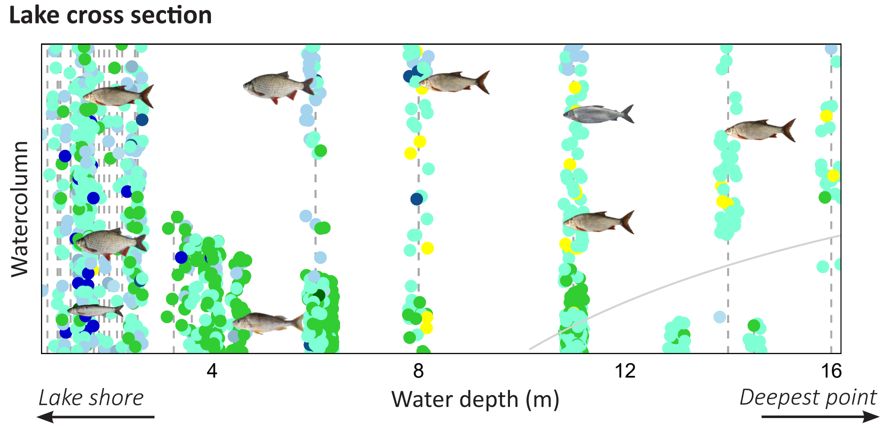


Lake Brenet

Depth distribution
Perch and roach dominated abundance across the depths in the benthic zone, while rudd and tench formed much of the biomass in the upper layers. Roach also dominated biomass across the depths in the open water, while tench and rudd formed much of the biomass in the uppermost layer.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Minnow (species unknown) DD
Phoxinus sp

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Lake Neuchatel
Rhine catchment

Lake environment

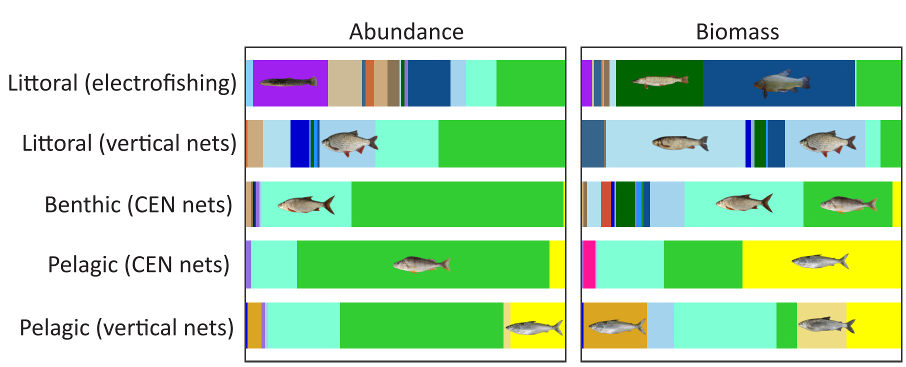
Lake Neuchatel is a large and deep lake at the southern foot of the Jura Mountains. Lakes Morat and Biel are connected to Lake Neuchatel by short (<10 km) channels. Lakes Brenet, Joux and Rousses are located upstream along the Thielle-Orbe (rivers). Lake Neuchatel was previously eutrophied, but was oligotrophic, with well-oxygenated deeper waters, at the time of sampling.

Fish community overview

26 fish species were recorded in Projet Lac, including 2 endemic and 4 non-native species. The fish community in Lake Neuchatel is similar to the neighbouring lakes Morat and Biel. The Palée (*Coregonus palaea*) is endemic to all three lakes, along with the endemic Bondelle (*Coregonus candidus*) in Lake Neuchatel. Perch dominated net catches by numbers in the littoral, benthic and pelagic habitats, with many affected by the "blackspot" flatworm parasite. Prevalence of the parasite was distinctly higher in the northeastern third of the lake. Cyprinids dominated the biomass of the benthic zone, while whitefish formed most of the fish biomass in the open water. The endemic Jaunet (*Salvelinus neocomensis*) is presumed extinct.

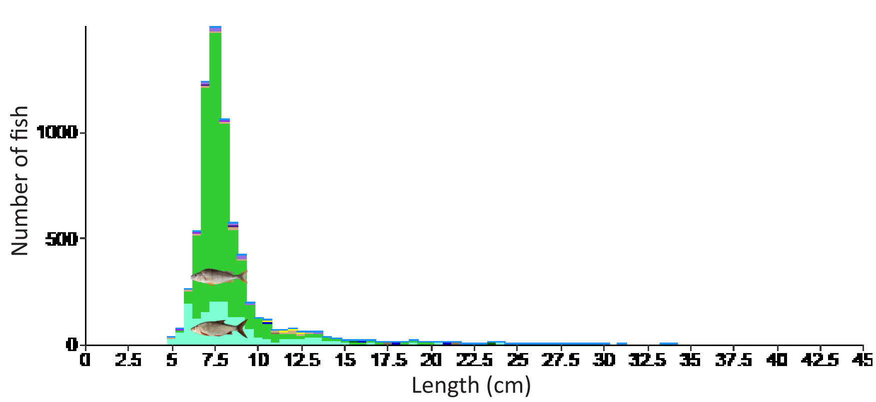
Community composition

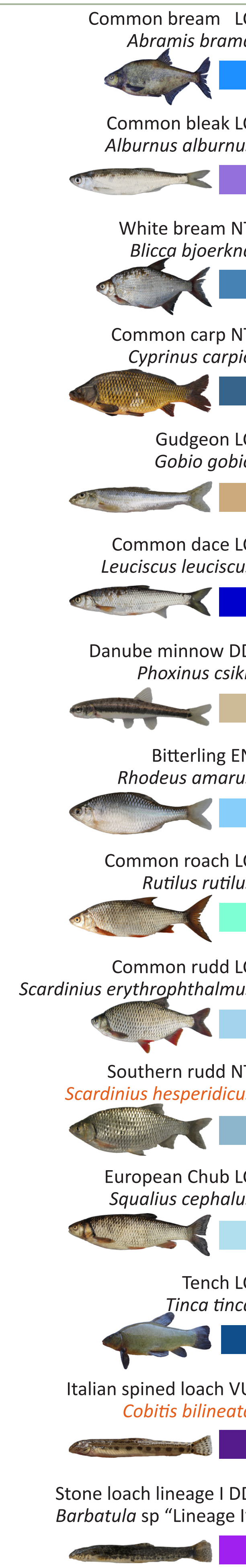
Near the lakeshore (littoral), stone loach and perch contributed the highest abundance by electrofishing, while tench and pike dominated the biomass. Littoral nets contained mostly perch, roach and rudd, with biomass mostly chub and rudd. Close to the lake floor (benthic), perch and roach dominated abundance and biomass. Most of the fish caught in open water (pelagic) were perch and roach, with biomass mostly whitefish.



Fish lengths

Fish caught in CEN nets were dominated by many small perch 6-8 cm and roach 6-9 cm.

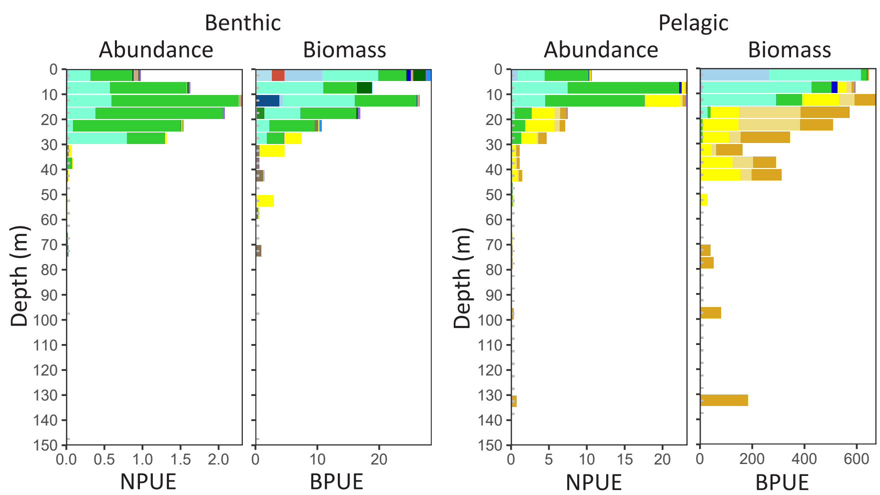




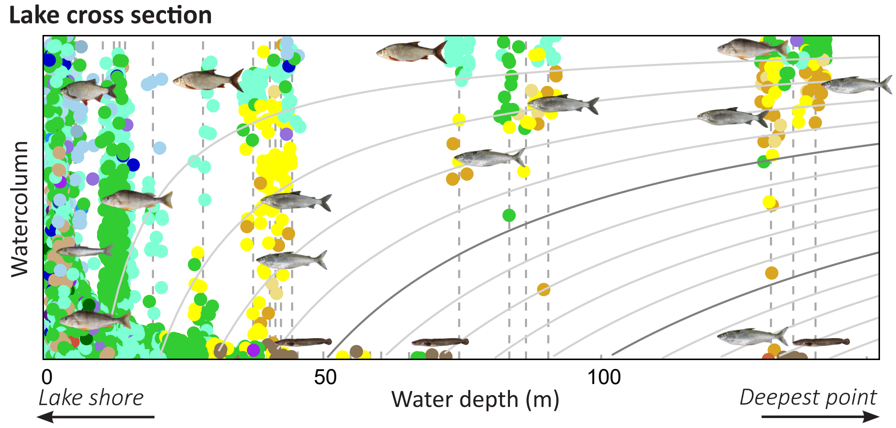
Lake Neuchatel

Depth distribution

Abundance of roach and perch in the benthic nets peaked at 10-15 m and dropped dramatically below 30 m. Benthic biomass followed a similar trend with a second peak close to the lake surface caused by rudd. Perch and roach were also abundant in the pelagic nets between 0-15 m, with whitefish most abundant 10-30 m. Pelagic biomass was layered by rudd 0-5 m, roach 0-15 m and whitefish 10-45 m. Burbot and sculpin were recorded from 140 m deep.



Lake cross section



Palée NT
Coregonus palaea

Bondelle NT
Coregonus candidus

Atlantic trout NT
Salmo trutta

Alpine lake perch LC
Perca fluviatilis "Yellow-orange form"

European river perch DD
Perca fluviatilis "Red form"

Pike-perch nn
Sander lucioperca

Pumpkinseed -
Lepomis gibbosus

Littoral lake sculpin NT
Cottus gobio "Aare lineage littoral"

Northern pike LC
Esox lucius

Wels catfish LC
Silurus glanis

Burbot LC
Lota lota

Fish species reported to occur in the lake but not recorded in Projet Lac

Common barbel NT
Barbus barbus

Prussian carp nn
Carassius gibelio

Goldfish nn
Carassius auratus

Common nase CR
Chondrostoma nasus

Lake char VU
Salvelinus umbla

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Largemouth bass / Blackbass nn
Micropterus salmoides

Three-spined stickleback (western) NT
Gasterosteus gymnurus

Three-spined stickleback (eastern) nn
Gasterosteus aculeatus

European eel CR
Anguilla anguilla

Brook lamprey EN
Lampetra planeri

Jaunet †
Salvelinus neocomensis

Lake Murten

Rhine catchment

Lake environment

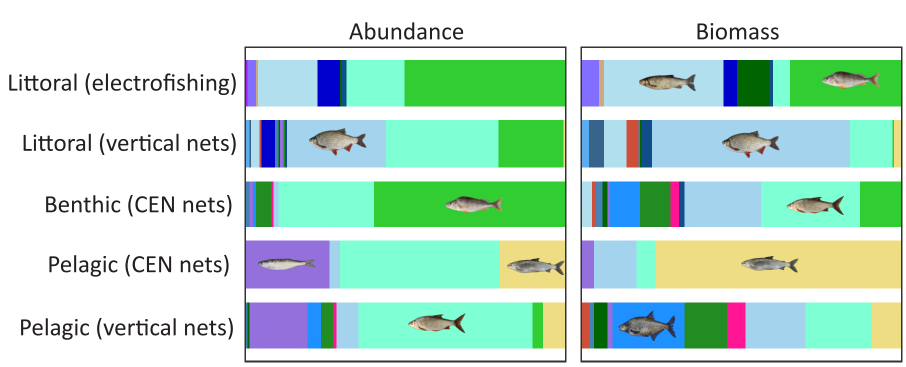
Lake Morat is a small lake compared to neighbouring lakes Neuchatel and Biel. The lake was mesotrophic at the time of sampling but had experienced severe eutrophication in the past century. There was no dissolved oxygen below 15 m deep around the time of sampling.

Fish community overview

23 fish species were recorded in Projet Lac, including 1 endemic and 4 non-native species. Fish in Lake Morat were dominated by cyprinids, predominantly roach, with chub and rudd (common and non-native southern) close to the lakeshore and bleak in open water. Perch was common in benthic habitats. No fish were recorded in the lower half of the lake. Failure to record burbot in the lake is noteworthy, with this species recorded in almost all other lakes in the Rhine catchment. The endemic Férit (*Coregonus restrictus*) is presumed extinct.

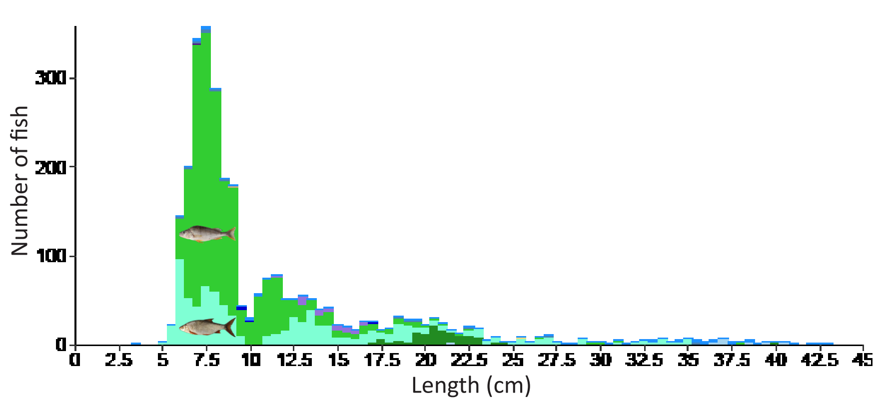
Community composition

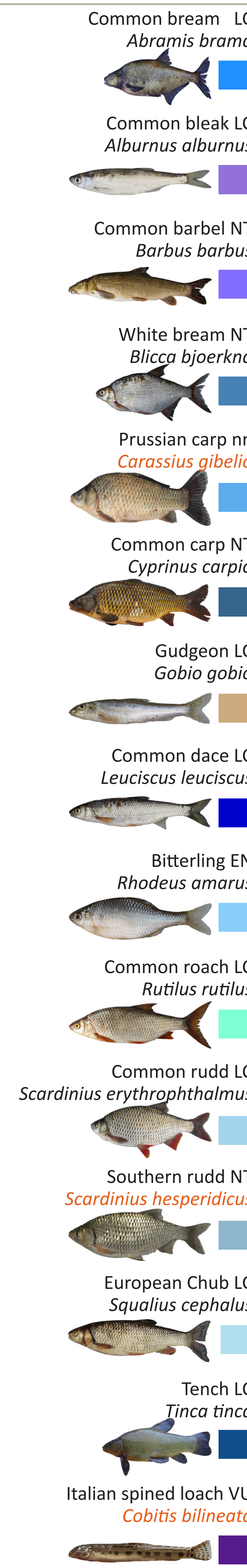
Near the lakeshore (littoral), perch, roach and chub were the most abundant fishes by electrofishing, while biomass was dominated by perch and chub. Littoral nets contained mostly rudd, roach and perch, while rudd made up most of the biomass. Close to the lake floor (benthic), perch and roach were the most abundant fishes, with rudd also contributing to biomass. Roach, bleak and whitefish most of the fish caught in the open water (pelagic) CEN nets, with biomass mostly whitefish. Biomass in pelagic vertical nets was diverse with a noteworthy contribution from bream.



Fish lengths

Fish caught in CEN nets were dominated by perch and roach with two peaks for each, likely reflecting age classes. Pikeperch 20-23 cm were also common.

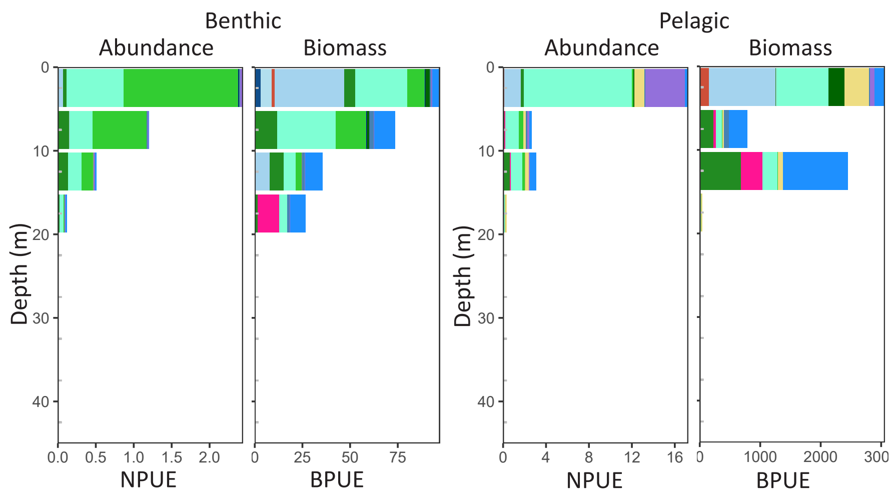




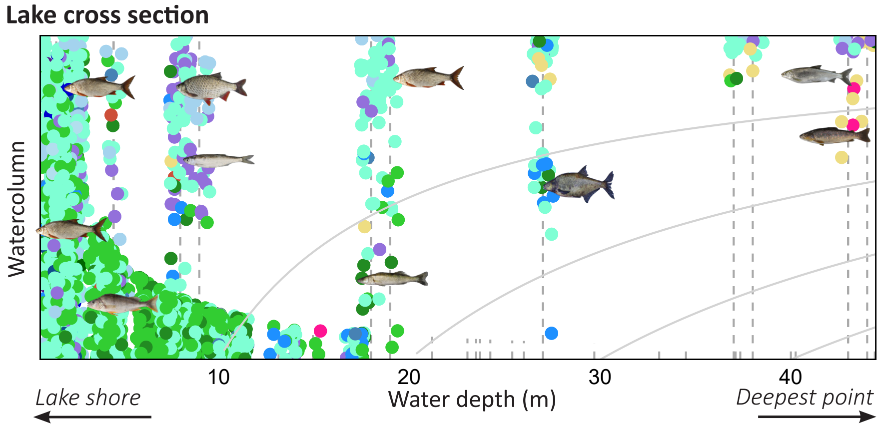
Lake Murten

Depth distribution

Perch and roach were most abundant in the shallowest layer of the benthic zone and consistently decreased with depth. Benthic biomass also decreased with depth. Abundance and biomass were also highest near the surface in the pelagic. Rudd, bleak and roach were common in open water in the shallow parts of the lake, with whitefish more common over deeper water. No fish below 20 m.

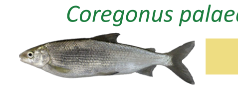


Lake cross section



Stone loach lineage I DD
Barbatula sp "Lineage I"

Palée NT
Coregonus palaea



Atlantic trout NT
Salmo trutta

Alpine lake perch LC
Perca fluviatilis "Yellow-orange form"

European river perch DD
Perca fluviatilis "Red form"

Pike-perch nn
Sander lucioperca

Northern pike LC
Esox lucius

Wels catfish LC
Silurus glanis

Fish species reported to occur in the lake but not recorded in Projet Lac

Spirlin VU
Alburnoides bipunctatus

Common nase CR
Chondrostoma nasus

Riffle dace VU
Telestes souffia aggassizi

Lake char VU
Salvelinus umbla

Rainbow trout nn
Oncorhynchus mykiss

Eurasian ruffe LC
Gymnocephalus cernua

Largemouth bass / Blackbass nn
Micropterus salmoides

European eel CR
Anguilla anguilla

Férit †
Coregonus restrictus

Lake Biel

Rhine catchment

Lake environment

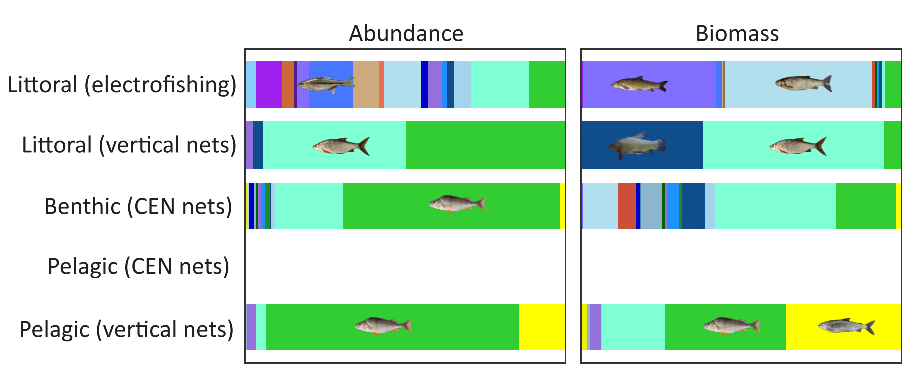
Lake Biel is part of the Aare (river) subcatchment and lies on the southern side of the Jura Mountains. The lake is intermediate in size and depth between the two neighbouring lakes Neuchatel and Morat. Lake Biel has experienced severe eutrophication but was oligo-mesotrophic at the time of sampling. The lake still experiences oxygen deficiencies in the deepest part of the lake.

Fish community overview

28 fish species were recorded in Projet Lac, including 2 endemic and 6 non-native species. Particularly high abundance, biomass and diversity of fish were recorded around the shoreline of Lake Biel by electrofishing. The only brook lampreys caught in Projet Lac were from this lake. Overall, catches were numerically dominated by perch, while roach formed much of the biomass in the benthic catches and whitefish dominated the biomass in open water. Very few fish were caught below 35 m deep. This was also one of the few lakes in the Rhine catchment where no Atlantic trout were recorded, suggesting very low numbers in the lake.

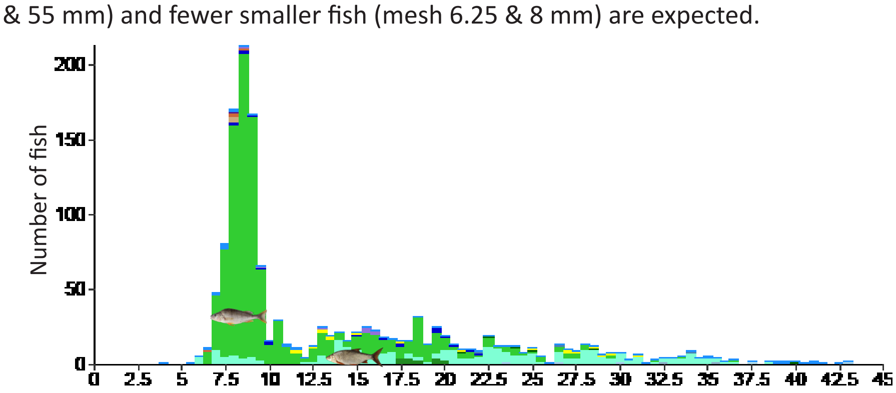
Community composition

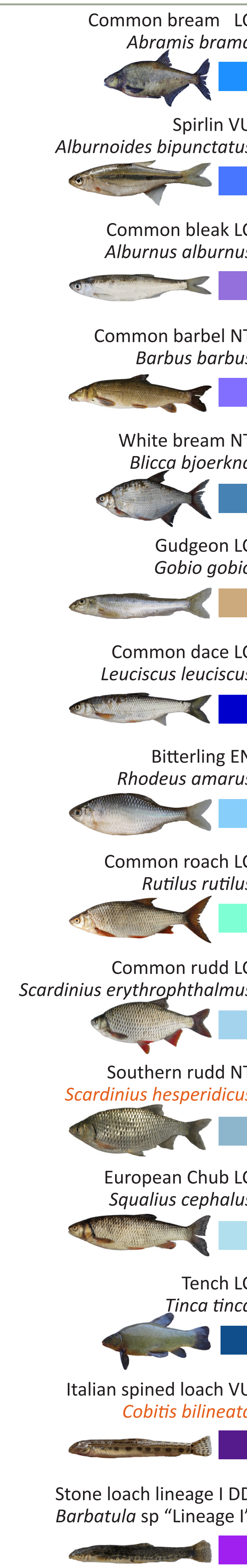
Near the lakeshore (littoral), catches by electrofishing were diverse, although biomass was dominated by barbel and chub. Littoral nets contained mostly roach and perch, with biomass mostly tench and roach. Close to the lake floor (benthic), most fish were perch and roach, with biomass mostly roach and perch. The open water (pelagic) was dominated by perch, while biomass was contributed mostly by perch, whitefish and roach.



Fish lengths

Nets used to sample Lake Biel contained different mesh areas so the length distribution is not directly comparable to other lakes. More larger fish (mesh 43 & 55 mm) and fewer smaller fish (mesh 6.25 & 8 mm) are expected.

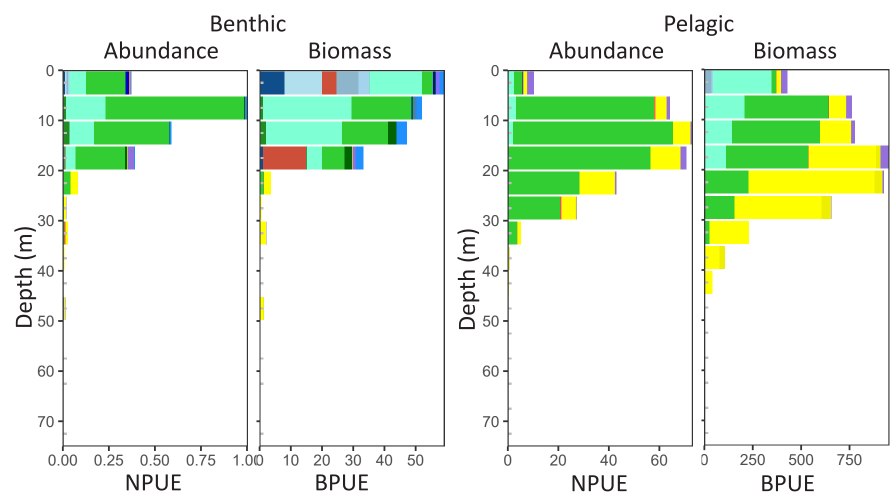




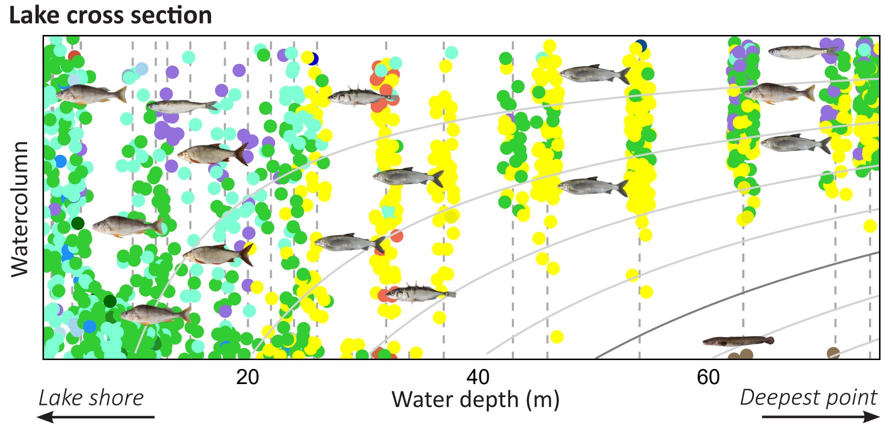
Lake Biel

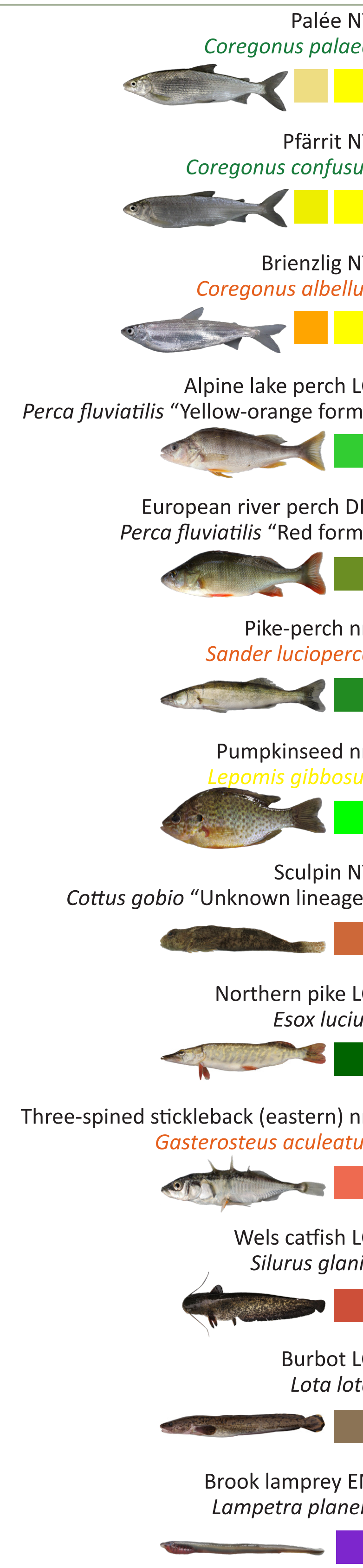
Depth distribution

Perch and roach dominated the benthic catches, with perch most abundant, peaking and 5-10 m, and roach forming most of the biomass in the upper 15 m. In the pelagic, abundance was very low near the surface. Abundance and biomass peaked at 10-20 m. Pelagic biomass showed smooth depth transitions from roach, to perch to whitefish. Whitefish dominated throughout the water-column over parts of the lake more than 25 m deep.



Lake cross section





Fish species reported to occur in the lake but not recorded in Projet Lac

Prussian carp nn
Carassius gibelio

Common nase CR
Chondrostoma nasus

Common carp NT
Cyprinus carpio

Minnow (species unknown) DD
Phoxinus sp

Riffle dace VU
Telestes souffia aggassizi

Atlantic trout NT
Salmo trutta

Lake char VU
Salvelinus umbla

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Largemouth bass / Blackbass nn
Micropterus salmoides

Sculpin (species unknown) DD
Cottus sp

European eel CR
Anguilla anguilla

Lake Thun

Rhine catchment

Lake environment

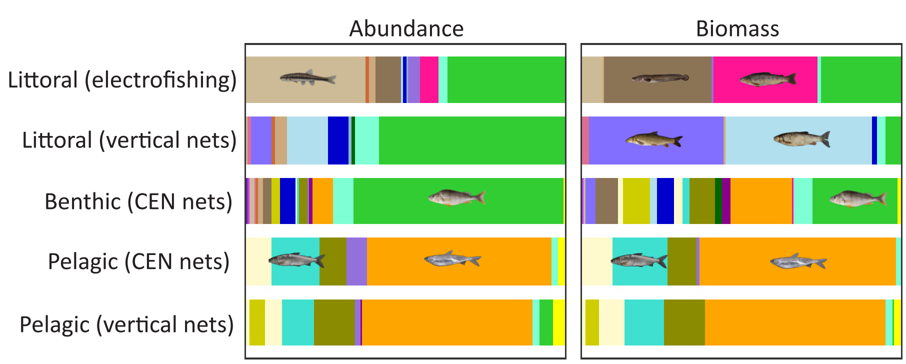
Lake Thun is a large and deep oligotrophic lake in the Aare (river) subcatchment on the northern edge of the Alps. Lake Brienz is immediately upstream. The twin lakes were never strongly eutrophied and have probably always had dissolved oxygen throughout the watercolumn. Lake Thun has a high proportion of modified littoral habitats.

Fish community overview

27 fish species were recorded in Projet Lac, including 10 endemic and 3 non-native species. The highest number of endemic fish species of all surveyed lakes was recorded in Lake Thun, including records of 6 endemic whitefish, 3 endemic char and 1 endemic sculpin species. Many, but not all, of the endemic species are shared with Brienz. Low catch rates were recorded in the littoral zone and shallow open water, however benthic catches of biomass were of a similar magnitude throughout the entire depth of the lake. In open water, the peak of abundance and biomass was deeper than in most lakes (consistent with other oligotrophic lakes).

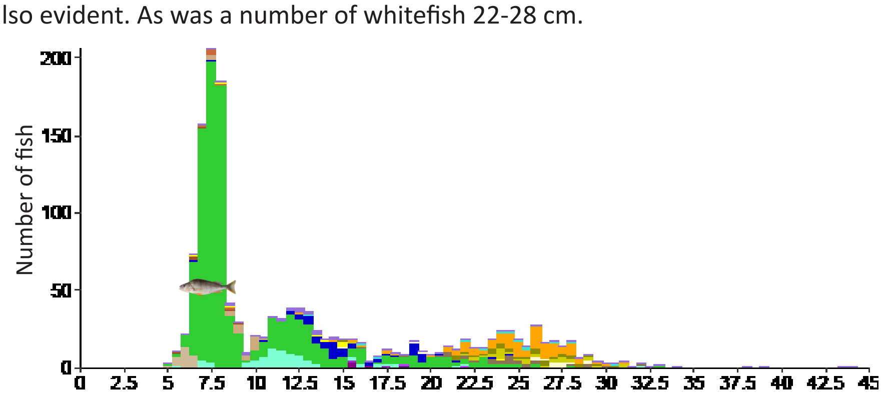
Community composition

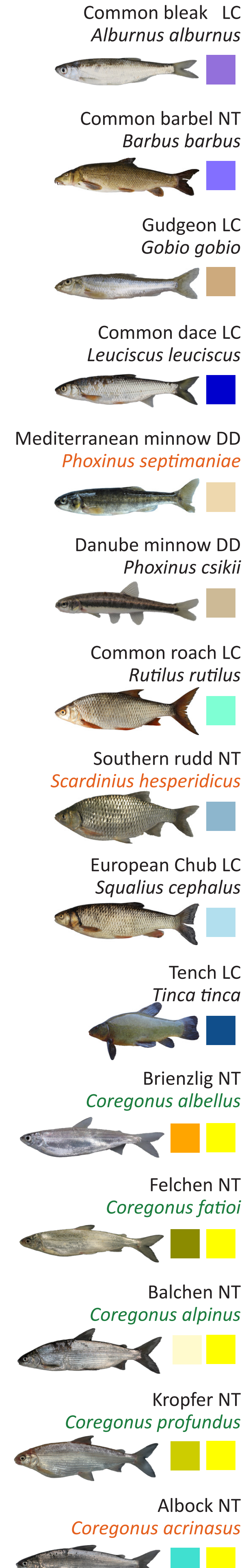
Near the lakeshore (littoral), gudgeon and perch dominated abundance, while biomass was mostly burbot, Atlantic trout and perch. Littoral nets contained mostly perch, with biomass mostly chub and barbel. Close to the lake floor (benthic), perch constituted most of the fish and much of the biomass, with whitefish and burbot also contributing to biomass. The open water (pelagic) was heavily dominated by whitefish.



Fish lengths

Fish caught in CEN nets were dominated by two cohorts of small perch 7-8 cm and 11-14 cm. A small peak of gudgeon around 6 cm and roach 10-13 cm were also evident. As was a number of whitefish 22-28 cm.





Lake Thun

Steinmann's Balchen NT
Coregonus steinmanni

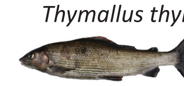
Atlantic trout NT
Salmo trutta

Orange-bellied char VU
Salvelinus sp "Limnetic Thun/Brienz"

Profundal dwarf char Thun VU
Salvelinus sp "Profundal-dwarf Thun"

Profundal extreme char Thun VU
Salvelinus sp "Profundal extreme Thun"

European grayling EN
Thymallus thymallus



Alpine lake perch LC
Perca fluviatilis "Yellow-orange form"

European river perch DD
Perca fluviatilis "Red form"

Littoral lake sculpin NT
Cottus gobio "Aare lineage littoral"

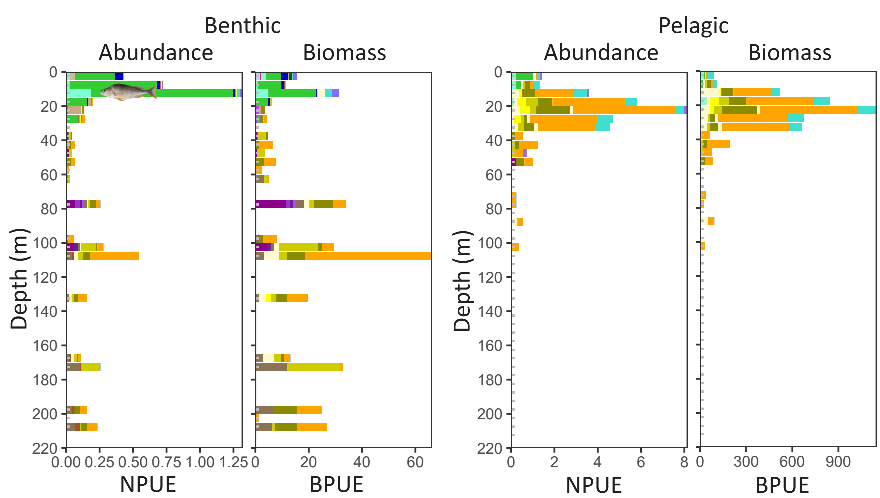
Profundal sculpin Thun NT
Cottus gobio "Profundal Thun"

Northern pike LC
Esox lucius

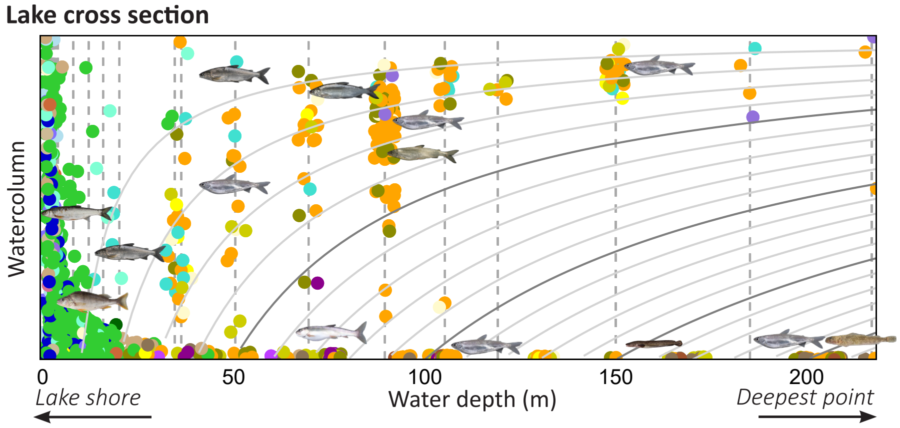
Burbot LC
Lota lota

Depth distribution

In the benthic nets, perch dominated the shallow layers to around 30 m, with whitefish, char and burbot common near the lake floor below 30 m to the deepest point. Benthic biomass was similar across the lake depths. Different species of whitefish dominated fish in the pelagic nets, with the highest catches at 20-25 m and dropping below 55 m. Few fish caught in open water below 50 m.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common bream LC
Abramis brama

White bream NT
Blicca bjoerkna

Common nase CR
Chondrostoma nasus

Common carp NT
Cyprinus carpio

Common rudd LC
Scardinius erythrophthalmus

Stone loach (species unknown) DD
Barbatula sp

Canadian lake trout nn
Salvelinus namaycush

Giant piscivorous char Thun VU
Salvelinus sp "Giant Thun"

Benthic char Thun / Brienz VU
Salvelinus sp "Benthic Thun/Brienz"

Rainbow trout nn
Oncorhynchus mykiss

Wels catfish LC
Silurus glanis

European eel CR
Anguilla anguilla

Brook lamprey EN
Lampetra planeri

Lake Brienz

Rhine catchment

Lake environment

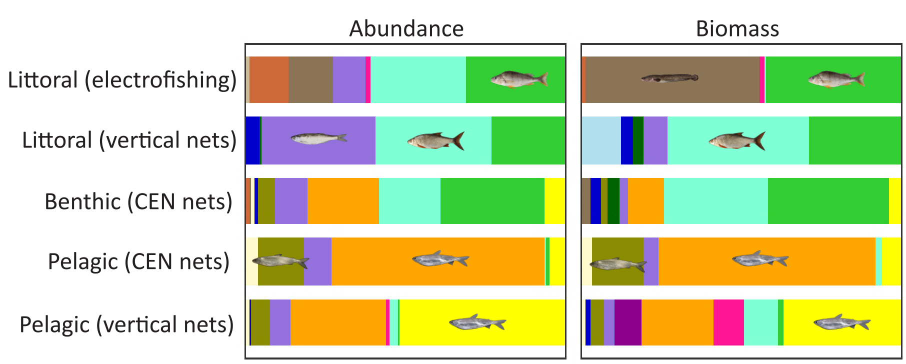
Lake Brienz is a large and very deep oligotrophic lake in the Aare (river) sub-catchment on the northern edge of the Alps. The average depth of this lake is the deepest of all surveyed northern perialpine lakes. Lake Thun is immediately downstream. The twin lakes were never strongly eutrophied and have probably always had dissolved oxygen throughout the watercolumn. Fine glacial sediments in the lake result in high turbidity, low light penetration and a shallow zone of primary productivity.

Fish community overview

16 fish species were recorded in Projet Lac, including 4 endemic and 0 non-native species. All but one of these endemic species are shared with Lake Thun. Lake Brienz was one of only two (of 35) surveyed lakes where no non-native species were recorded (the other was Lake Walen). Among the highest whole-lake catch rates of whitefish by abundance were also recorded in this lake, contributed by the four recorded endemic whitefish species. The lowest catch rates in the littoral zone by electrofishing were recorded in the lake, with several widespread cyprinid species, tench, gudgeon and rudd, absent from the catches.

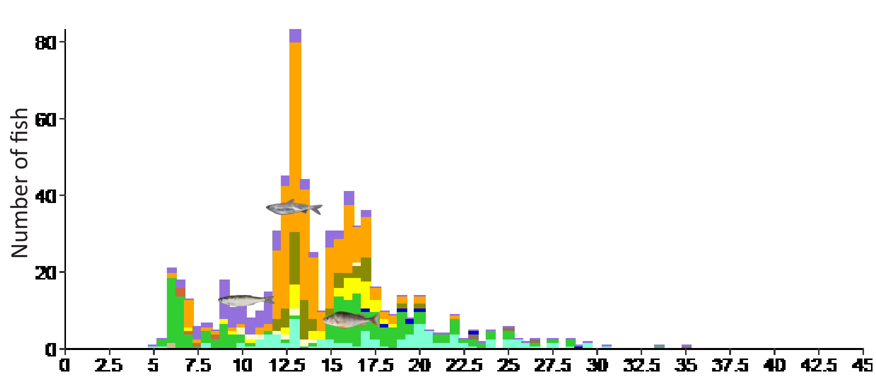
Community composition

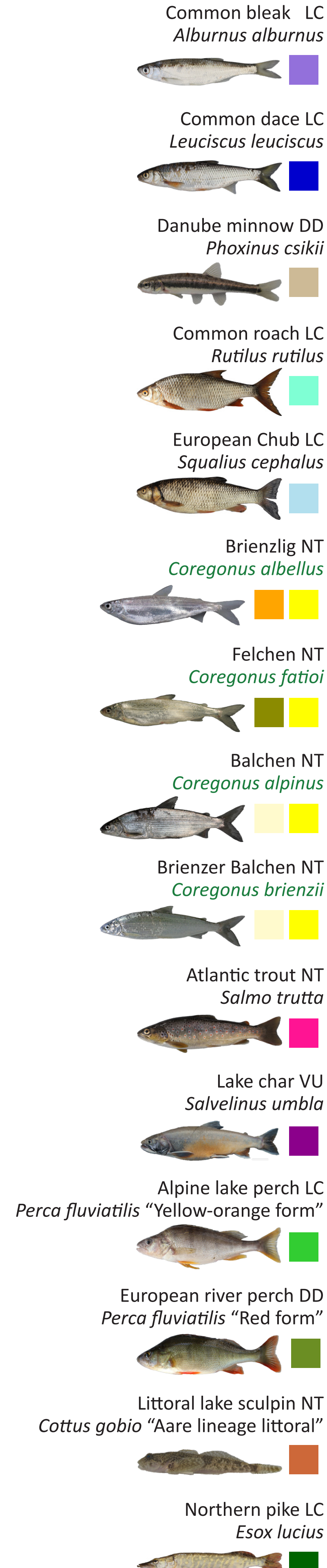
Near the lakeshore (littoral), electrofishing catches were a mix of low numbers of perch, roach, sculpin, burbot and bleak, while biomass was dominated by burbot and perch. Littoral nets contained many bleak and roach, with a high biomass of roach and perch. Close to the lake floor (benthic), nets contained mostly perch, whitefish and roach, with biomass again dominated by perch and roach. The open water (pelagic) contained mostly different species of whitefish, along with Atlantic trout, char and bleak.



Fish lengths

Fish caught in CEN nets were dominated by whitefish 12-17 cm. Bleak 8-17 cm were also evident, with a high proportion of larger perch and roach.



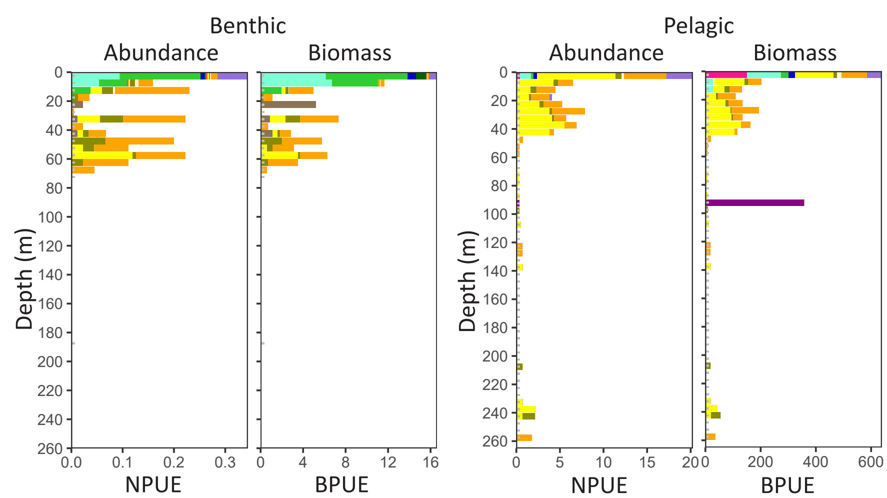


Lake Brienz

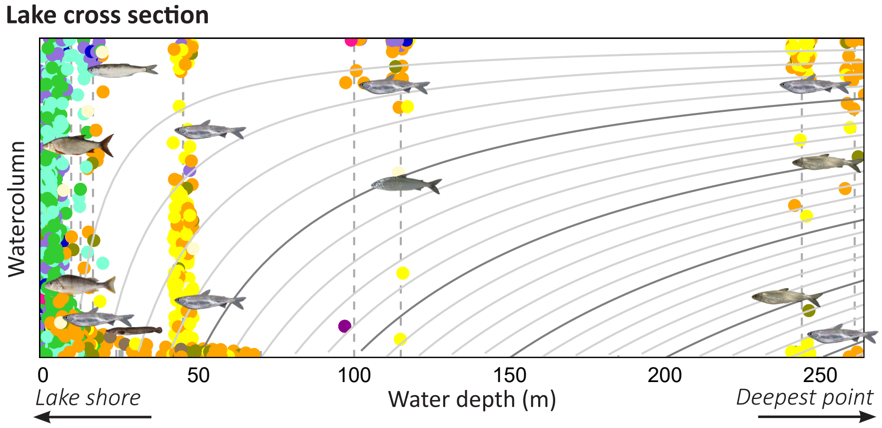
Burbot LC
Lota lota

Depth distribution

Perch and roach were mainly confined to the upper 10 m of the benthic zone, while whitefish dominated 10-70 m. Only one benthic net was set below 75 m, which caught no fish. Whitefish dominated the fish in the pelagic zone, with fish caught to the deepest point of the lake. A large char was caught around 90 m from the surface.

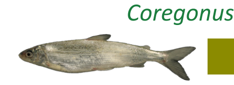


Lake cross section

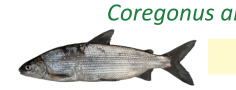


Brienzlig NT
Coregonus albellus

Felchen NT
Coregonus fatioi



Balchen NT
Coregonus alpinus



Brienzer Balchen NT
Coregonus brienzii

Fish species reported to occur in the lake but not recorded in Projet Lac

Common bream LC
Abramis brama

Spirlin VU
Alburnoides bipunctatus

Common barbel NT
Barbus barbus

Common carp NT
Cyprinus carpio

Gudgeon LC
Gobio gobio

Common rudd LC
Scardinius erythrophthalmus

Tench LC
Tinca tinca

Stone loach (species unknown) DD
Barbatula sp

Limnetic char Brienz VU
Salvelinus sp "Limnetic Brienz"

Benthic char Thun / Brienz VU
Salvelinus sp "Benthic Thun/Brienz"

Canadian lake trout nn
Salvelinus namaycush

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Lake Zug

Rhine catchment

Lake environment

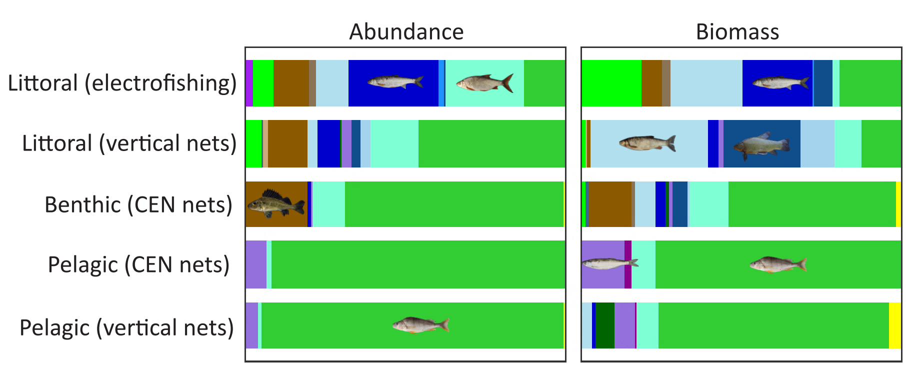
Lake Zug is a large and deep eutrophic lake in the Reuss (river) subcatchment on the northern edge of the Alps. The lake was previously heavily eutrophied. In the year of sampling it had no dissolved oxygen below 140m water depth.

Fish community overview

19 fish species were recorded in Projet Lac, including 1 endemic and 2 non-native species. Very high numbers of perch were caught in the upper layers of the open water and benthic habitats. Non-native ruffe were common in the littoral and deeper benthic catches. Very few fish were caught below 30 m deep, although several burbot were caught at 80 m. Whitefish contributed less than 5% of the catches in open water and only 3 char were caught in the lake. *Coregonus* sp “Zugeralbeli” is presumed extinct. A second extinct endemic species, *Coregonus* sp “Zuger Kropfer”, has recently been discovered from museum collections.

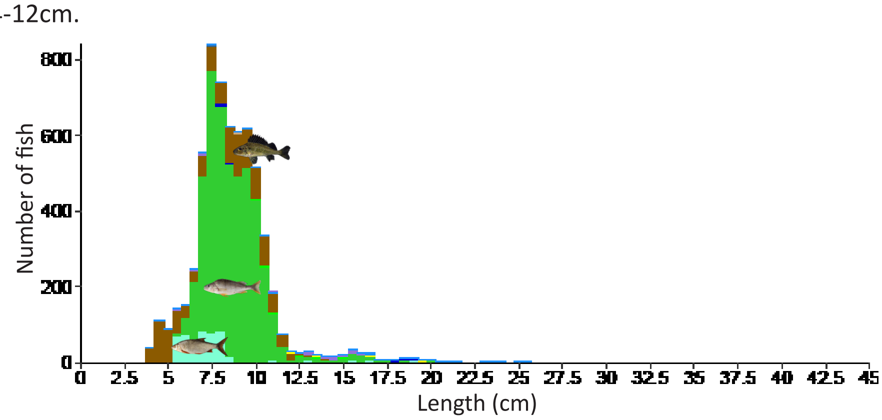
Community composition

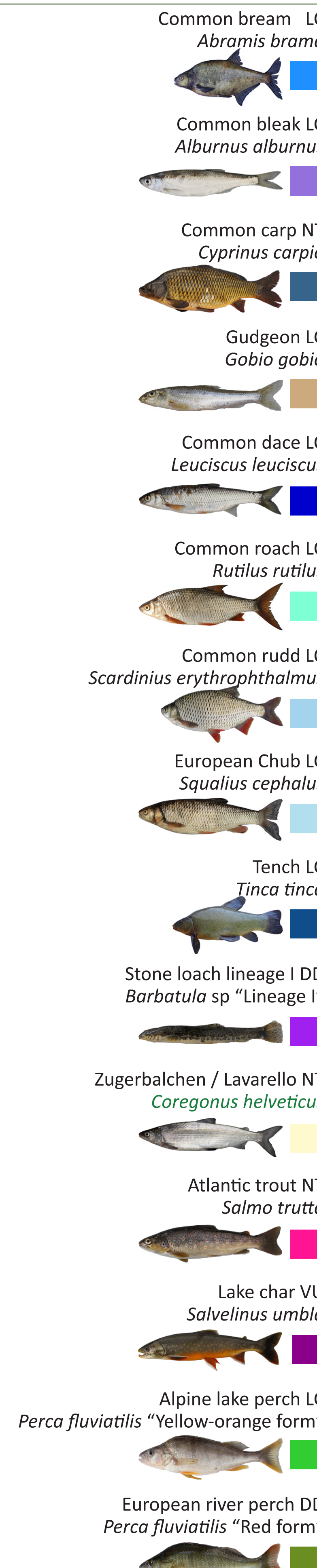
Near the lakeshore (littoral), dace and roach were the most common fish caught by electrofishing, with biomass mostly dace, chub, perch and non-native pumpkinseed. Littoral nets were dominated by perch and roach, with biomass mostly chub and tench. Close to the lake floor (benthic), perch dominated abundance and biomass, while roach and non-native ruffe also made substantial contributions. The open water (pelagic) was heavily dominated by perch, with contributions from roach and bleak.



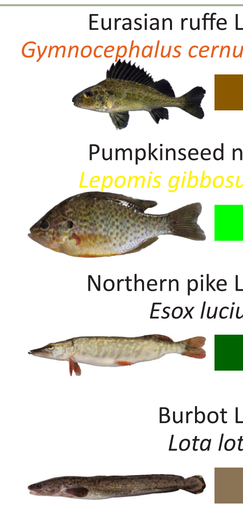
Fish lengths

Fish caught in CEN nets were heavily dominated by small perch 7-11 cm. Small roach 5-8 cm were also evident. Non-native ruffe were common, ranging from 4-12cm.



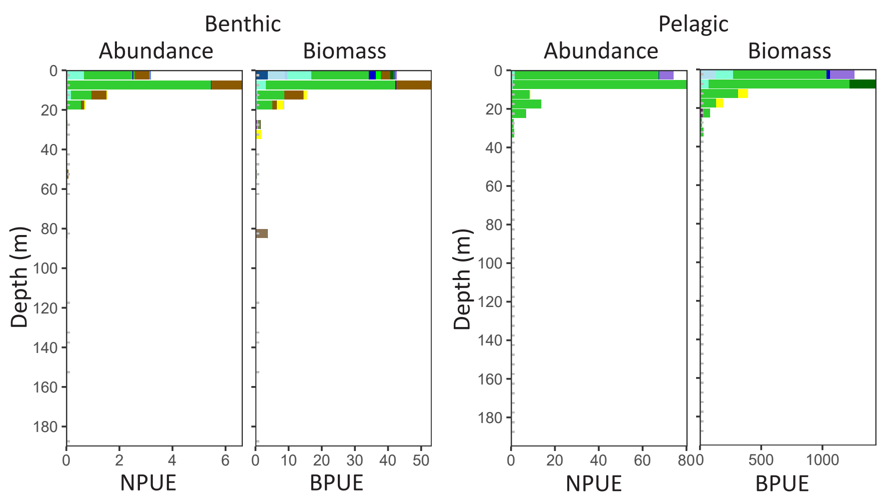


Lake Zug

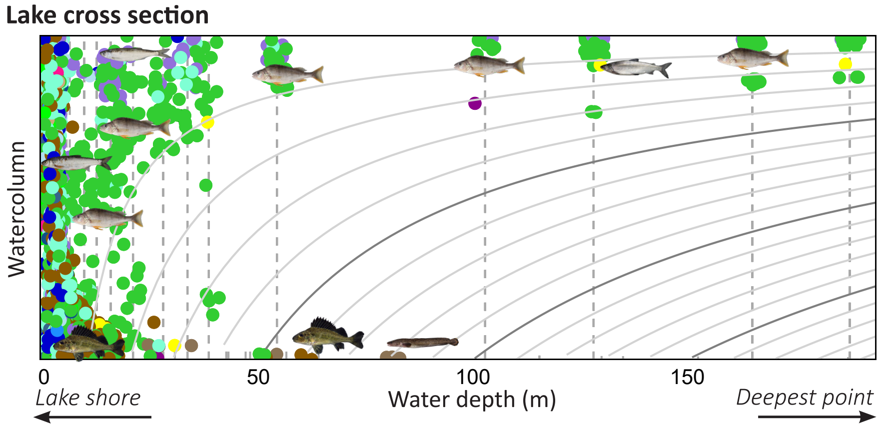


Depth distribution

Benthic fish were dominated by perch and non-native ruffe in the upper 20 m. Very few fish were caught below 20 m, with 8 fish caught between 50-85 m and no fish below 85 m. Pelagic nets were also dominated by perch, with small contributions from bleak and one large pike. Deeper perch were likely caught in the net as it was being raised. No fish were caught in the pelagic zone below 35 m.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Spirlin VU
Alburnoides bipunctatus

Common barbel NT
Barbus barbus

White bream NT
Blicca bjoerkna

Rainbow trout nn
Oncorhynchus mykiss

Pike-perch nn
Sander lucioperca

Sculpin (species unknown) DD
Cottus sp

European eel CR
Anguilla anguilla

Zugeralbeli †
Coregonus sp "Zugeralbeli"

Zuger Kropfer †
Coregonus sp "Zuger Kropfer"

Lake Lucerne

Rhine catchment

Lake environment

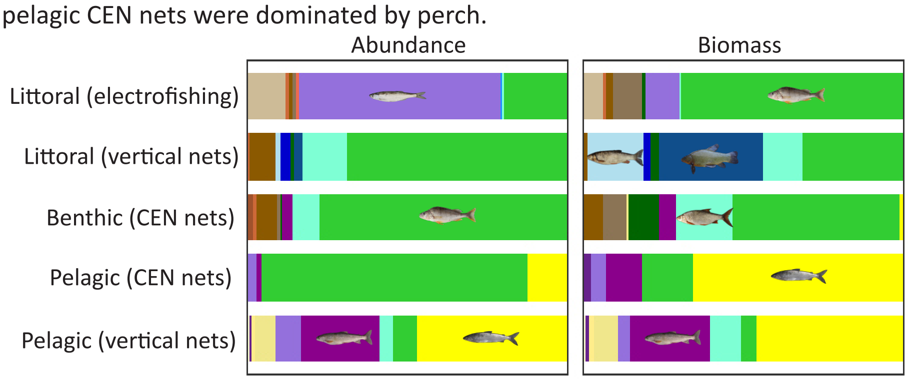
Lake Lucerne is a large and deep lake oligotrophic lake in the Reuss (river) sub-catchment on the northern edge of the Alps. The lake consists of multiple deep basins that are separated by shallower narrow stretches and have different environmental conditions and histories. Lake Lucerne experienced mild eutrophication and was mesotrophic in the 1970s and 1980s. Vitznau and Gersau basins were moderately affected by deep-water oxygen deficiencies during this period, while the Urner basis was consistently oxygenated.

Fish community overview

27 fish species were recorded in Projet Lac, including 7 endemic and 3 non-native species. High number of endemic species caught in Lake Lucerne resulted in a high uniqueness of the fish community. This lake was also unusual among the perialpine lakes for its high biomass of char. Numbers of char in open water peaked between 35 - 60 m from the surface, immediately above were the whitefish between 10 - 35 m, with perch, roach and bleak near the surface. Char were also common in benthic catches below 40 m, along with burbot, while perch were common close to the lakeshore. A relatively high biomass of non-native ruffe was recorded in the benthic habitats of Kreuztrichter and adjacent basins. *Salmo* cf. *schiefermuelleri* is presumed extinct.

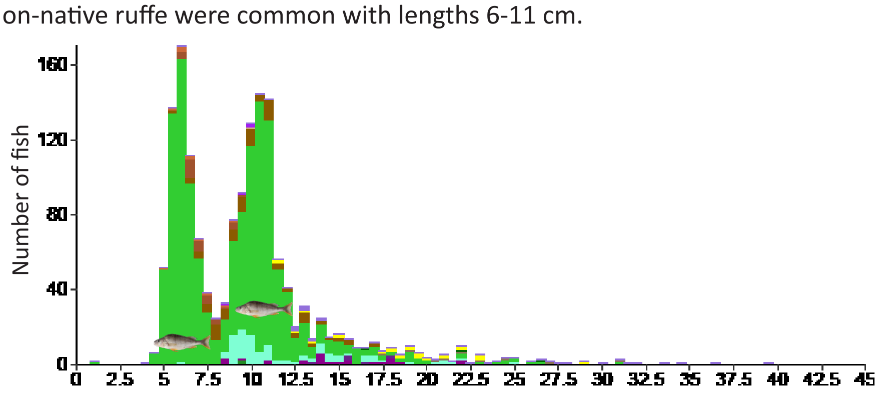
Community composition

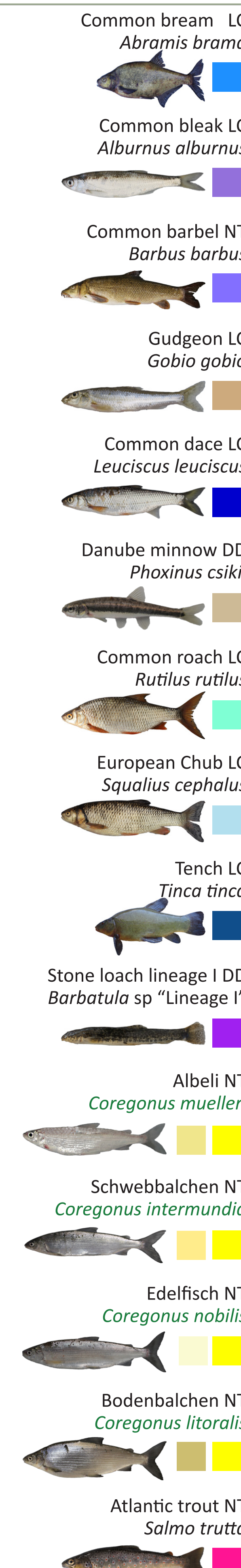
Near the lakeshore (littoral), electrofishing catches were dominated by bleak, followed by perch and gudgeon, with biomass mostly perch. Littoral nets and nets close to the lake floor (benthic), were dominated by perch, with contributions from roach and non-native ruffe. Biomass in littoral nets was mostly perch and tench, while biomass in benthic nets was mostly perch and roach. In the open water (pelagic), biomass was dominated by whitefish, followed by char and perch. Similar patterns were seen in the vertical pelagic nets, while the pelagic CEN nets were dominated by perch.



Fish lengths

Fish caught in CEN nets were dominated by two cohorts of perch 6-7 cm and 9-12 cm. Roach were common in lengths 8-17 cm, with char of similar sizes. Non-native ruffe were common with lengths 6-11 cm.

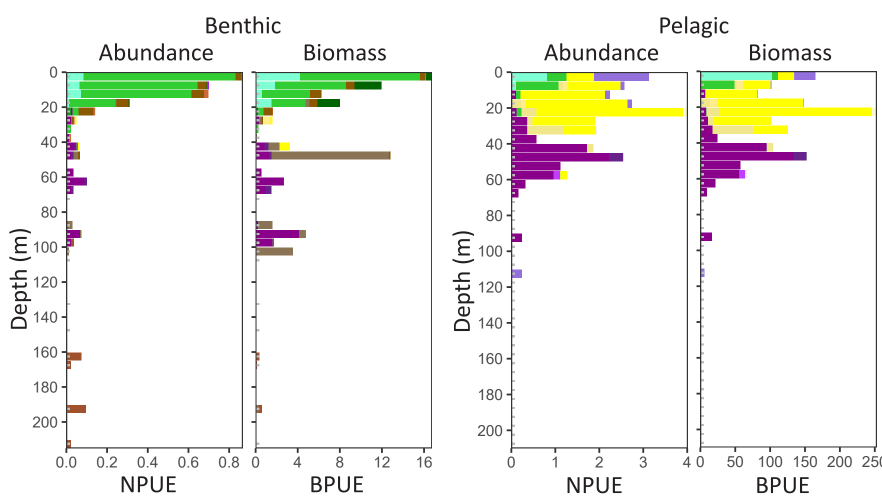




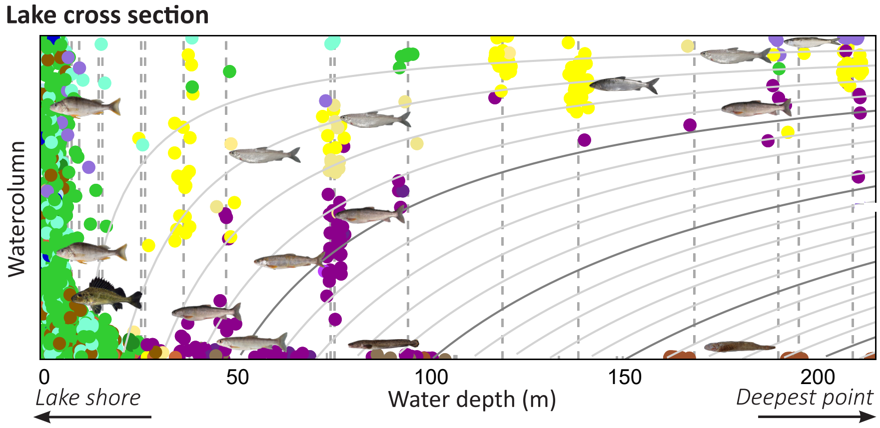
Lake Lucerne

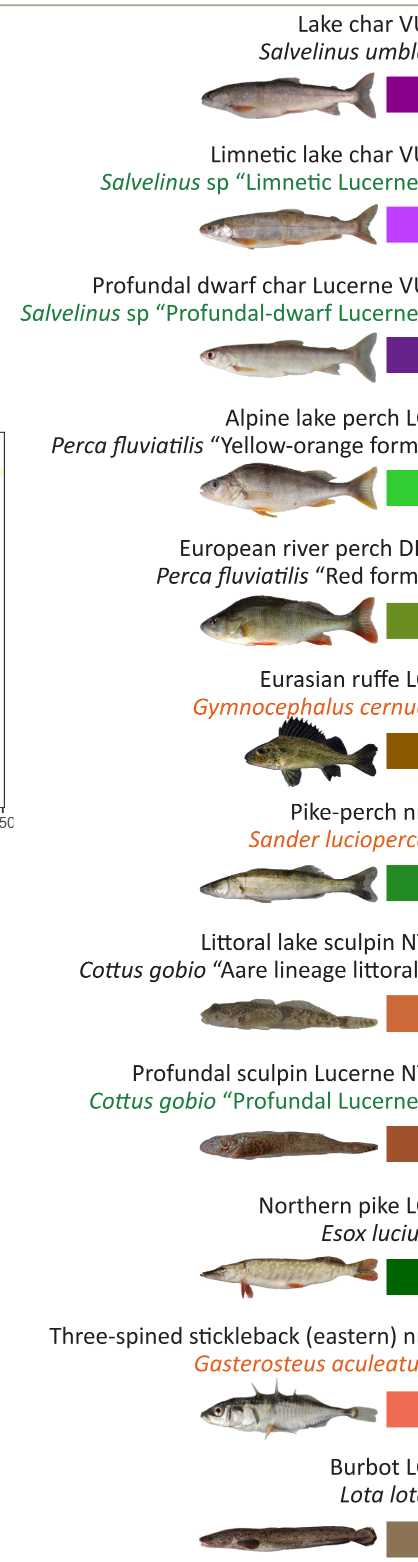
Depth distribution

Perch dominated the upper 20 m of the benthic zone, along with roach and non-native ruffe. Pike also contributed to biomass in shallower benthic layers. Char and burbot dominated between 40 m to 100 m, with sculpin below, to the deepest point of the lake. In the open water, roach, perch and bleak were confined to the upper 10 m. Whitefish dominated abundance and biomass between 15-35 m, with char the dominant fish between 35-70 m.



Lake cross section





Fish species reported to occur in the lake but not recorded in Projet Lac

Spirlin VU
Alburnoides bipunctatus

White bream NT
Blicca bjoerkna

Common nase CR
Chondrostoma nasus

Common carp NT
Cyprinus carpio

Common rudd LC
Scardinius erythrophthalmus

Riffle dace VU
Telestes souffia aggassizi

Pelagic Schwebbalchen NT
Coregonus suspensus

Giant piscivorous char Lucerne VU
Salvelinus sp "Giant Lucerne"

Canadian lake trout nn
Salvelinus namaycush

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Pumpkinseed nn
Lepomis gibbosus

European eel CR
Anguilla anguilla

Brook lamprey EN
Lampetra planeri

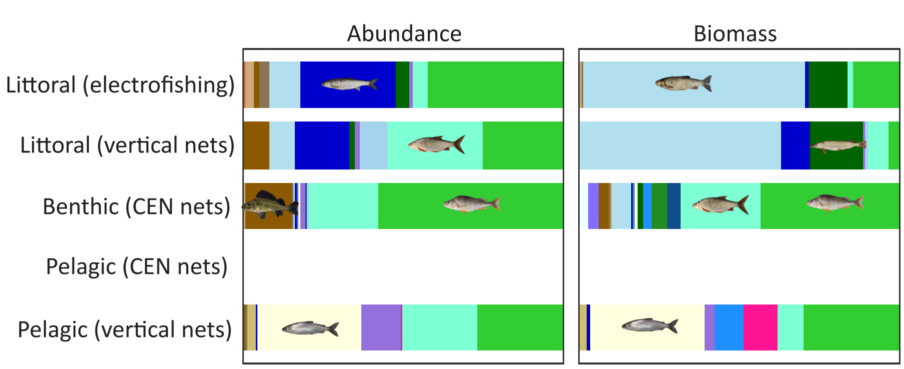
Schwebforelle †
Salmo schiefermuelleri

Lake Sarnen
Rhine catchment

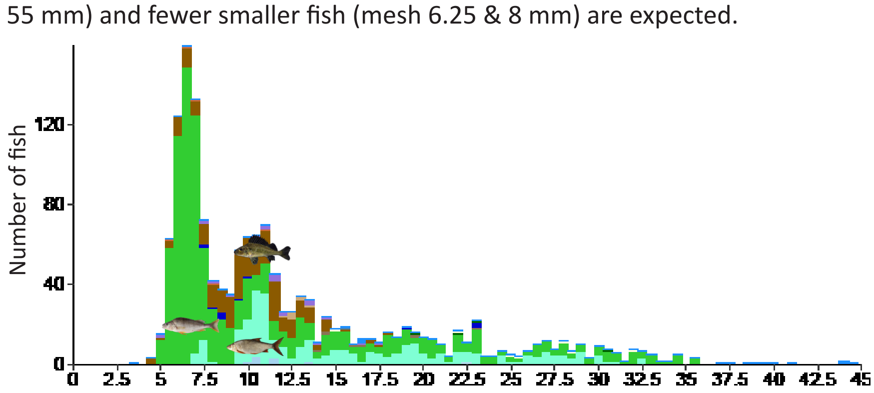
Lake environment
Lake Sarnen is a relatively small, oligotrophic lake in the Reuss (river) sub-catchment on the northern edge of the Alps. Lake Lucerne lies a short distance downstream. The lake experienced mild oxygen deficiencies close to the deepest point of the lake during its mesotrophic period in the 21st century.

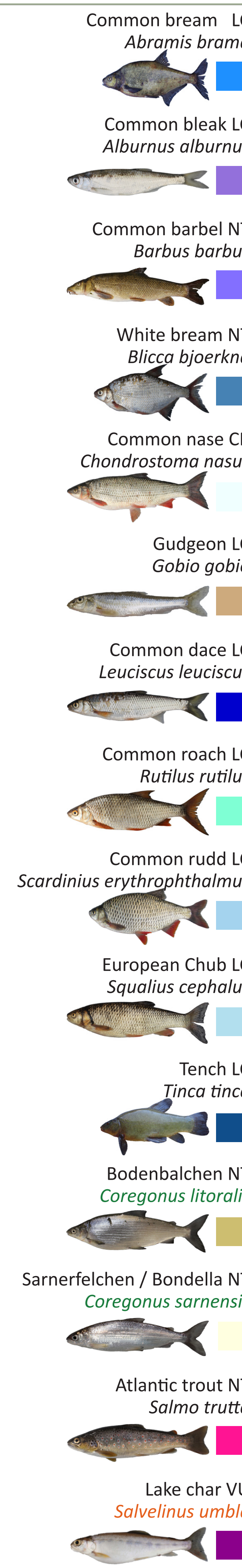
Fish community overview
22 fish species were recorded in Projet Lac, including 2 endemic and 3 non-native species. A relatively high number of native species were recorded in Lake Sarnen considering its size, including the only record of nose carp in Projet Lac. Perch were abundant in the upper 10 m of benthic habitats, with dace and roach also common in the intertidal. Many large chub were also caught close the the lakeshore. Non-native ruffe were common in benthic habitats. Whitefish dominated the abundance and biomass of fish caught in open water.

Community composition
Near the lakeshore (littoral), electrofishing catches were dominated by perch and dace, while biomass was mostly chub. Littoral nets contained a high proportion of roach and perch, with biomass again dominated by chub, along with pike. Close to the lake floor (benthic), perch was most abundant, with roach and non-native ruffe. Biomass was dominated by perch and roach. The open water (pelagic) contained a high proportion of whitefish and perch, with roach and bleak also contributing to abundance. No CEN nets were deployed in the pelagic zone.

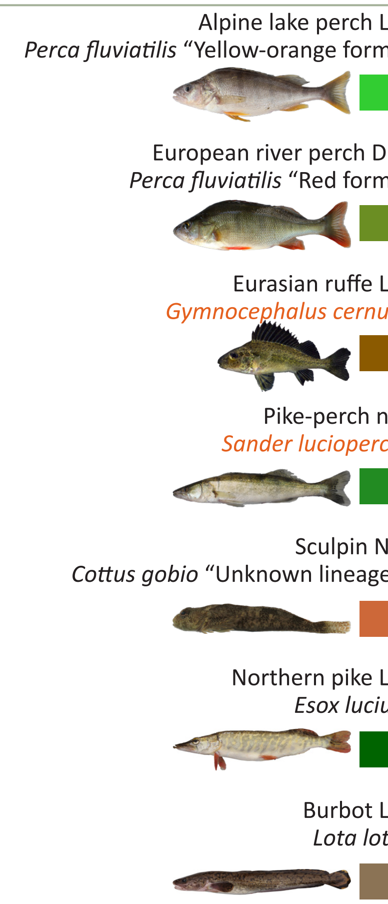


Fish lengths
Nets used to sample Lake Sarnen contained different mesh areas so the length distribution is not directly comparable to other lakes. More larger fish (mesh 43 & 55 mm) and fewer smaller fish (mesh 6.25 & 8 mm) are expected.



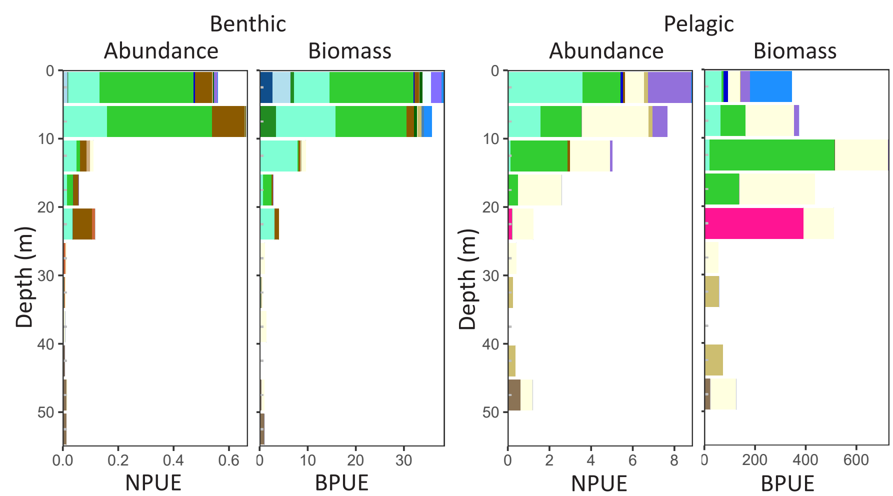


Lake Sarnen

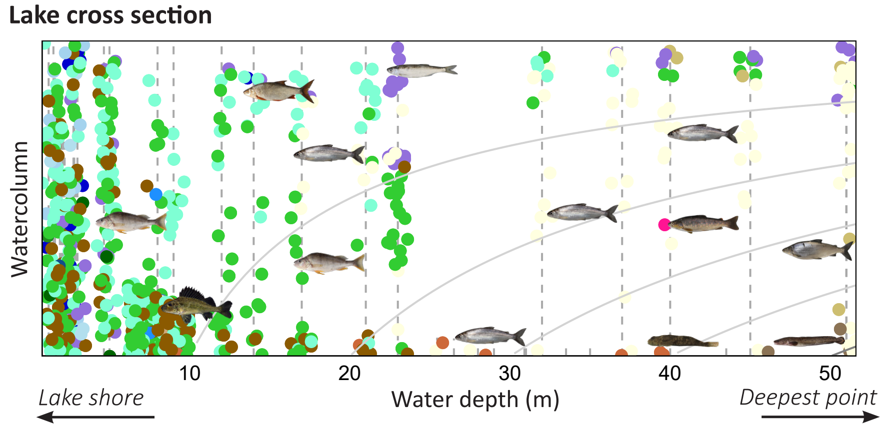


Depth distribution

Perch and roach dominated abundance and biomass near the lake floor to around 10 m, below which catches dropped markedly. Non-native ruffe contributed a noteworthy proportion of abundance to 25 m. In open water, roach and bleak dominated near the surface, with perch and whitefish below. A large lake trout was caught at 23 m deep. Fish were caught down to the deepest point of the lake.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common carp NT
Cyprinus carpio

Stone loach (species unknown) DD
Barbatula sp

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

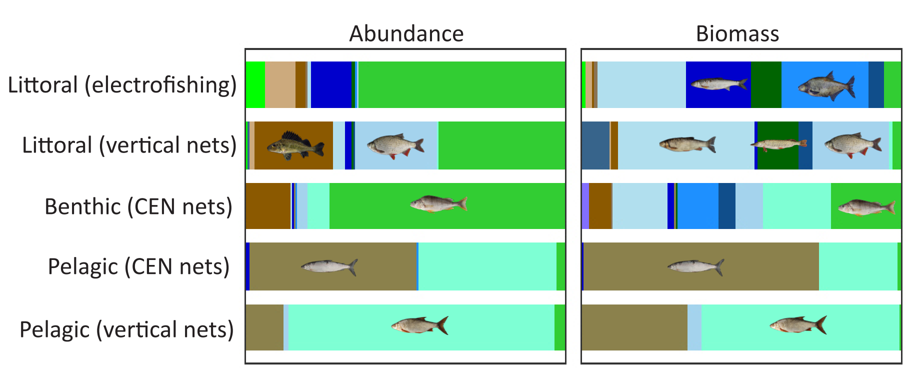
European eel CR
Anguilla anguilla

Lake Hallwil
Rhine catchment

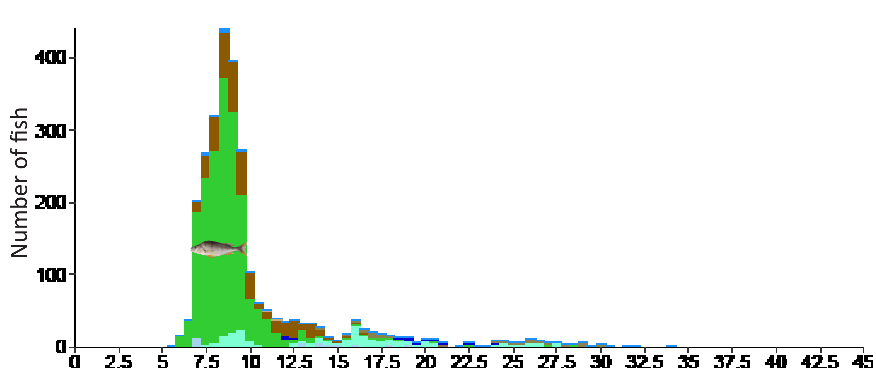
Lake environment
Lake Hallwil is today a mesotrophic and warm midland lake. This lake experienced the strongest eutrophication last century of all surveyed lakes (peak total phosphorus 260 ?g/L). The effects of this are still seen today with severe oxygen deficiencies below the thermocline (>15 m). The lake has a comparatively high proportion of near-natural littoral habitats.

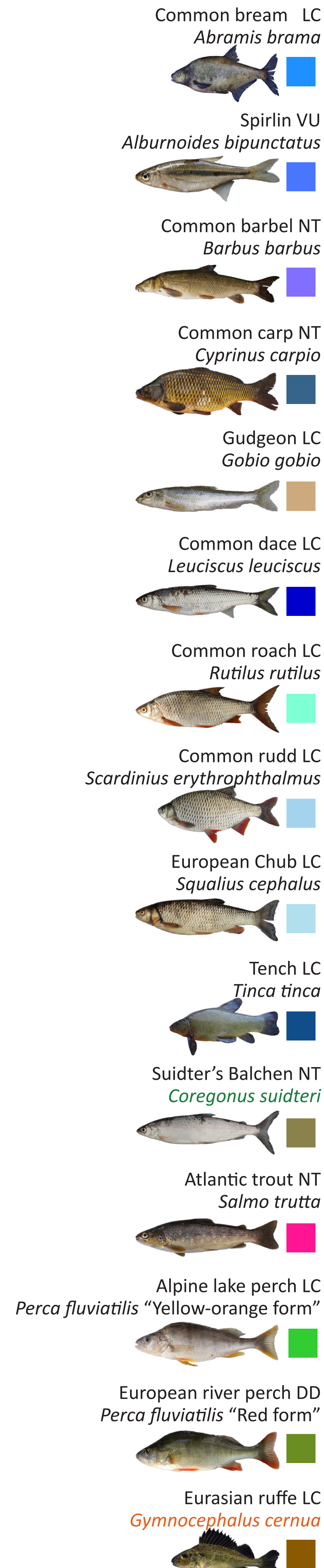
Fish community overview
20 fish species were recorded in Projet Lac, including 1 endemic and 3 non-native species. A very high abundance and biomass of roach were caught in open water, along with whitefish (Coregonus suidteri). Perch and non-native ruffe were the most common fish in the benthic habitats, while cyprinids dominated the biomass. Very few fish were caught below 15 m deep. Notably, neither bleak nor char were recorded in the lake.

Community composition
Near the lakeshore (littoral), electrofishing catches were dominated by perch, with chub, bream and dace contributing high proportions to biomass. Littoral nets contained many perch, rudd and non-native ruffe. Biomass was mostly chubb, followed by rudd and pike. Close to the lake floor (benthic), abundance was dominated by perch followed by non-native ruffe, with biomass spread relatively evenly among multiple species. The open water (pelagic) was heavily dominated by whitefish and roach.



Fish lengths
Fish caught in CEN nets were dominated by small perch 7-10 cm, along with roach 8-10 cm and 13-20 cm, and non-native ruffe 7-14 cm.





Lake Hallwil

Pike-perch nn
Sander lucioperca

Pumpkinseed nn
Lepomis gibbosus

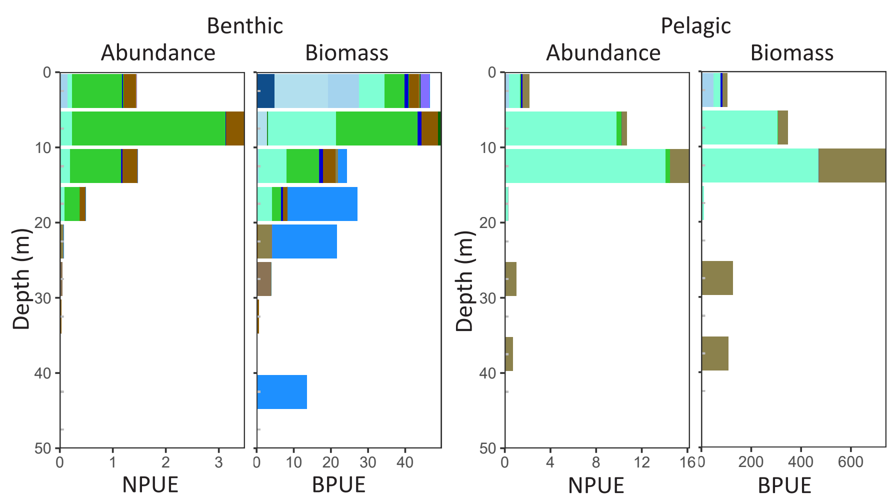
Sculpin NT
Cottus gobio "Unknown lineage"

Northern pike LC
Esox lucius

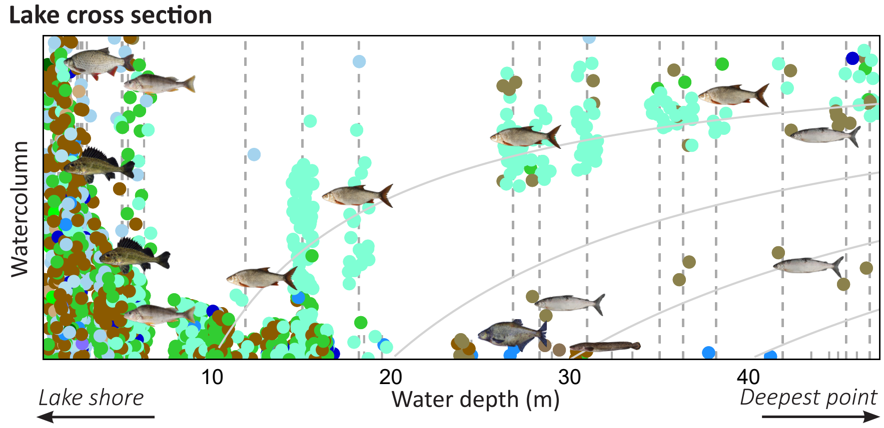
Burbot LC
Lota lota

Depth distribution

Benthic catches were dominated by large numbers of small perch, as well as non-native ruffe, to 20 m. A mix of cyprinids contributed to biomass in the shallowest layer, with perch and roach below, and bream peaking in biomass 15-20 m. In open water, roach dominated abundance and biomass, which increased to 10-15 m. Whitefish also occured around this depth and deeper below.



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common bleak LC
Alburnus alburnus

White bream NT
Blicca bjoerkna

Stone loach (species unknown) DD
Barbatula sp

Lake char VU
Salvelinus umbla

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

European eel CR
Anguilla anguilla

Upper Lake Zurich

Rhine catchment

Lake environment

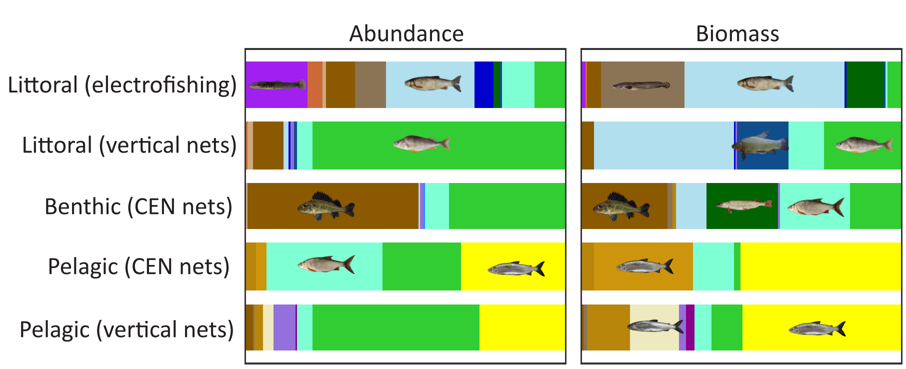
Upper Lake Zurich an oligotrophic lake in the Limat (River) subcatchment. The lake is considerably smaller and shallower than its sister immediately downstream Lake Zurich and has experienced lesser anthropogenic effects in terms of nutrient pollution and modification of littoral habitats. Despite this, the lake still suffers from oxygen deficiencies in the deeper half of the lake towards the end of the stratification period in autumn.

Fish community overview

20 fish species were recorded in Projet Lac, including 3 endemic and 1 non-native species. Low numbers of fish caught in open water. Biomass was dominated by whitefish, with decent numbers of roach and perch also caught. Non-native ruffe was the most abundant fish caught in benthic habitats, with perch and chub common in the littoral zone. A high number of stone loach were also caught in the electrofishing catches in the littoral zone. Also noteworthy is the absence of trout among the catches in the lake.

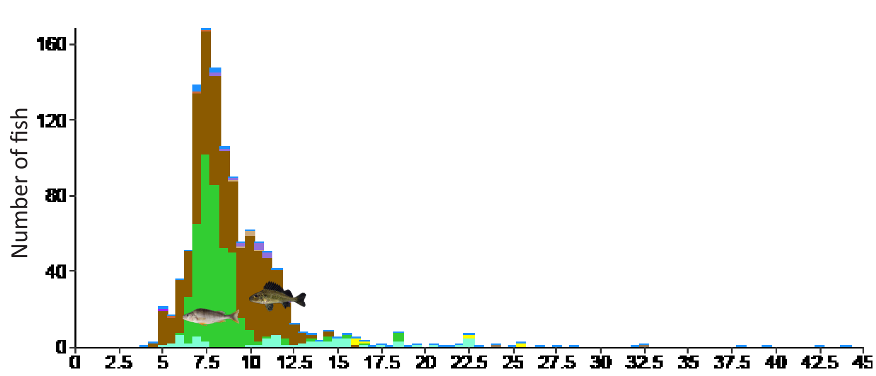
Community composition

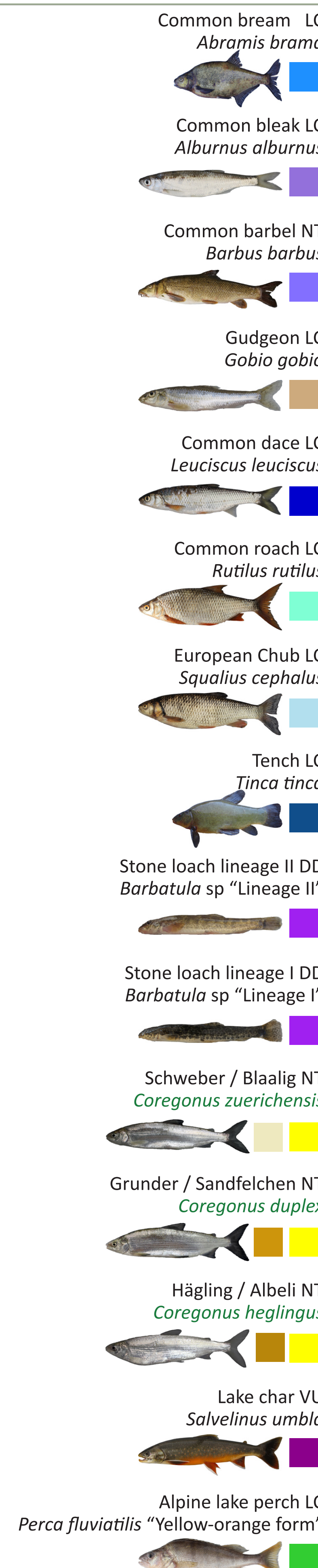
Near the lakeshore (littoral), electrofishing catches were dominated by chub and stone loach ("Lineage I"), with biomass mostly chub and burbot. Littoral nets were dominated by perch, with chub forming most of the biomass. Close to the lake floor (benthic), non-native ruffe dominated abundance, along with perch, while roach and pike also contributed to biomass. Abundance in open water (pelagic) was dominated by roach, perch and whitefish, with biomass mostly whitefish.



Fish lengths

Fish caught in CEN nets were dominated by non-native ruffe 5-12 cm and small perch 7-9 cm.





Upper Lake Zurich

Depth distribution

Perch and non-native ruffe were common in the shallow benthic zone to 20 m, below which catches dropped markedly. In open water, abundance was highest at 10-15 m and biomass 20-30 m. Bleak and roach were caught close to the surface, perch were abundant between 5-20 m, with whitefish contributing most of the biomass between 10-30 m.

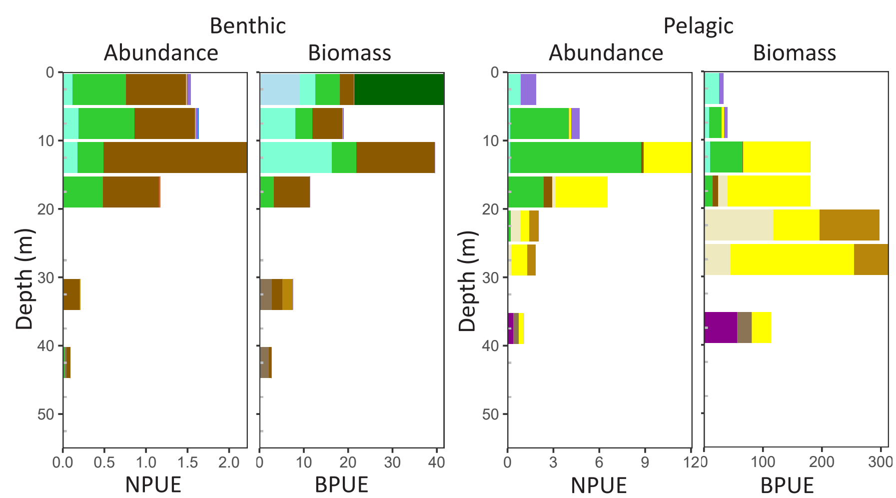
European river perch DD
Perca fluviatilis "Red form"

Eurasian ruffe LC
Gymnocephalus cernua

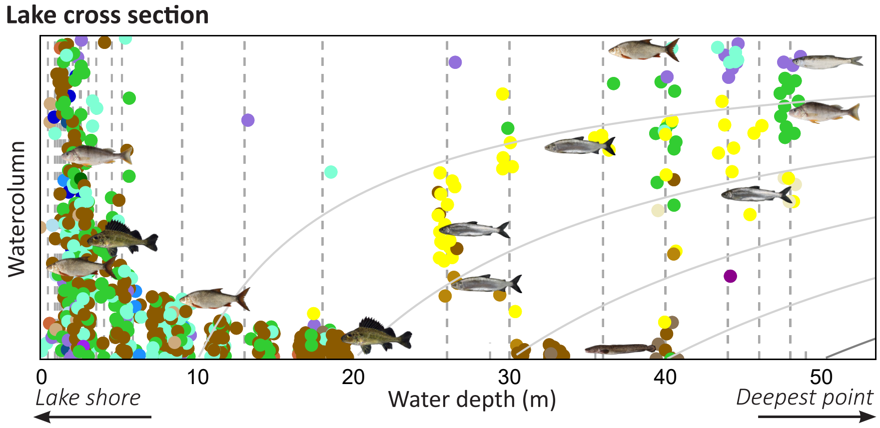
Littoral lake sculpin NT
Cottus gobio "Aare lineage littoral"

Northern pike LC
Esox lucius

Burbot LC
Lota lota



Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

White bream NT
Blicca bjoerkna

Common carp NT
Cyprinus carpio

Common rudd LC
Scardinius erythrophthalmus

Atlantic trout NT
Salmo trutta

European grayling EN
Thymallus thymallus

European eel CR
Anguilla anguilla

Lake Zurich (lower lake)

Rhine catchment

Lake environment

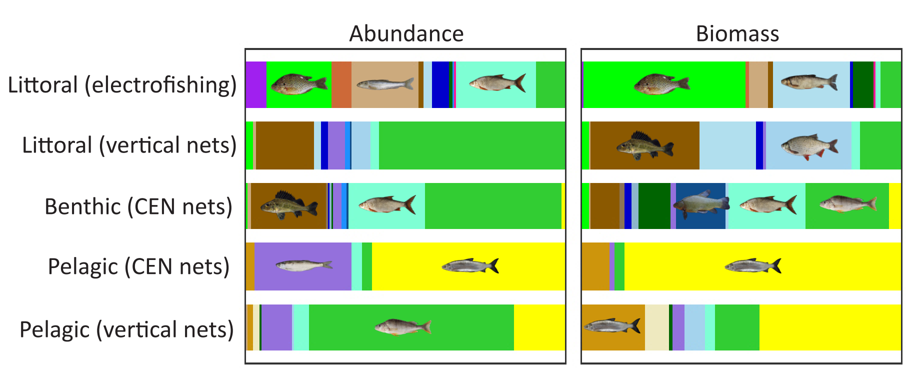
Lake Zurich is in the Limat (River) subcatchment, immediately downstream of the shallower Upper Lake Zurich. Lake Zurich is currently mesotrophic, however very little of these nutrients reach the surface waters. Weaker vertical mixing in recent years contributes to the low nutrients in surface waters, an increasingly large zone of low oxygen near the lake floor at the deepest point of the lake, a second zone of low oxygen (< 4mg/L) around the thermocline and increasing biomass of cyanobacteria (Planktothrix). This lake had the lowest proportion of near-natural habitats of all surveyed lakes.

Fish community overview

21 fish species were recorded in Projet Lac, including 2 endemic and 3 non-native species. Fish abundance in gillnets were dominated by perch, with biomass dominated by whitefish. No fish were caught below 80 m due to hypoxia. Very high biomass of non-native pumpkinseed in the littoral zone and ruffe in the littoral and benthic zone. Genetic analysis of samples collected by Projet Lac confirmed the presence of three species of whitefish in the lake.

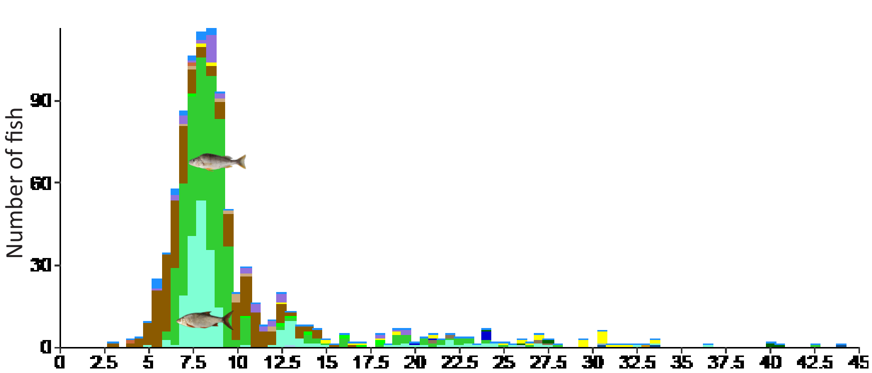
Community composition

Near the lakeshore (littoral), electrofishing catches were mostly non-native pumpkinseed, gudgeon and roach, with biomass dominated by pumpkinseed and chub. Littoral nets were dominated by perch, with non-native ruffe. Biomass was mostly ruffe, with chub and rudd. Close to the lake floor (benthic), perch, roach and non-native ruffe were most abundant. These species also formed much of the biomass. Whitefish and bleak were common in the open water (pelagic) CEN nets, while perch dominated the pelagic vertical nets. Pelagic biomass was dominated by whitefish."



Fish lengths

Fish caught in CEN nets were dominated by roach, perch and non-native ruffe, of similar sizes 6-9 cm.



Common bream LC
Abramis brama

Common bleak LC
Alburnus alburnus

Common carp NT
Cyprinus carpio

Gudgeon LC
Gobio gobio

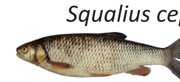
Common dace LC
Leuciscus leuciscus

Common roach LC
Rutilus rutilus

Common rudd LC
Scardinius erythrophthalmus

Southern rudd NT
Scardinius hesperidicus

European Chub LC
Squalius cephalus



Tench LC
Tinca tinca

Stone loach lineage I DD
Barbatula sp "Lineage I"

Schweber / Blaalig NT
Coregonus zuerichensis

Grunder / Sandfelchen NT
Coregonus duplex

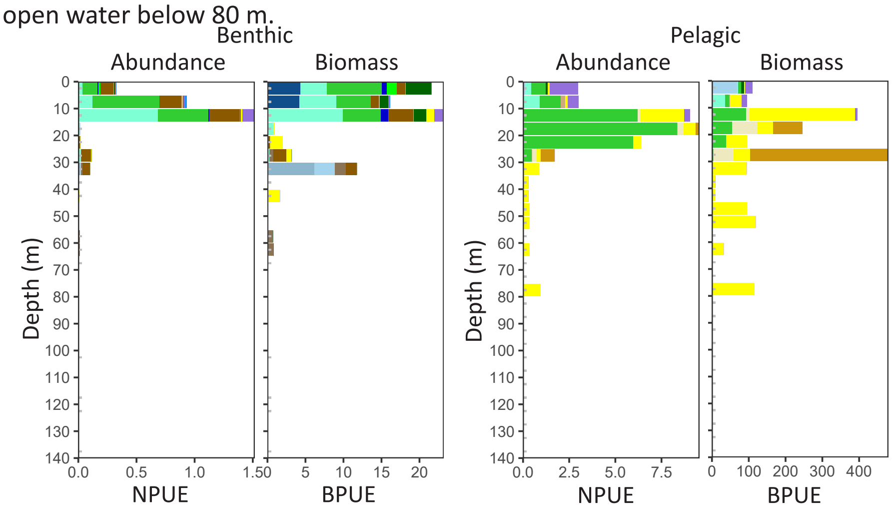
Atlantic trout NT
Salmo trutta

Alpine lake perch LC
Perca fluviatilis "Yellow-orange form"

Lake Zurich (lower lake)

Depth distribution

Catches near the lake floor were highest in the upper 15 m, with most fish caught 10-15 m. Benthic abundance was mostly perch, roach and non-native ruffe, while tench also contributed to biomass in benthic habitats. Very few fish were caught near the lake floor below 15 m, and no fish caught below 65 m. Bleak and perch dominated the open water above the shallow parts of the lake, with perch catches highest 10-25 m below the surface. Particularly high numbers of perch were recorded in one vertical net. Whitefish dominated the deeper open water, with the highest biomass 10-80 m. No fish were caught in open water below 80 m.



European river perch DD
Perca fluviatilis "Red form"

Eurasian ruffe LC
Gymnocephalus cernua

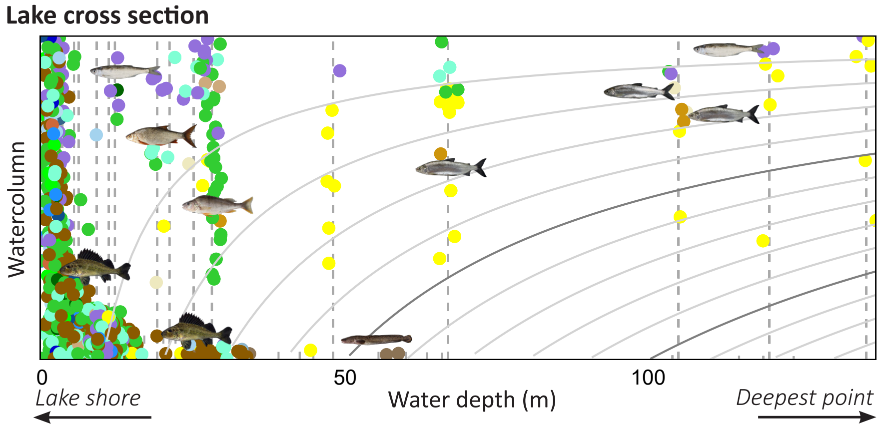
Pumpkinseed nn
Lepomis gibbosus

Littoral lake sculpin NT
Cottus gobio "Aare lineage littoral"

Northern pike LC
Esox lucius

Burbot LC
Lota lota

Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Spirlin VU
Alburnoides bipunctatus

Common barbel NT
Barbus barbus

White bream NT
Blicca bjoerkna

Prussian carp nn
Carassius gibelio

Goldfish nn
Carassius auratus

Common nase CR
Chondrostoma nasus

Minnow (species unknown) DD
Phoxinus sp

Hägling / Albeli NT
Coregonus heglingus

Lake char VU
Salvelinus umbla

Canadian lake trout nn
Salvelinus namaycush

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Three-spined stickleback (eastern) nn
Gasterosteus aculeatus

Wels catfish LC
Silurus glanis

Black bullhead nn
Ameiurus melas

European eel CR
Anguilla anguilla

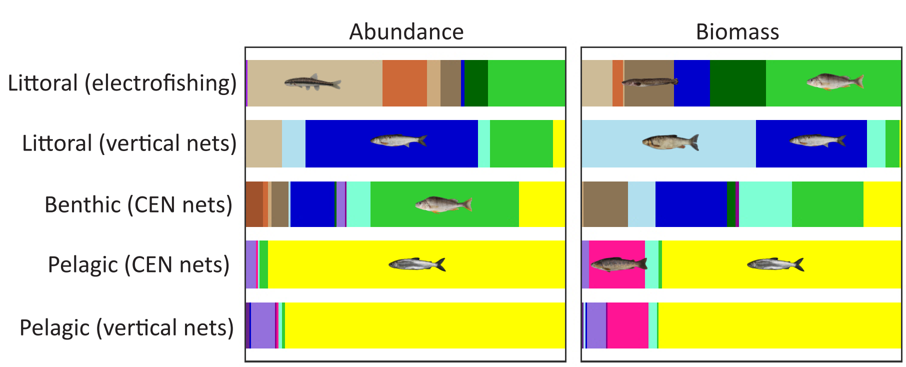
Brook lamprey EN
Lampetra planeri

Lake Walen
Rhine catchment

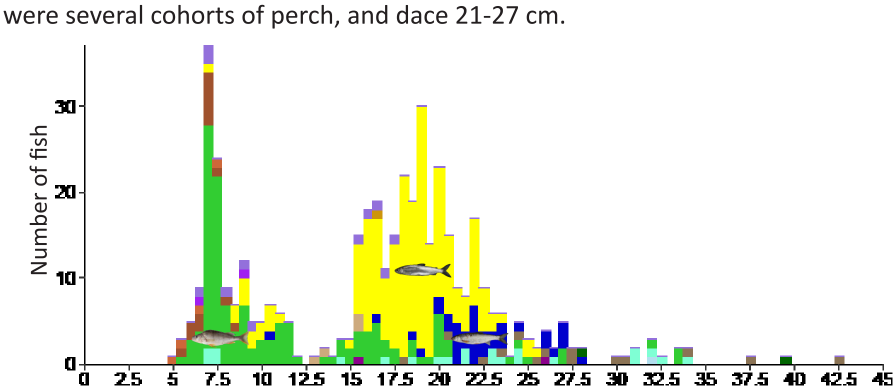
Lake environment
Lake Walen is an ultra-oligotrophic lake, located a short distance upstream from Upper Lake Zurich in the Limat (river) subcatchment. The surface waters of the lake remain cool and the lake is well-oxygenated throughout the year. A high proportion (75%) of shoreline habitats are in a near-natural state. The redirection of the Linth (river) into Lake Walen in early 1800 created issues with turbidity and sedimentation.

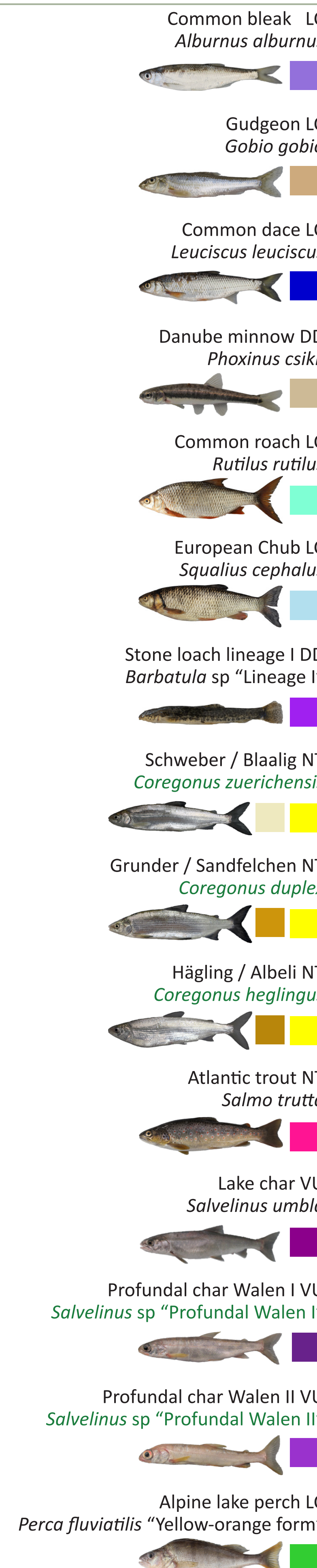
Fish community overview
20 fish species were recorded in Projet Lac, including 6 endemic and 0 non-native species. Community composition in Lake Walen is close to what we would expect from a typical large, oligotrophic, cool-water, perialpine lake. Abundance and biomass in the littoral gillnets were the lowest of all surveyed lakes. No non-native species were recorded (one of only two lakes where this was the case). A high number of endemic species were recorded in the lake, including 3 species of whitefish, 2 char and a sculpin. Whitefish heavily dominated the fish caught in open water, along with a reasonable biomass of trout. Burbot were common with whitefish in the benthic catches.

Community composition
Near the lakeshore (littoral), electrofishing catches were dominated by gudgeon, along with perch and sculpin, while biomass was mostly perch, pike and burbot. Littoral nets caught few fish, which were mostly dace, while chub and dace dominated biomass. Close to the lake floor (benthic), perch dominated abundance, along with dace and whitefish, while biomass was distributed among these species plus roach and burbot. The open water (pelagic) was heavily dominated by whitefish, with bleak also contributing to abundance, and Atlantic trout to biomass.



Fish lengths
Fish caught in CEN nets were dominated by whitefish 15-23 cm. This dominance of medium-sized whitefish was unique among the surveyed lakes. Also evident were several cohorts of perch, and dace 21-27 cm.

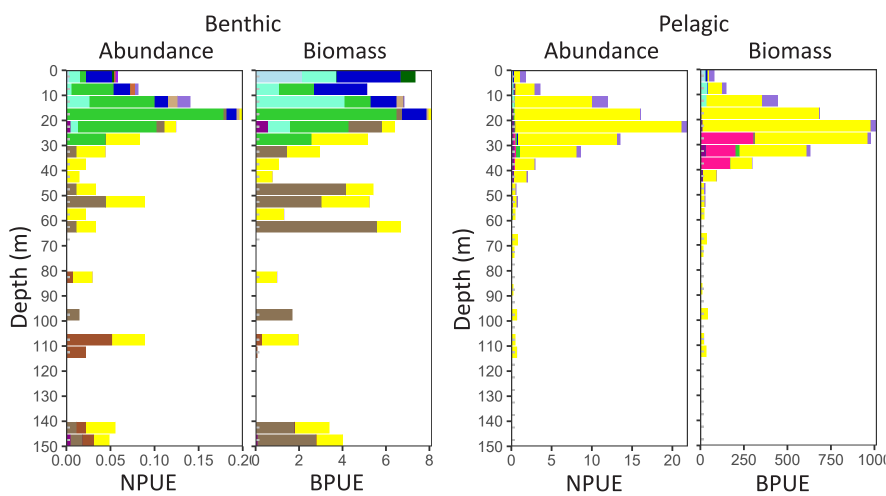




Lake Walen

Depth distribution

Dace were common in the benthic zone near the surface, with perch abundance peaking 15-20 m. Whitefish, burbot and sculpin dominated below 30 m. Benthic biomass was of a similar magnitude throughout the depths. Whitefish, burbot and sculpin were caught at the deepest point of the lake. In the pelagic, whitefish catches peaked 20-25 m, with trout also contributing to biomass 25-40 m.



European river perch DD
Perca fluviatilis "Red form"

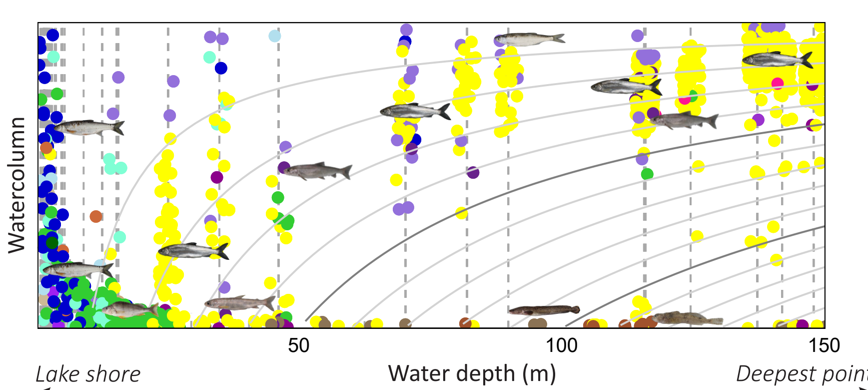
Littoral lake sculpin NT
Cottus gobio "Aare lineage littoral"

Profundal sculpin Walen NT
Cottus gobio "Profundal Walen"

Northern pike LC
Esox lucius

Burbot LC
Lota lota

Lake cross section



Fish species reported to occur in the lake but not recorded in Projet Lac

Common bream LC
Abramis brama

Common barbel NT
Barbus barbus

White bream NT
Blicca bjoerkna

Common nase CR
Chondrostoma nasus

Common carp NT
Cyprinus carpio

Common rudd LC
Scardinius erythrophthalmus

Tench LC
Tinca tinca

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

European eel CR
Anguilla anguilla

Upper Lake Constance

Rhine catchment

Lake environment

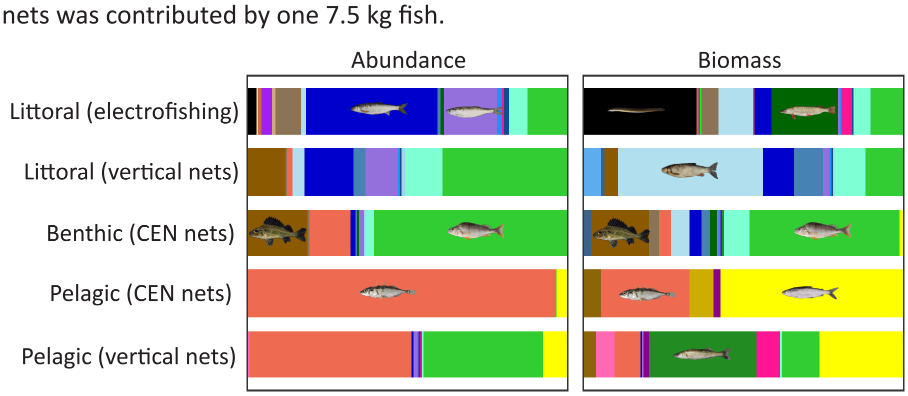
Upper Lake Constance is the largest lake in the Rhine catchment. The lake was oligotrophic at the time of sampling, but had experienced hyper-eutrophic conditions during the past century. Oxygen was present throughout the water column in the year of sampling.

Fish community overview

31 fish species were recorded in Projet Lac, including 4 endemic and 6 non-native species. Highest number of fish species of all northern perialpine lakes were recorded in Upper Lake Constance. Several individuals of the believed-extinct endemic profundal char were recovered, as well as the first record of a blunt-snout gudgeon in the lake and Switzerland. Very high catches of non-native stickleback in open water, along with high numbers of non-native ruffe in the benthic zone. This was the only northern perialpine lake where eels were recorded. The kilch (Coregonus gutturosus) is presumed extinct.

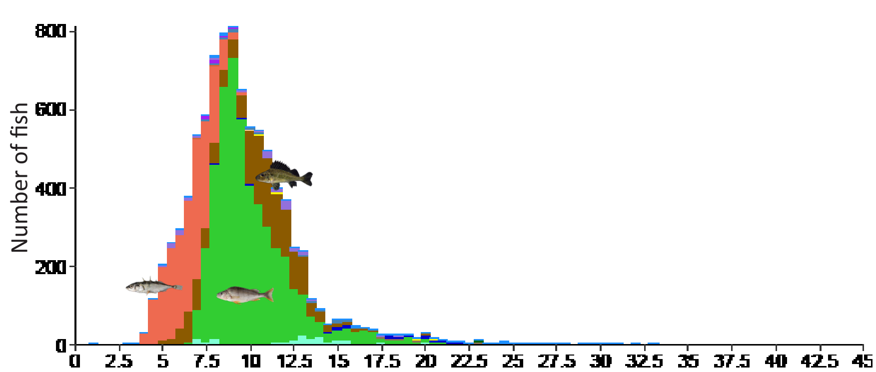
Community composition

Near the lakeshore (littoral), electrofishing catches were dominated by dace and bleak, with much biomass contributed by eels and pike. Littoral nets contained a high proportion of perch, along with several other species, including non-native ruffe. Close to the lake floor (benthic), nets were dominated by perch, along with ruffe and non-native stickleback. In the open water (pelagic), abundance was dominated by stickleback, while biomass was dominated by whitefish. The high % biomass of non-native pikeperch in the pelagic vertical nets was contributed by one 7.5 kg fish.



Fish lengths

Fish caught in CEN nets were dominated by small perch 8-13 cm, 15-17 cm, non-native stickleback 4-8 cm and non-native ruffe 6-13 cm.



Common bream LC
Abramis brama

Common bleak LC
Alburnus alburnus

White bream NT
Blicca bjoerkna

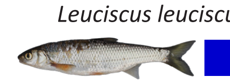
Prussian carp nn
Carassius gibelio

Common carp NT
Cyprinus carpio

Gudgeon LC
Gobio gobio

Blunt-snout gudgeon DD
Gobio obtusirostris

Common dace LC
Leuciscus leuciscus



Common roach LC
Rutilus rutilus

Common rudd LC
Scardinius erythrophthalmus

European Chub LC
Squalius cephalus

Tench LC
Tinca tinca

Stone loach lineage II DD
Barbatula sp "Lineage II"

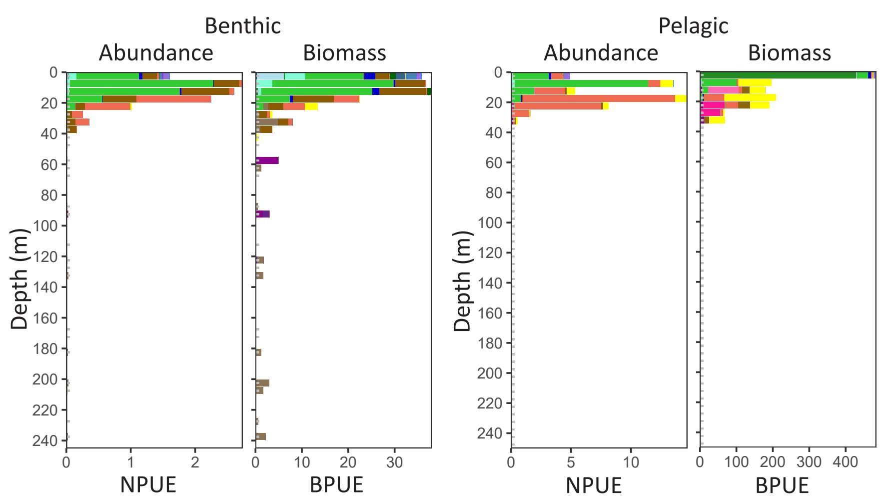
Blaufelchen NT
Coregonus wartmanni

Sandfelchen NT
Coregonus arenicolus

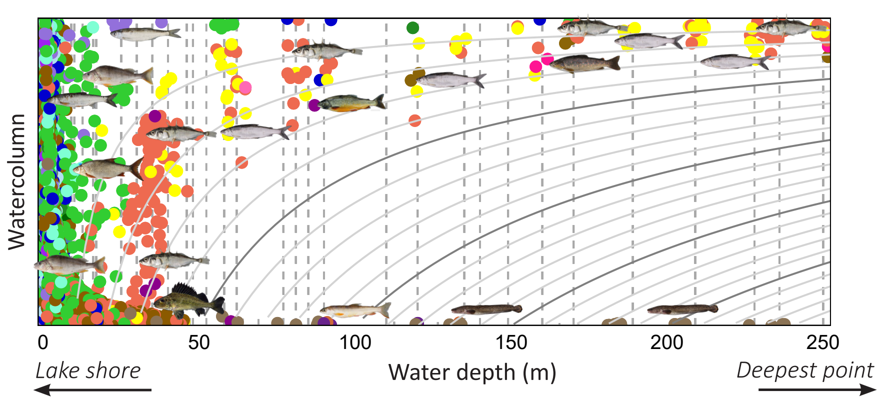
Upper Lake Constance

Depth distribution

Perch and non-native ruffe formed most of the catch in the benthic nets to 15 m, with non-native stickleback mostly deeper 15-35 m. Char and burbot formed most of benthic biomass below 40 m. In the open water, perch dominated the upper 10 m, with stickleback abundant 10-30 m. Whitefish dominated the pelagic biomass 5-25 m. No fish were caught in open water below 40 m. In the benthic zone, burbot were present to the deepest point of the lake.



Lake cross section



Gangfisch NT
Coregonus macrophthalmus

Atlantic trout NT
Salmo trutta

Lake char VU
Salvelinus umbla

Profundal char CR
Salvelinus profundus

Rainbow trout nn
Oncorhynchus mykiss

Alpine lake perch LC
Perca fluviatilis "Yellow-orange form"

European river perch DD
Perca fluviatilis "Red form"

Eurasian ruffe LC
Gymnocephalus cernua

Pike-perch nn
Sander lucioperca

Pumpkinseed nn
Lepomis gibbosus

Rhine river sculpin NT
Cottus gobio "Rhine lineage"

Northern pike LC
Esox lucius

Three-spined stickleback (eastern) nn
Gasterosteus aculeatus

Wels catfish LC
Silurus glanis

European eel CR
Anguilla anguilla

Burbot LC
Lota lota

Fish species reported to occur in the lake but not recorded in Projet Lac

Spirlin VU
Alburnoides bipunctatus

Common barbel NT
Barbus barbus

Common nase CR
Chondrostoma nasus

Minnow (species unknown) DD
Phoxinus sp

Riffle dace VU
Telestes souffia aggassizi

Spiny loach (species unknown) DD
Cobitis sp

European grayling EN
Thymallus thymallus

Black bullhead nn
Ameiurus melas

Brook lamprey EN
Lampetra planeri

Lower Lake Constance

Rhine catchment

Lake environment

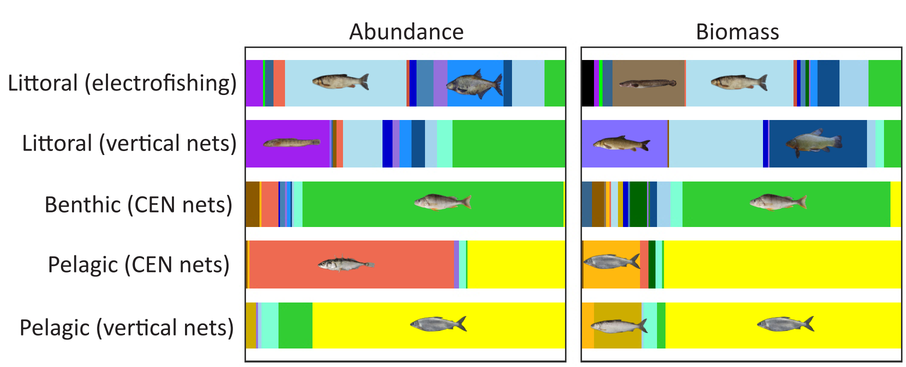
Lower Lake Constance is a mesotrophic lake, located immediately downstream of Upper Lake Constance. The lake experience strongly eutrophic conditions in the late 1970s. Lower Lake Constance consists of multiple basins (Rheinsee, Gnadensee, Zellersee) which have different environmental conditions. Oxygen deficiencies are common below the thermocline of most of the lake basins in autumn.

Fish community overview

25 fish species were recorded in Projet Lac, including 2 endemic and 5 non-native species. Whitefish formed more than 90% of the fish biomass caught in open water, however non-native stickleback formed 60% of fish caught in in the pelagic CEN gillnets. Perch dominated the benthic zone, with cyprinids (chub, bream), and burbot common near the lakeshore. Noteworthy absences from Projet Lac catches include sculpin, char and gudgeon.

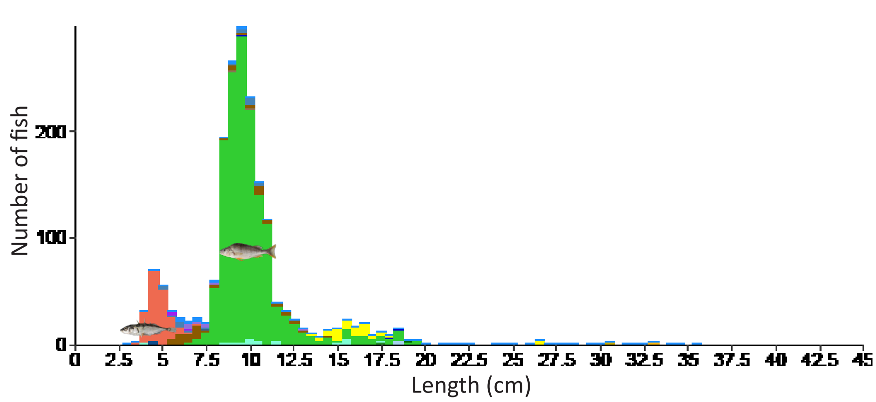
Community composition

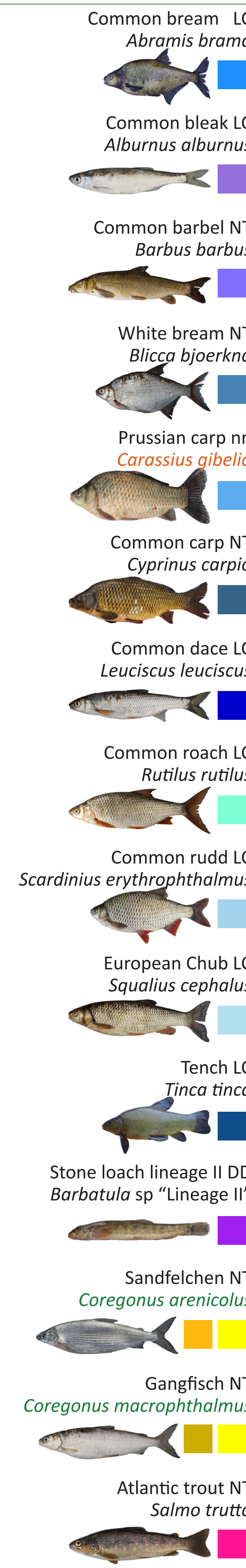
Near the lakeshore (littoral), electrofishing catches were dominated by chub and bream, with biomass mostly chub and burbot. Littoral nets were dominated by perch and stone loach, with biomass mostly barbel, chub and tench. Close to the lake floor (benthic), perch heavily dominated abundance and biomass. The open water (pelagic) was dominated by whitefish, however non-native stickleback formed around 60% of fish caught in the pelagic CEN nets. Very few stickleback were caught in the pelagic vertical nets due to the larger minimum mesh size.



Fish lengths

Fish caught in CEN nets were dominated by small perch 8-11 cm and small non-native stickleback 4-6 cm.

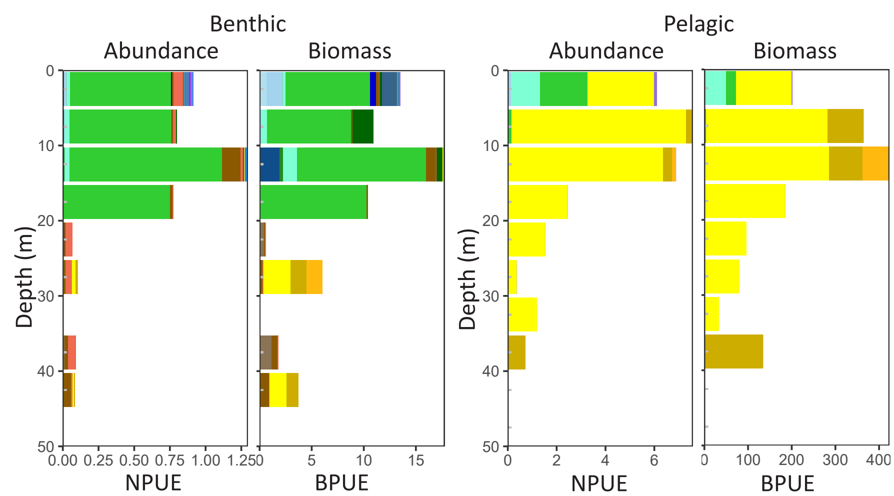




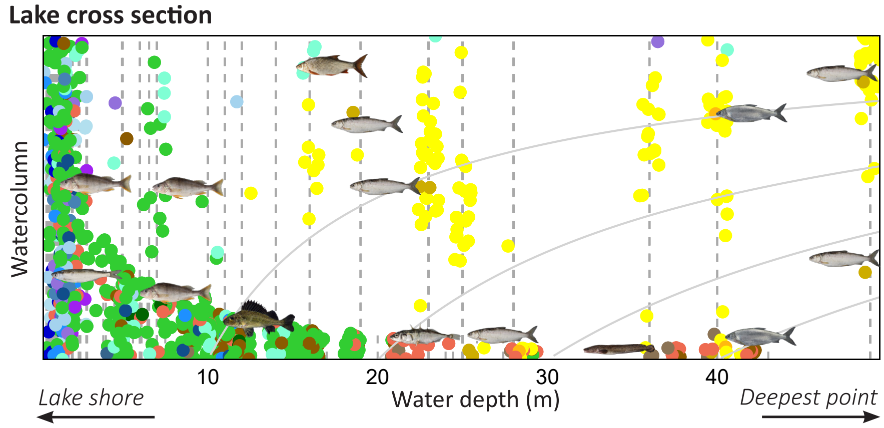
Lower Lake Constance

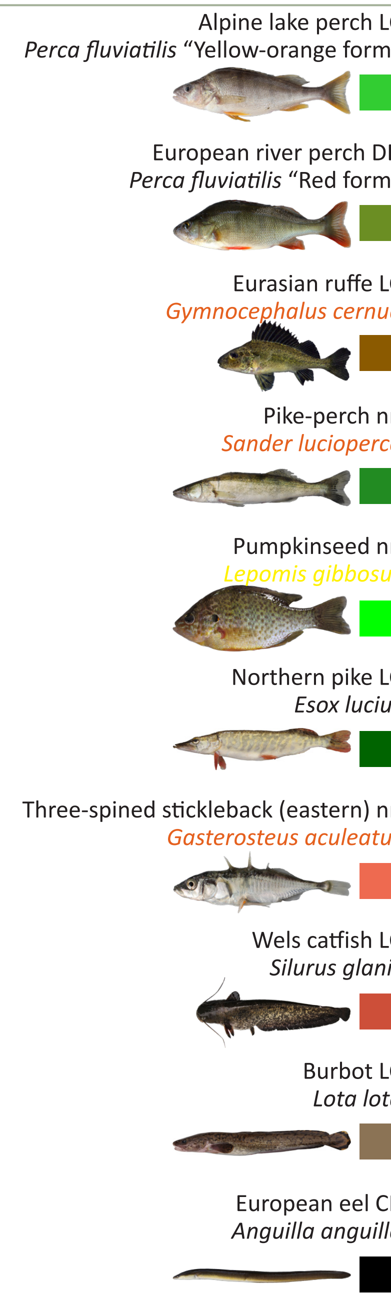
Depth distribution

Benthic fish were heavily dominated by perch, with catches of a similar magnitude 0-20 m, and only two perch caught below this depth. Deeper-caught benthic fish were mostly non-native stickleback and non-native ruffe, along with whitefish and burbot. Pelagic fish in vertical nets were heavily dominated by whitefish with catches peaking 5-15 m.



Lake cross section





Fish species reported to occur in the lake but not recorded in Projet Lac

Goldfish nn
Carassius auratus

Gudgeon LC
Gobio gobio

Minnow (species unknown) DD
Phoxinus sp

Bitterling EN
Rhodeus amarus

Lake char VU
Salvelinus umbla

Rainbow trout nn
Oncorhynchus mykiss

European grayling EN
Thymallus thymallus

Sculpin (species unknown) DD
Cottus sp

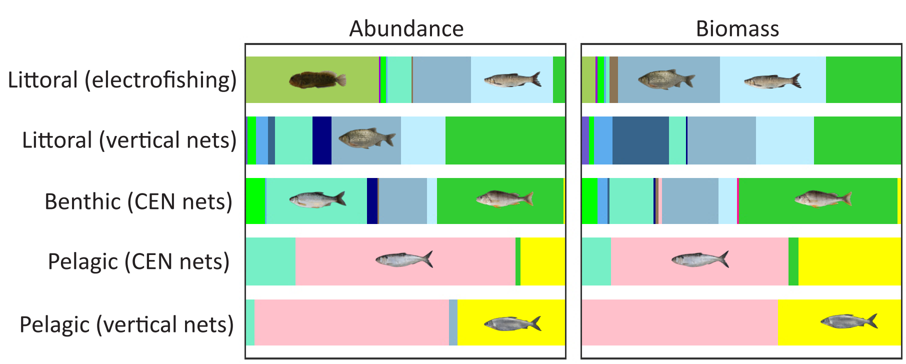
Brook lamprey EN
Lampetra planeri

Lake Garda
Po catchment

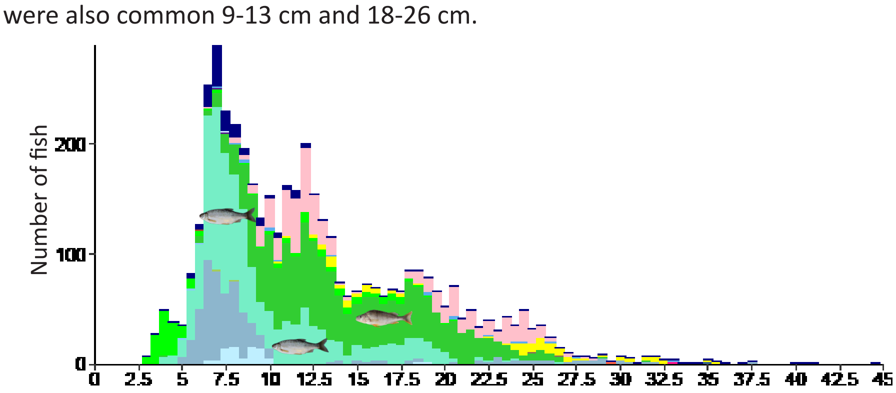
Lake environment
Lake Garda is by far the largest southern perialpine lake and was also the lowest elevation lake surveyed in Project Lac. The deepest point of the lake is 280 m below sea level. The lake has a particularly long retention time owing to its large volume and relatively small outflow. Lake Garda was mesotrophic at the time of sampling and has not been strongly eutrophied.

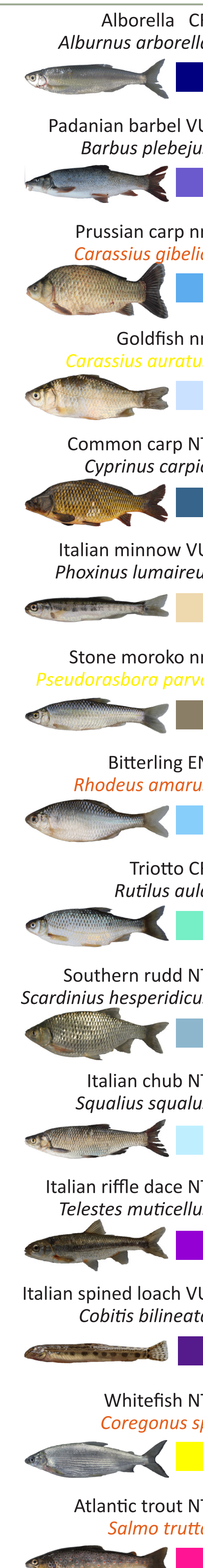
Fish community overview
26 fish species were recorded in Projet Lac, including 1 endemic and 9 non-native species. Catches in open water were dominated by agone, along with non-native whitefish. Freshwater blenny were common near the lakeshore, with southern rudd and Italian chub. Fish were caught in the benthic zone across the full depth profile to the deepest point of the lake, however only two fish were caught in open water below 50 m from the surface. Lake Garda was the only southern perialpine lake where tench was not recorded in the catches. It was also the only southern perialpine where an endemic species was recorded: carpione del Garda.

Community composition
Near the lakeshore (littoral), electrofishing catches were dominated by the freshwater blenny, along with Italian chub and southern rudd, while biomass was mostly chub, rudd and perch. Littoral nets contained mostly perch, southern rudd, Italian chub and triotto, with carp also contributing to biomass. Close to the lake floor (benthic), abundance and biomass were dominated by perch, along with triotto and southern rudd. The open water (pelagic) was dominated by agone, with non-native whitefish and triotto.



Fish lengths
Fish caught in CEN nets contained a high proportion of medium-sized perch 9-22 cm, many triotto 6-20 cm, small southern rudd 6-9 cm. Two sizes of agone were also common 9-13 cm and 18-26 cm.

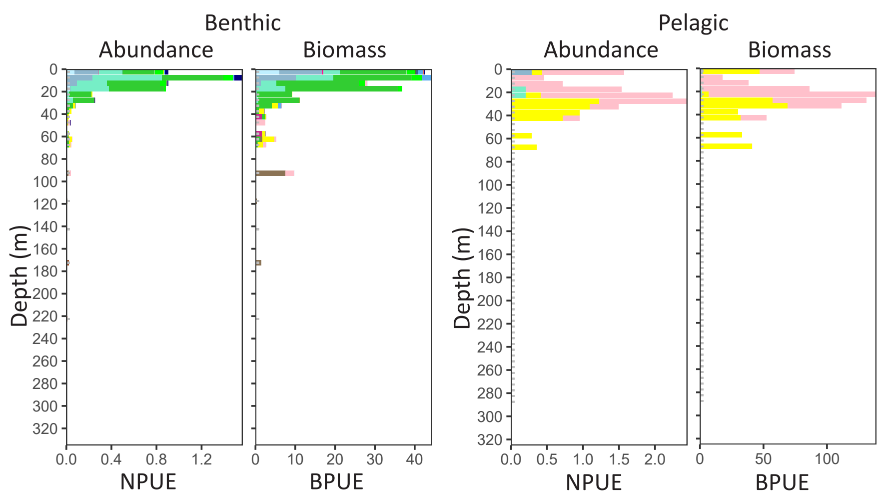




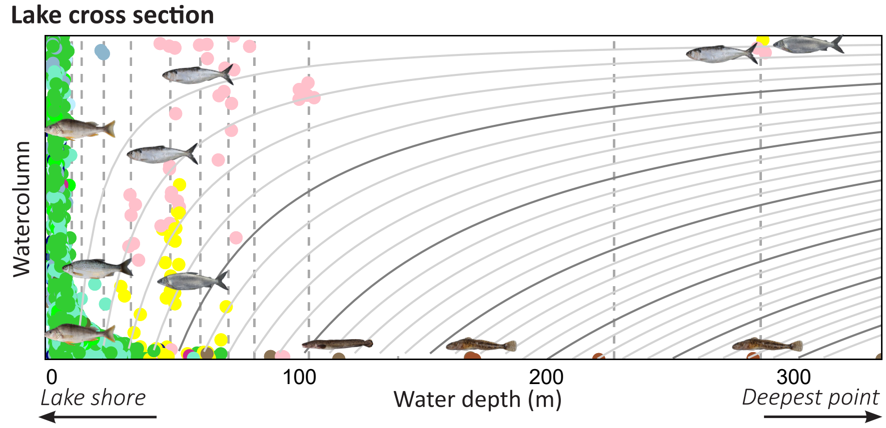
Lake Garda

Depth distribution

Benthic catches, mostly perch, triotto and southern rudd, were highest in the upper 20 m. Only a few agone, burbot and profundal sculpin were caught below 80 m. In the open water, agone were generally caught shallower (0-30 m deep) than the non-native whitefish (25-70 m). Fish were caught in the benthic zone to the deepest point of the lake, however very few fish were caught in open water over the deeper parts of the lake. Agone were most common in the upper layers of open water in shallower parts of the lake (<100 m).



Lake cross section



Carpione del Garda DD
Salmo carpio

European river perch DD
Perca fluviatilis "Red form"

Freshwater blenny NT
Salaria fluviatilis "Italian lineage"

Pumpkinseed nn
Lepomis gibbosus

Largemouth bass / Blackbass nn
Micropterus salmoides

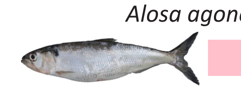
Padanian goby EN
Padogobius bonelli

Profundal Po lake sculpin NT
Cottus sp "Profundal Po"

Southern pike DD
Esox cisalpinus

Black bullhead nn
Ameiurus melas

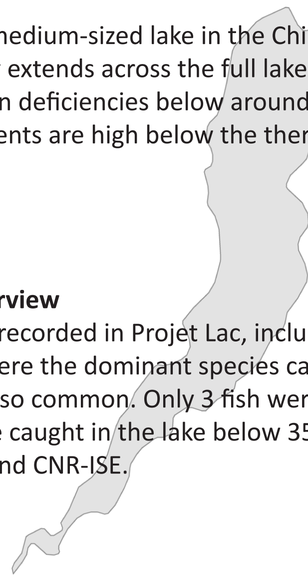
Agone VU
Alosa agone



Burbot LC
Lota lota

Lake Idro

Po catchment



Lake environment

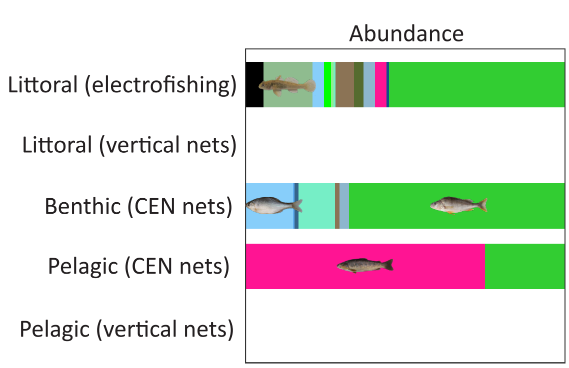
Lake Idro is a deep, medium-sized lake in the Chiese (river) subcatchment. Vertical mixing rarely extends across the full lake depth. The lake experiences deep-water oxygen deficiencies below around 40 m, as well as blooms of cyanobacteria. Nutrients are high below the thermocline but low in the surface waters above.

Fish community overview

14 fish species were recorded in Projet Lac, including 0 endemic and 5 non-native species. Perch were the dominant species caught near the lake floor, with the Padanian goby also common. Only 3 fish were caught in open water from 40 nets. No fish were caught in the lake below 35 m. The fish of Lake Idro were surveyed by GRAIA and CNR-ISE.

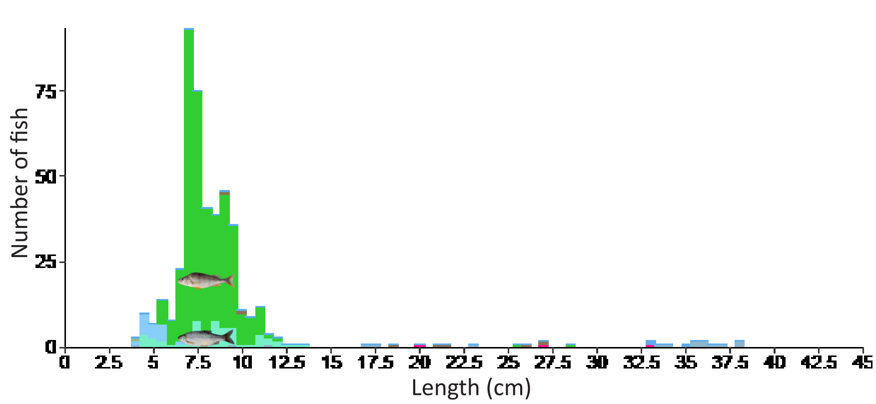
Community composition

Near the lakeshore (littoral), electrofishing catches were dominated by perch, along with Padanian goby. Close to the lake floor (benthic), perch dominated abundance, along with triotto and non-native bitterling. Only four fish were caught in open water (pelagic): 1 small perch and 3 non-native Atlantic trout were caught between 0-10 m.



Fish lengths

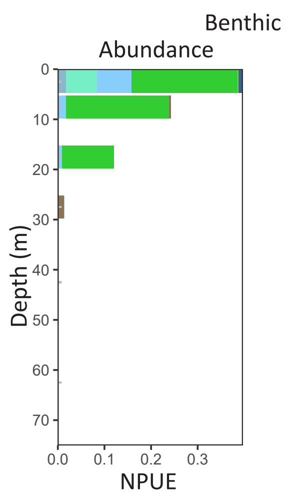
Fish caught in CEN nets were dominated by small perch 7-9 cm, triotto 5-12 cm and non-native bitterling 4-6 cm.



Lake Idro

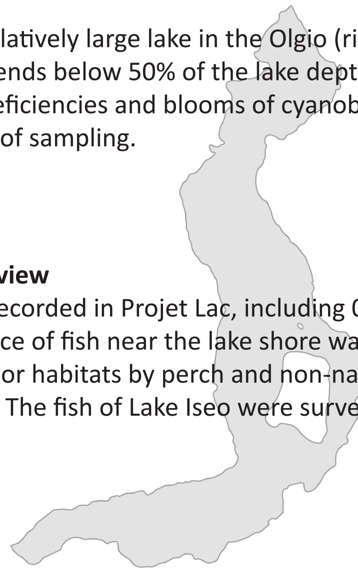
Depth distribution

Perch dominated the shallow layers to 20 m, burbot between 20-35 m and no fish below 35 m. No fish were caught in pelagic CEN nets below 10 m. Vertical nets were not used to sample the fish of Lake Idro, so a two-dimensional depth distribution cannot be shown.



Lake Iseo

Po catchment



Lake environment

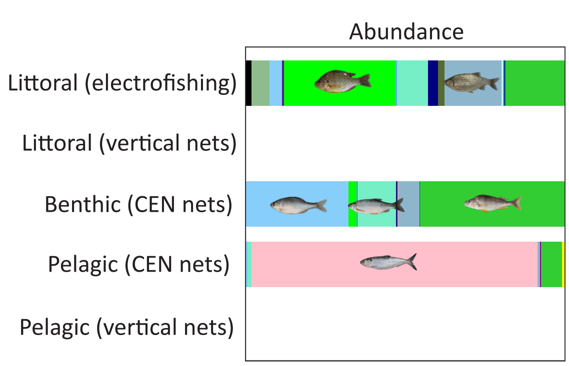
Lake Iseo is a deep, relatively large lake in the Olgio (river) subcatchment. Vertical mixing rarely extends below 50% of the lake depth. The lake experiences deep-water oxygen deficiencies and blooms of cyanobacteria. The lake was eutrophic at the time of sampling.

Fish community overview

22 fish species were recorded in Projet Lac, including 0 endemic and 7 non-native species. Abundance of fish near the lake shore was dominated by exotic pumpkinseed, lake floor habitats by perch and non-native bitterling, and the open water by agone. The fish of Lake Iseo were surveyed by GRAIA and CNR-ISE.

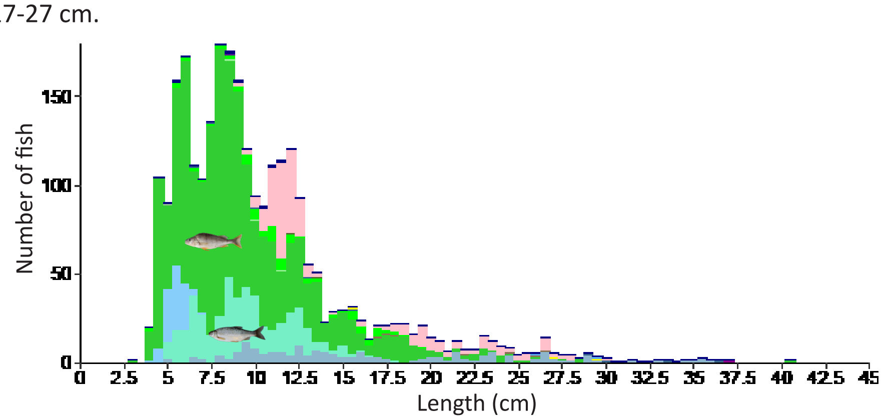
Community composition

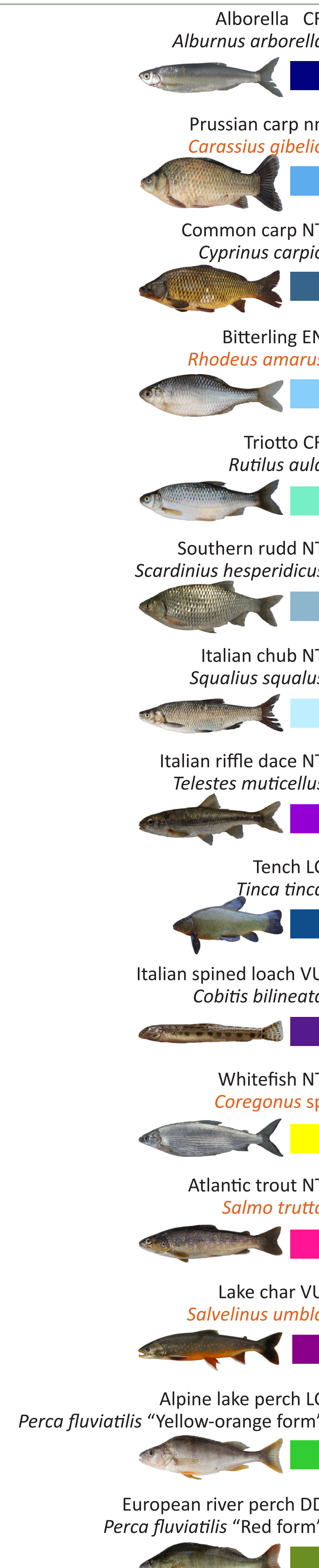
Near the lakeshore (littoral), electrofishing catches were dominated by exotic pumpkinseed, with perch and southern rudd also common. Close to the lake floor (benthic), catches were dominated by perch and non-native bitterling, with triotto and southern rudd also contributing. The open water (pelagic) was heavily dominated by agone.



Fish lengths

Fish caught in CEN nets were dominated by perch 4-20 cm, triotto 5-13 cm and bitterling 5- 6 cm. Two size groups of agone were also evident 11-13 cm and 17-27 cm.

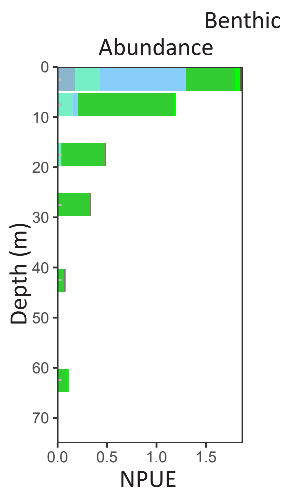


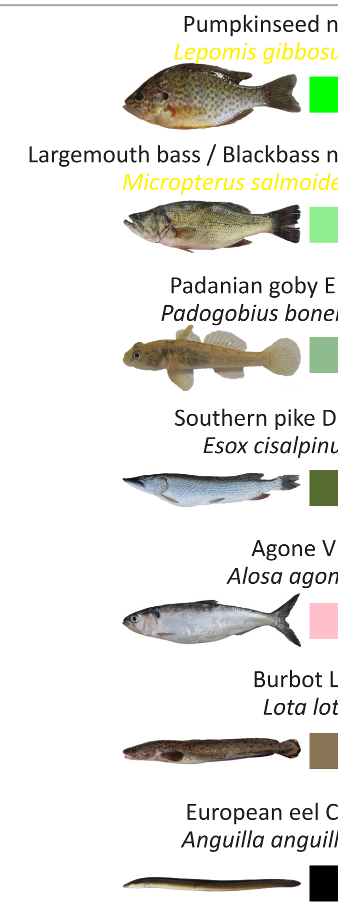


Lake Iseo

Depth distribution

Perch dominated benthic catches throughout the depths (although perch deeper than 30 m were likely caught while the net was being deployed/re-trieved). Non-native bitterling and southern rudd were most common near the lake shore. In pelagic CEN nets, agone were most abundant near the surface, with numbers decreasing down through the depth zones to 30 m. No fish were caught below 40 m. Vertical nets were not used to sample the fish of Lake Iseo, so a two-dimensional depth distribution cannot be shown.





Lake Maggiore

Po catchment

Lake environment

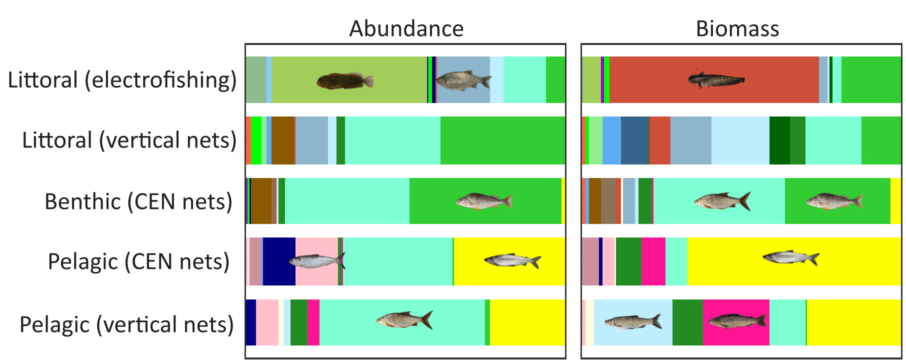
Lake Maggiore is a large and deep lake in the Ticino (river) subcatchment, a short distance away from lakes Lugano and Varese. The lake experienced mild eutrophication over the past century, but was mesotrophic at the time of sampling and had oxygen throughout the watercolumn. The lake experiences very high fluctuations in water level.

Fish community overview

36 fish species were recorded in Projet Lac, including 0 endemic and 14 non-native species. Highest number of non-native species of all surveyed lakes were recorded in Lake Maggiore. Perch and non-native roach dominated the shallow benthic zone. Freshwater blenny was very common near the lakeshore. In the open water, non-native roach were common near the surface not far from the shore, while non-native whitefish (lavarello and bondella) and agone were dominated towards the middle of the lake. No fish were caught below 35 m in open water. This was the only lake where twaite shad were recorded.

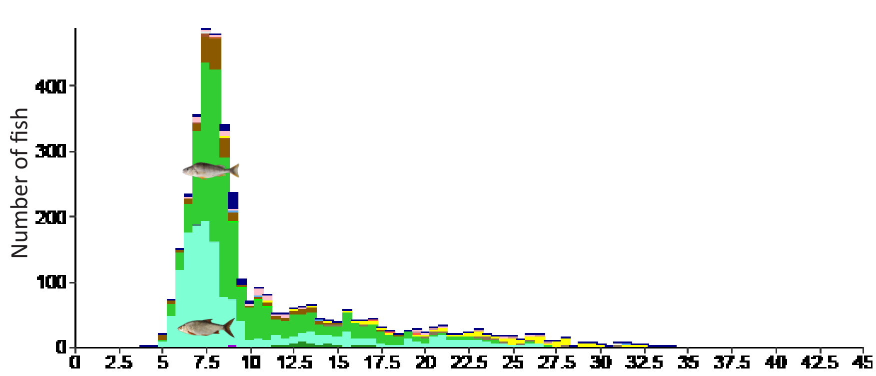
Community composition

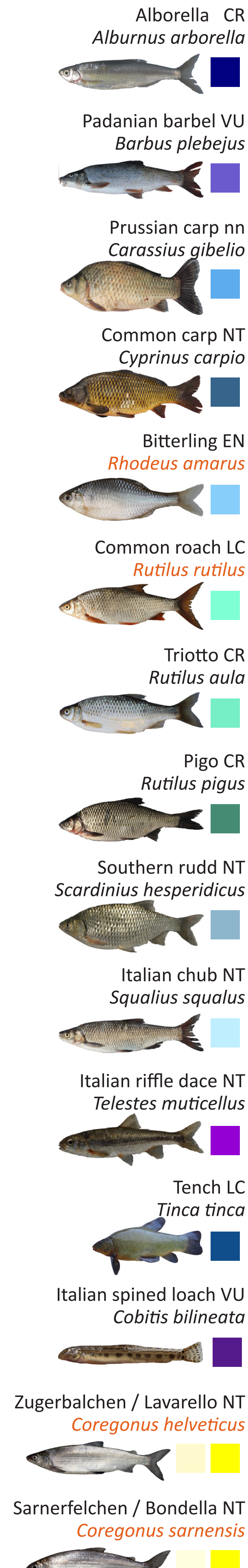
Near the lakeshore (littoral), electrofishing catches were dominated by freshwater blenny, along with southern rudd. Biomass was dominated by two large non-native wels catfish. Littoral nets contained a high proportion of perch and non-native roach, with biomass distributed among many different species. Close to the lake floor (benthic), perch and roach dominated abundance and biomass. The open water (pelagic) was mostly roach, non-native whitefish, with some agone. Pelagic biomass was mostly whitefish, with contributions from Italian chub, non-native Atlantic trout.



Fish lengths

Fish caught in CEN nets were dominated by small perch 6-9 cm and roach 6-9 cm. Larger fish were mostly whitefish.

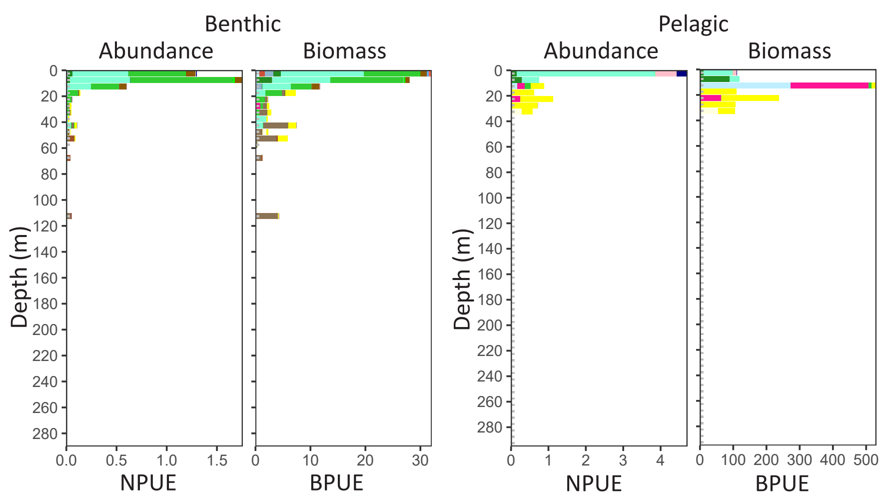




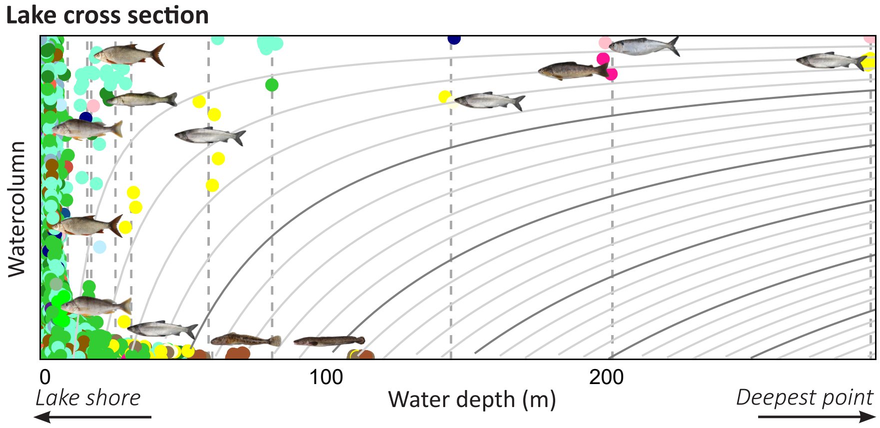
Lake Maggiore

Depth distribution

Benthic catches were highest in the upper 10 m, dominated by perch and non-native roach. Deeper benthic fish were mostly burbot, profundal sculpin and non-native whitefish. In the pelagic, roach dominated the surface layer, with catches of whitefish highest between 15-35 m. Very few fish were caught in open water, with none caught below 35 m. Benthic nets consistently contained fish, however no benthic nets were set below 125 m, so it is uncertain whether fish are present in this deep benthic habitat.



Lake cross section



Atlantic trout NT
Salmo trutta

Marble trout CR
Salmo marmoratus

Rainbow trout nn
Oncorhynchus mykiss

Alpine lake perch LC
Perca fluviatilis “Yellow-orange form”

European river perch DD
Perca fluviatilis “Red form”

Eurasian ruffe LC
Gymnocephalus cernua

Pike-perch nn
Sander lucioperca

Freshwater blenny NT
Salaria fluviatilis “Italian lineage”

Pumpkinseed nn
Lepomis gibbosus

Largemouth bass / Blackbass nn
Micropterus salmoides

Padanian goby EN
Padogobius bonelli

Po littoral / stream sculpin NT
Cottus sp “Po lineage”

Profundal Po lake sculpin NT
Cottus sp “Profundal Po”

Northern pike LC
Esox lucius

Southern pike DD
Esox cisalpinus

Three-spined stickleback (Adriatic lineage) DD
Gasterosteus gymnurus

Wels catfish LC
Silurus glanis

Black bullhead nn
Ameiurus melas

Agone VU
Alosa agone

Twaite shad DD
Alosa fallax

Burbot LC
Lota lota

Fish species reported to occur in the lake but not recorded in Projet Lac

Common bream LC
Abramis brama

Italian nase CR
Chondrostoma soetta

Gudgeon DD
Gobio sp

Italian loach CR
Sabanejewia larvata

Lake char VU
Salvelinus umbla

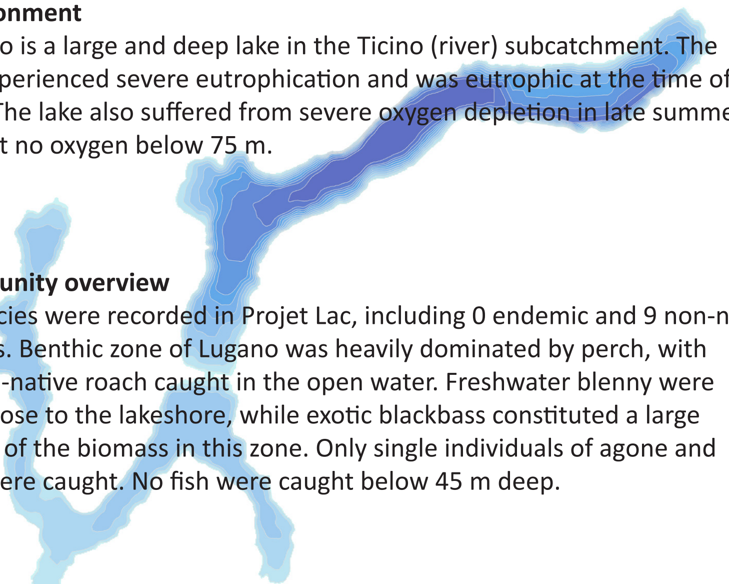
European grayling EN
Thymallus thymallus

European eel CR
Anguilla anguilla

Lombardy lamprey DD
Lampetra zanandreai

Lake Lugano

Po catchment



Lake environment

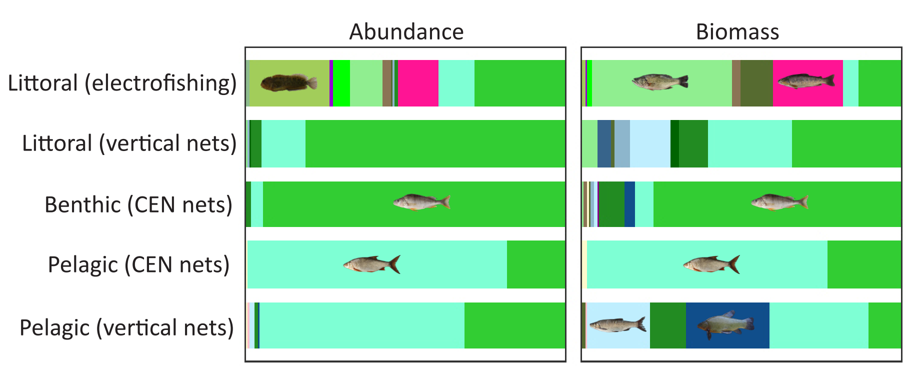
Lake Lugano is a large and deep lake in the Ticino (river) subcatchment. The lake has experienced severe eutrophication and was eutrophic at the time of sampling. The lake also suffered from severe oxygen depletion in late summer with almost no oxygen below 75 m.

Fish community overview

24 fish species were recorded in Projet Lac, including 0 endemic and 9 non-native species. Benthic zone of Lugano was heavily dominated by perch, with mostly non-native roach caught in the open water. Freshwater blenny were common close to the lakeshore, while exotic blackbass constituted a large proportion of the biomass in this zone. Only single individuals of agone and alborella were caught. No fish were caught below 45 m deep.

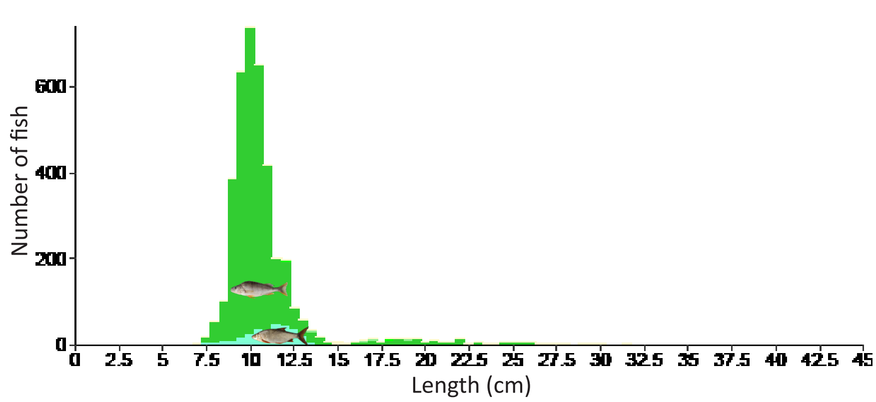
Community composition

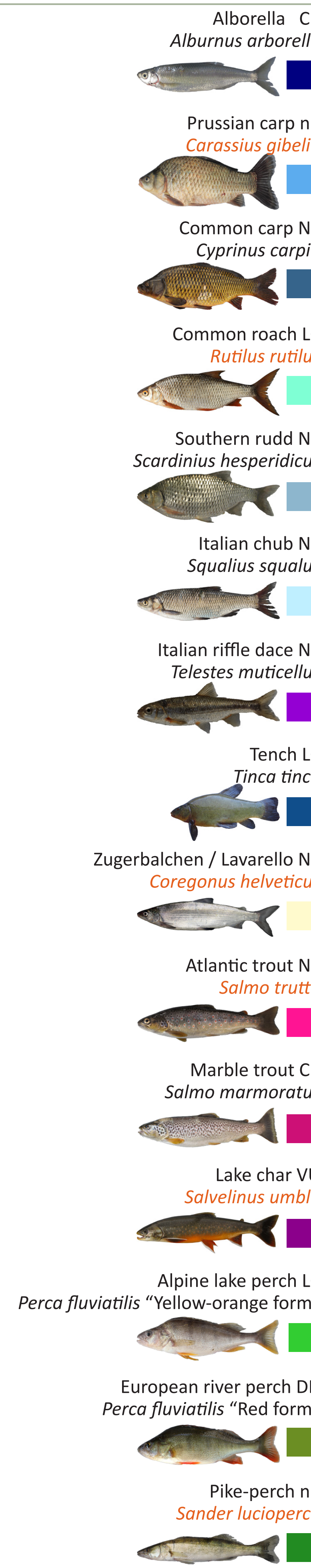
Near the lakeshore (littoral), electrofishing catches were dominated by perch and freshwater blenny, with biomass mainly exotic blackbass and non-native Atlantic trout. In the littoral nets, abundance was heavily dominated by perch, with non-native roach also contributing to biomass. Close to the lake floor (benthic), perch heavily dominated abundance and biomass. The open water (pelagic) was dominated by roach, with perch, with tench, Italian chub and non-native pikeperch also contributing to biomass.



Fish lengths

Fish caught in CEN nets were very heavily dominated by small perch 9-12 cm, along with non-native roach 10-13 cm.

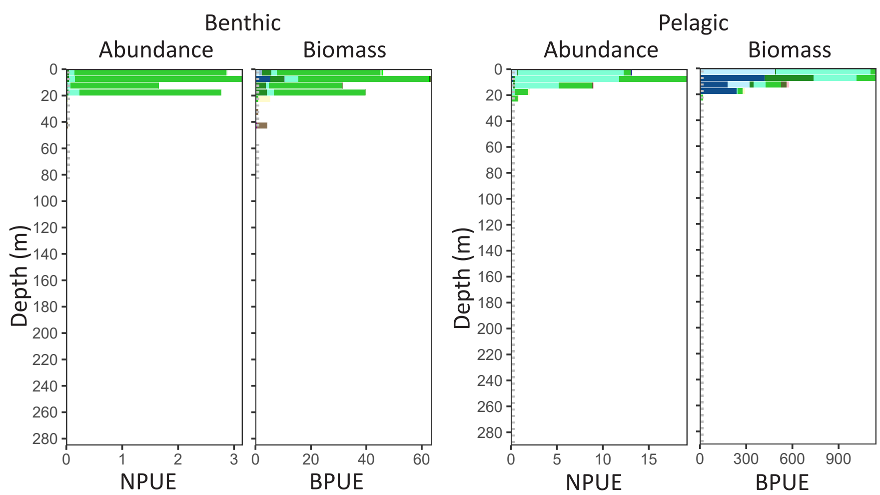




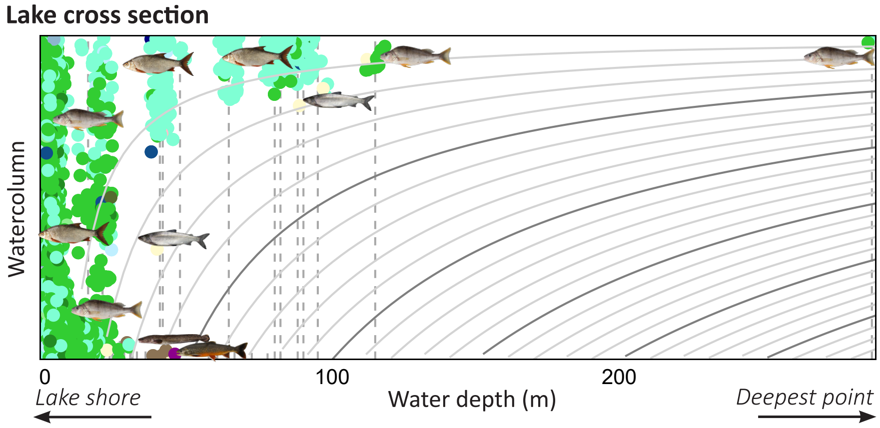
Lake Lugano

Depth distribution

The vast majority of fish were caught in the upper 20 m of the lake and no fish were caught below 50 m. Perch dominated catches near the lake floor to 20 m, with burbot and non-native whitefish among the few fish caught below 20 m. Non-native roach and perch dominated abundance in the upper layers of the pelagic, with tench and Italian chub contributing to biomass. No fish were caught below 30 m in open water. Fish were only caught in the upper 20 % of the lake.



Lake cross section



Freshwater blenny NT
Salaria fluviatilis "Italian lineage"

Pumpkinseed nn
Lepomis gibbosus

Largemouth bass / Blackbass nn
Micropterus salmoides

Padanian goby EN
Padogobius bonelli

Northern pike LC
Esox lucius

Southern pike DD
Esox cisalpinus

Agone VU
Alosa agone

Burbot LC
Lota lota

European eel CR
Anguilla anguilla

Fish species reported to occur in the lake but not recorded in Projet Lac

Padanian barbel VU
Barbus plebejus

Italian nase CR
Chondrostoma soetta

Gudgeon DD
Gobio sp

Triotto CR
Rutilus aula

Pigo CR
Rutilus pigus

Rainbow trout nn
Oncorhynchus mykiss

Sculpin (species unknown) DD
Cottus sp

Wels catfish LC
Silurus glanis

Black bullhead nn
Ameiurus melas

Lombardy lamprey DD
Lampetra zanandreai

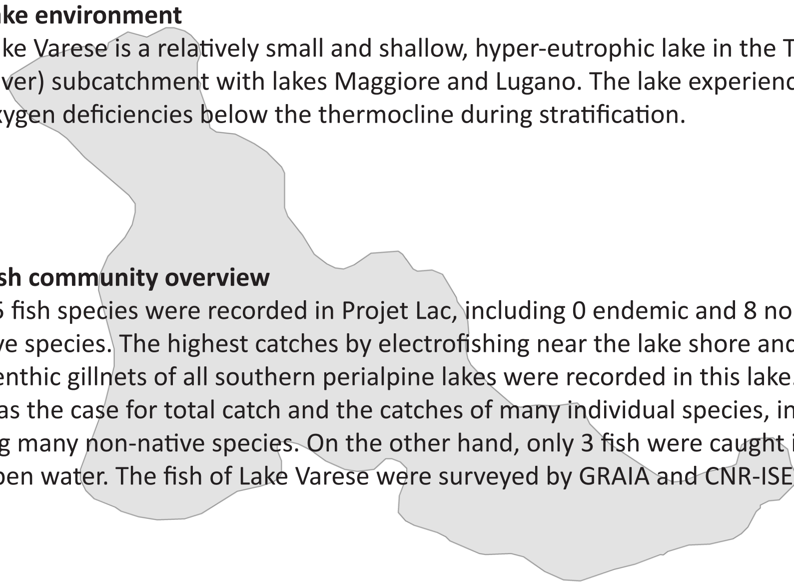
Twaite shad †
Alosa fallax

Lake Varese

Po catchment

Lake environment

Lake Varese is a relatively small and shallow, hyper-eutrophic lake in the Ticino (river) subcatchment with lakes Maggiore and Lugano. The lake experiences oxygen deficiencies below the thermocline during stratification.

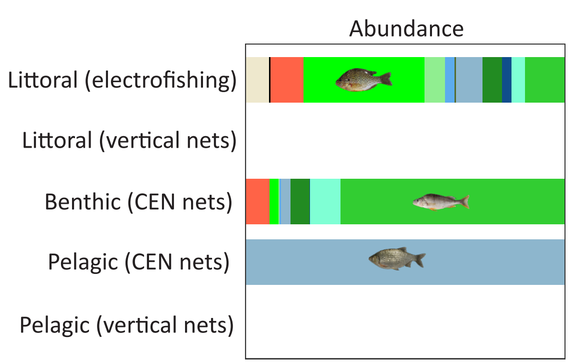


Fish community overview

15 fish species were recorded in Projet Lac, including 0 endemic and 8 non-native species. The highest catches by electrofishing near the lake shore and benthic gillnets of all southern perialpine lakes were recorded in this lake. This was the case for total catch and the catches of many individual species, including many non-native species. On the other hand, only 3 fish were caught in the open water. The fish of Lake Varese were surveyed by GRAIA and CNR-ISE.

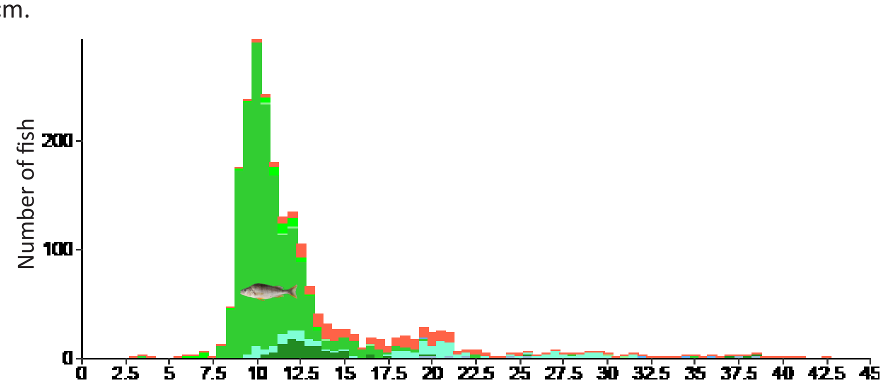
Community composition

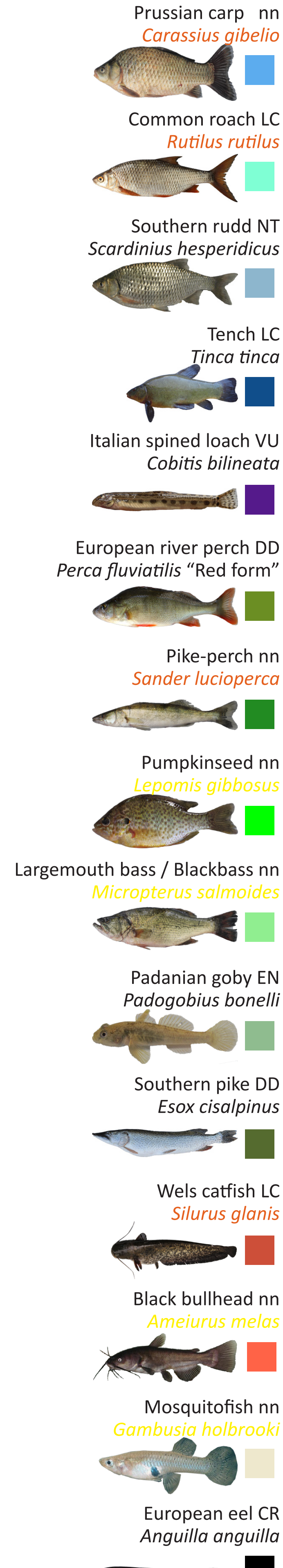
Near the lakeshore (littoral), electrofishing catches were dominated by exotic pumpkinseed. Perch, non-native black bullhead, exotic mosquitofish, southern rudd and exotic blackbass were also abundant. Close to the lake floor (benthic), perch dominated the catches, with black bullhead, non-native pikeperch and non-native roach also contributing. Only three fish (southern rudd) were caught in open water (pelagic).



Fish lengths

Fish caught in CEN nets were dominated by small perch 9-13 cm, with small pikeperch 11-15 cm also evident. Black bullhead were mostly between 11-21 cm.

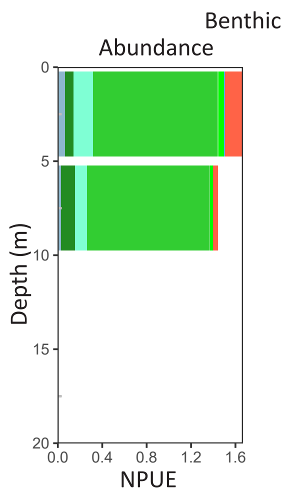




Lake Varese

Depth distribution

Perch dominated benthic fish to 10 m. The 3 southern rudd caught in open water were between 0-10 m. No fish were caught in the lake below 10 m. Vertical nets were not used to sample the fish of Lake Varese so a two-dimensional depth distribution cannot be shown.

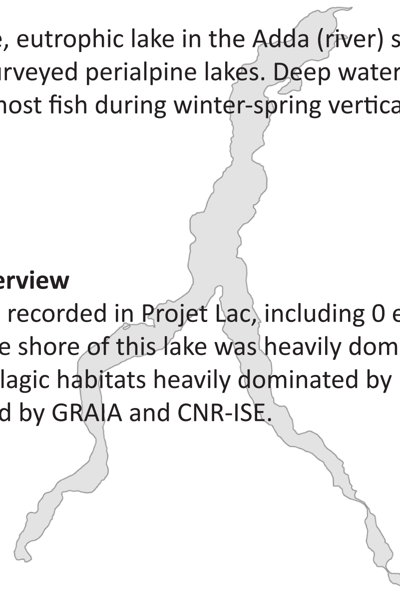


Lake Como

Po catchment

Lake environment

Lake Como is a large, eutrophic lake in the Adda (river) subcatchment. This was the deepest of all surveyed perialpine lakes. Deep water oxygen concentrations were sufficient for most fish during winter-spring vertical mixing.

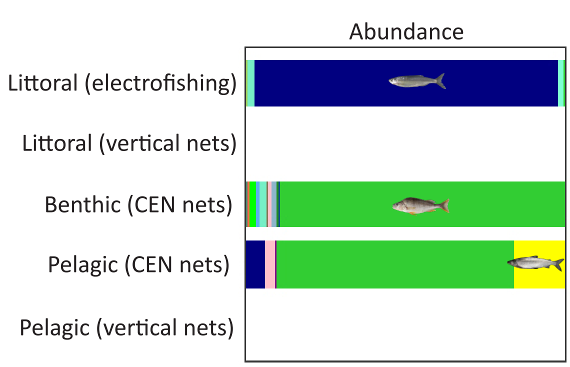


Fish community overview

26 fish species were recorded in Projet Lac, including 0 endemic and 9 non-native species. The lake shore of this lake was heavily dominated by alborella, with benthic and pelagic habitats heavily dominated by perch. The fish of Lake Como were surveyed by GRAIA and CNR-ISE.

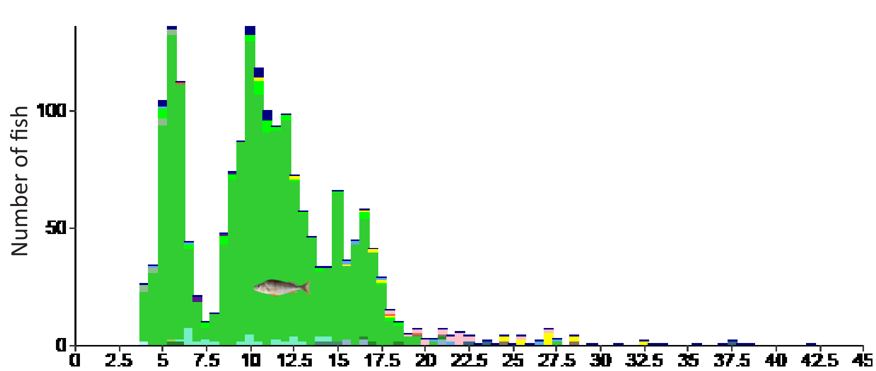
Community composition

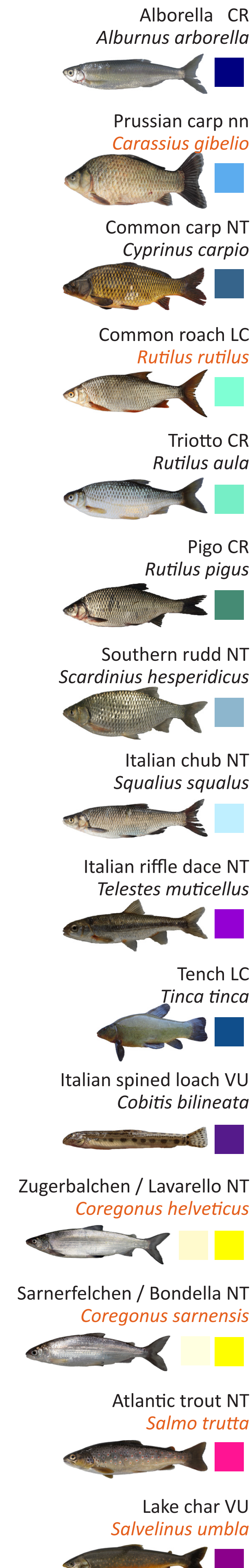
Near the lakeshore (littoral), electrofishing catches were heavily dominated by alborella. Close to the lake floor (benthic), perch formed more than 90% of recorded fish. The open water (pelagic) also contained mostly perch, with non-native whitefish.



Fish lengths

Fish caught in CEN nets were heavily dominated by perch with several cohorts evident: 4-7 cm, 8-13 cm and 16-18 cm.

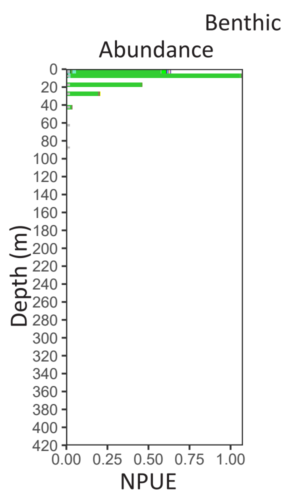




Lake Como

Depth distribution

Perch abundance was highest 5-10 m and declined with depth. No fish were caught between 50-75 m, however 1 burbot was caught between 75-100 m. No benthic nets were set below 100 m. Fish were caught in open water to 50 m, including non-native char and non-native whitefish, with no nets set below this depth. Vertical nets were not used to sample the fish of Lake Como, so a two-dimensional depth distribution cannot be shown.



European river perch DD
Perca fluviatilis "Red form"

Pike-perch nn
Sander lucioperca

Freshwater blenny NT
Salaria fluviatilis "Italian lineage"

Pumpkinseed nn
Lepomis gibbosus

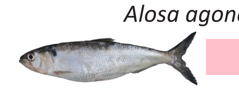
Padanian goby EN
Padogobius bonelli

Po littoral / stream sculpin NT
Cottus sp "Po lineage"

Southern pike DD
Esox cisalpinus

Black bullhead nn
Ameiurus melas

Agone VU
Alosa agone

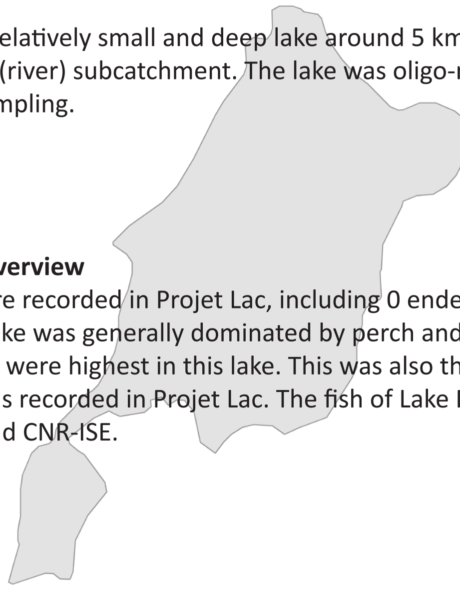


Burbot LC
Lota lota

European eel CR
Anguilla anguilla

Lake Mezzola

Po catchment



Lake environment

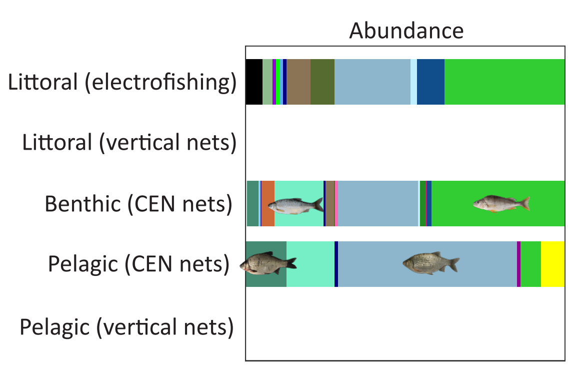
Lake Mezzola is a relatively small and deep lake around 5 km upstream of Lake Como in the Adda (river) subcatchment. The lake was oligo-mesotrophic around the time of fish sampling.

Fish community overview

26 fish species were recorded in Projet Lac, including 0 endemic and 10 non-native species. The lake was generally dominated by perch and southern rudd. Catch rates of pigo were highest in this lake. This was also the only lake where the Italian nase was recorded in Projet Lac. The fish of Lake Mezzola were surveyed by GRAIA and CNR-ISE.

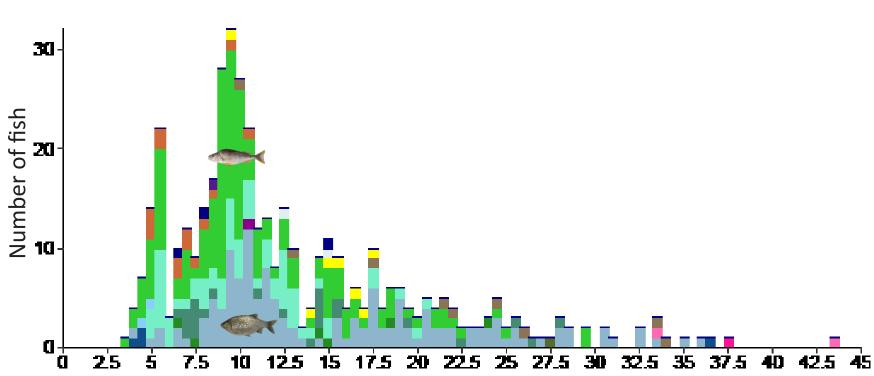
Community composition

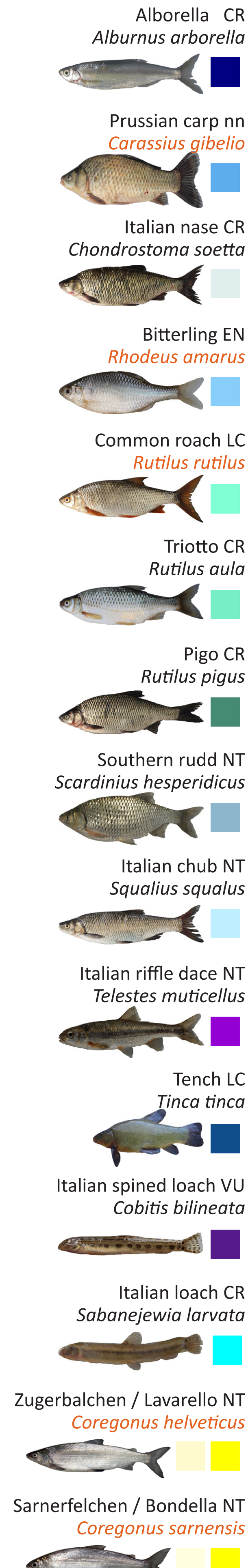
Near the lakeshore (littoral), electrofishing catches were dominated by perch and southern rudd. Close to the lake floor (benthic), perch and southern rudd were again dominant, along with triotto. The open water (pelagic) was also dominated by southern rudd, with pigo, triotto, perch and non-native whitefish.



Fish lengths

Fish caught in CEN nets were dominated by a large size range of southern rudd 8-26 cm. Small perch were also common 8-11 cm.

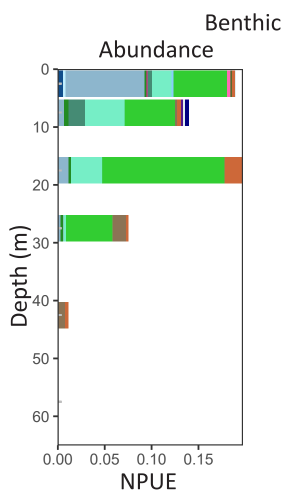




Lake Mezzola

Depth distribution

Southern rudd were common in the benthic zone near the surface, with perch common in depth zones to 35 m. A burbot and a sculpin were caught between 35-50 m, with no fish caught in the net set between 50-75 m. In the pelagic, southern rudd were similarly abundant in depth layers to 30 m. Two non-native whitefish were caught between 30-40 m, with no pelagic nets set below this. Vertical nets were not used to sample the fish of Lake Mezzola, so a two-dimensional depth distribution cannot be shown.



Atlantic trout NT
Salmo trutta

Lake char VU
Salvelinus umbla

Rainbow trout nn
Oncorhynchus mykiss

European river perch DD
Perca fluviatilis “Red form”

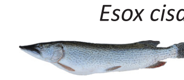
Pike-perch nn
Sander lucioperca

Pumpkinseed nn
Lepomis gibbosus

Padanian goby EN
Padogobius bonelli

Po littoral / stream sculpin NT
Cottus sp “Po lineage”

Southern pike DD
Esox cisalpinus

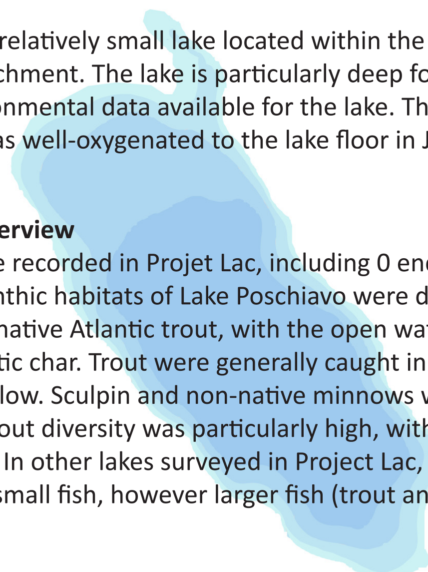


Burbot LC
Lota lota

European eel CR
Anguilla anguilla

Lake Poschiavo

Po catchment



Lake environment

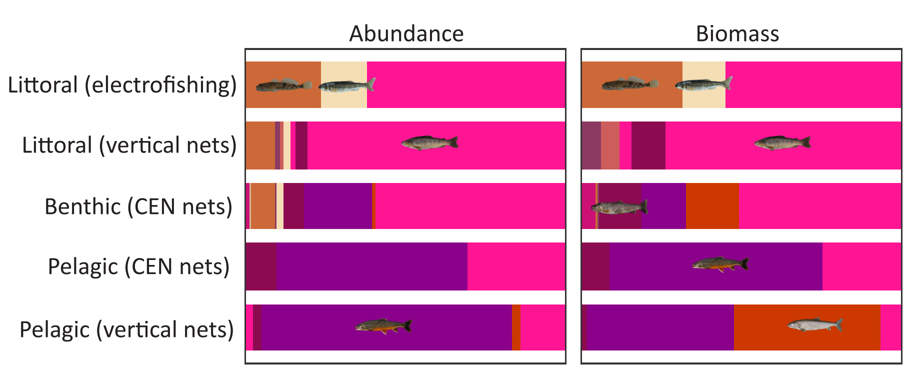
Lake Poschiavo is a relatively small lake located within the Alps, high in the Adda (river) subcatchment. The lake is particularly deep for is surface area. There is little environmental data available for the lake. The lake was mesotrophic in 1995 and was well-oxygenated to the lake floor in July 2007.

Fish community overview

10 fish species were recorded in Projet Lac, including 0 endemic and 6 non-native species.The benthic habitats of Lake Poschiavo were dominated heavily dominated by non-native Atlantic trout, with the open water dominated by non-native and exotic char. Trout were generally caught in the shallower depth layers, with char below. Sculpin and non-native minnows were common close to the lakeshore. Trout diversity was particularly high, with 3 native and 2 non-native species. In other lakes surveyed in Project Lac, the fish community was dominated by small fish, however larger fish (trout and char) dominated in Lake Poschiavo.

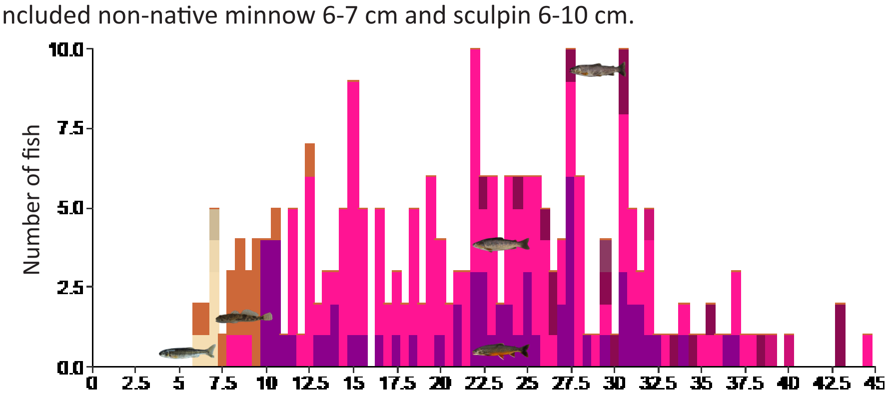
Community composition

Near the lakeshore (littoral), abundance and biomass of fish in electrofishing was dominated by small, non-native Atlantic trout, followed by sculpin and non-native minnow. Littoral nets were heavily dominated by Atlantic trout. Close to the lake floor (benthic), Atlantic trout also formed most of the abundance, with non-native lake char, while biomass also included Poschiavo lake trout, char and exotic Canadian lake trout. The open water (pelagic) was heavily dominated by char, with Atlantic trout. Canadian lake trout also contributed to biomass in vertical nets.



Fish lengths

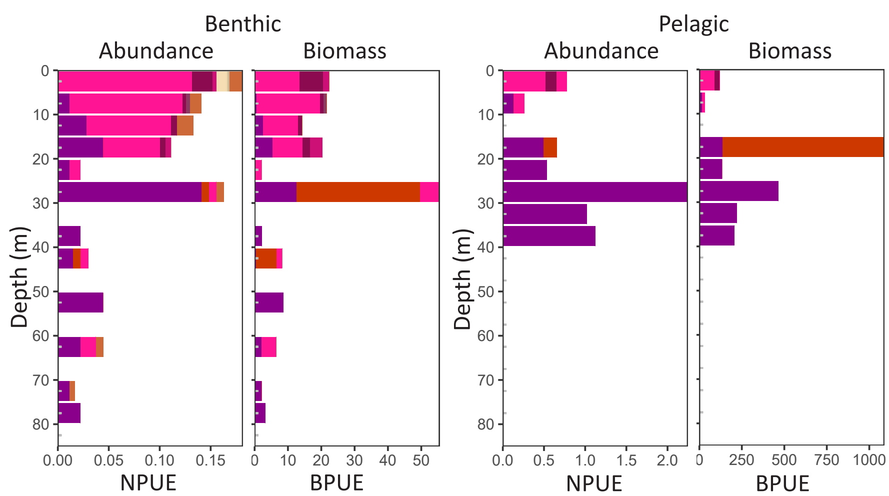
Fish caught in CEN nets were dominated by non-native Atlantic trout 12-32 cm, non-native char 10-37 cm and Poschaivo lake trout 22-43 cm. Smaller fish included non-native minnow 6-7 cm and sculpin 6-10 cm.



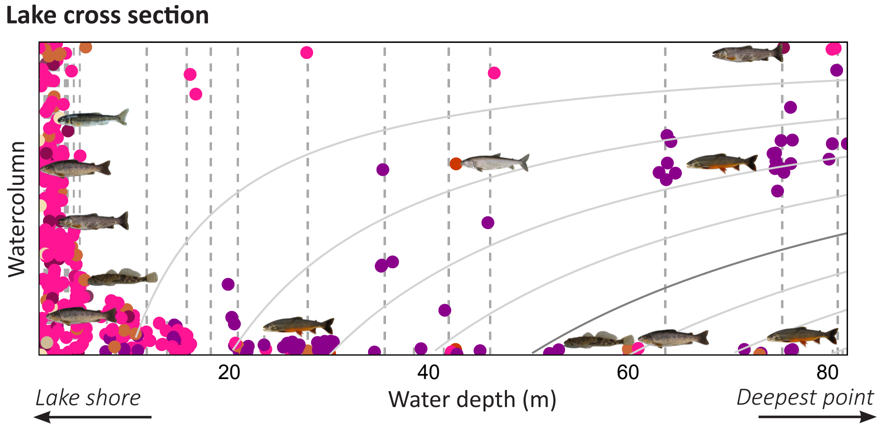
Lake Poschiavo

Depth distribution

Non-native Atlantic trout, Poschiavo lake trout, sculpin and non-native minnows dominated the shallow benthic nets, with abundance generally declining with depth. Non-native char began to dominate from 25 m to the deepest point of the lake. In the pelagic, Atlantic trout were caught mostly in the surface layers, with char mostly caught between 15-40 m. No fish were caught in open water below 40 m.



Lake cross section

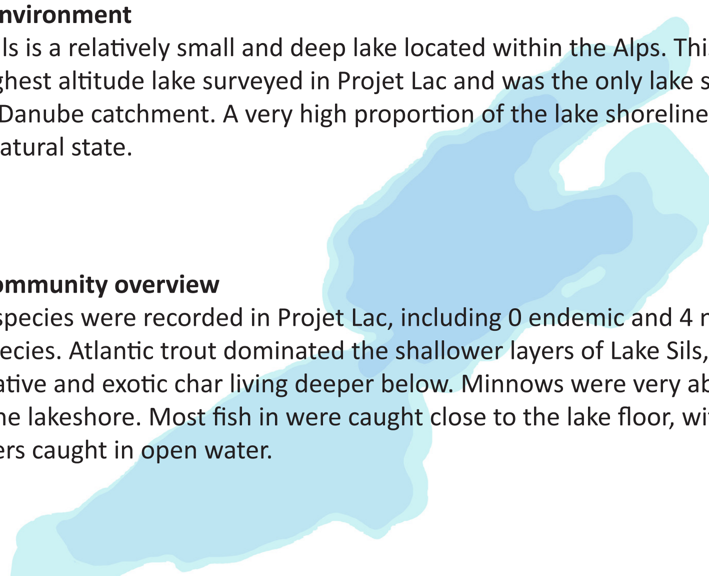


Fish species reported to occur in the lake but not recorded in Projet Lac

Southern rudd NT
Scardinius hesperidicus

Lake Sils

Danube catchment



Lake environment

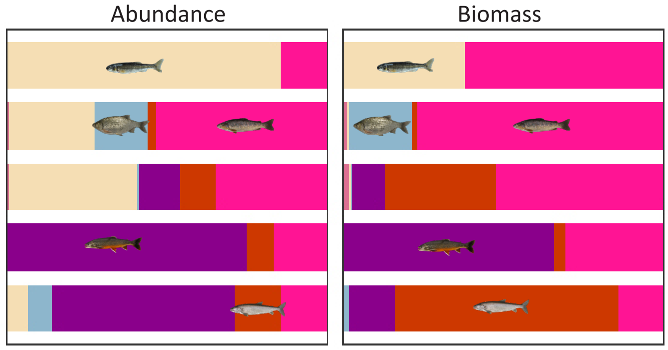
Lake Sils is a relatively small and deep lake located within the Alps. This was the highest altitude lake surveyed in Projet Lac and was the only lake surveyed in the Danube catchment. A very high proportion of the lake shoreline is in a near-natural state.

Fish community overview

8 fish species were recorded in Projet Lac, including 0 endemic and 4 non-native species. Atlantic trout dominated the shallower layers of Lake Sils, with non-native and exotic char living deeper below. Minnows were very abundant near the lakeshore. Most fish in were caught close to the lake floor, with low numbers caught in open water.

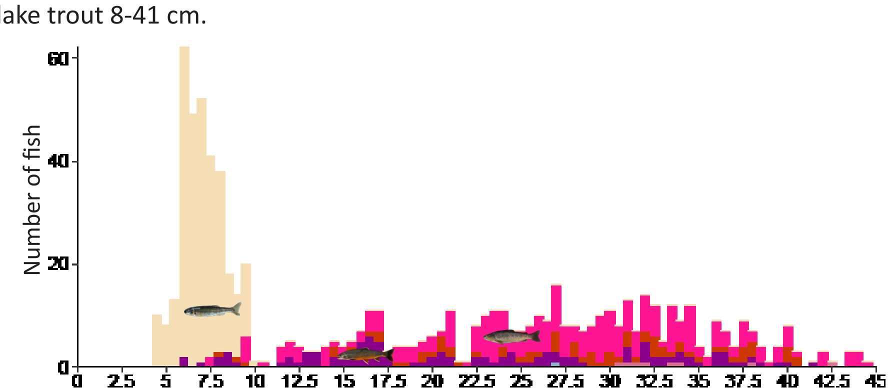
Community composition

Near the lakeshore (littoral), electrofishing abundance was dominated by minnow, with biomass dominated by Atlantic trout. Littoral nets were also dominated by Atlantic trout, with minnow contributing to abundance and southern rudd contributing to abundance and biomass. Close to the lake floor (benthic), abundance was dominated by minnow and Atlantic trout, while biomass was mostly Atlantic trout and exotic Canadian lake trout. The open water (pelagic) was dominated by non-native char, with Atlantic trout and Canadian lake trout also contributing to biomass.



Fish lengths

Fish caught in CEN nets were dominated by small minnow 5-9 cm and large salmonids: Atlantic trout 9- 45 cm, non-native char 6-40 cm and exotic Canadian lake trout 8-41 cm.



Mediterranean minnow DD
Phoxinus septimaniae

Danube minnow DD
Phoxinus csikii

Southern rudd NT
Scardinius hesperidicus

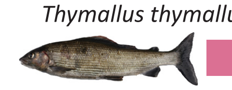
Atlantic trout NT
Salmo trutta

Danube trout CR
Salmo labrax

Lake char VU
Salvelinus umbla

Canadian lake trout nn
Salvelinus namaycush

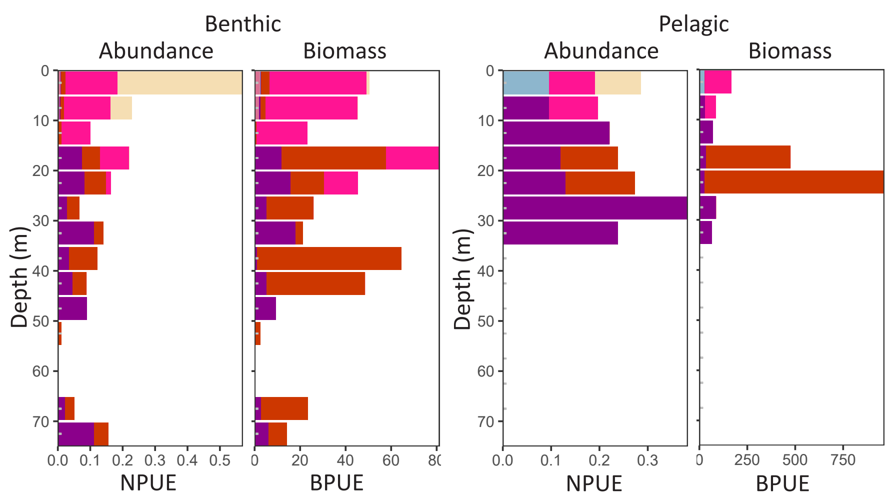
European grayling EN
Thymallus thymallus



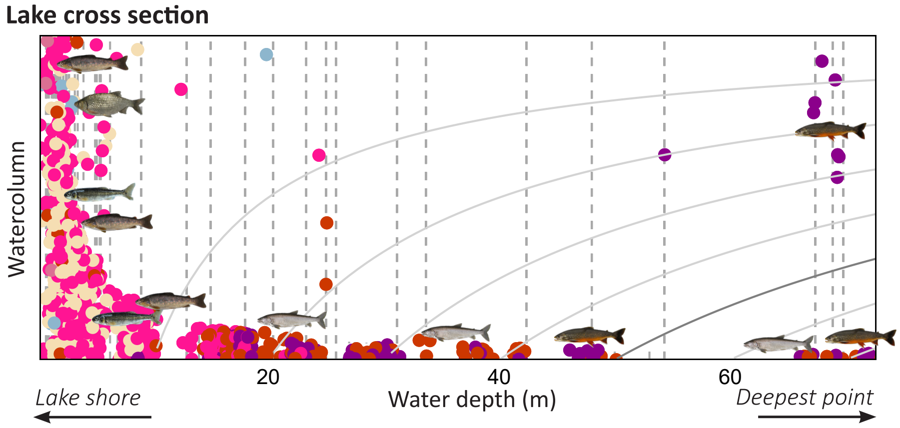
Lake Sils

Depth distribution

Minnow dominated benthic abundance near the surface, with Atlantic trout common between 0-20 m and non-native char and exotic Canadian lake trout below 15 m. In the pelagic, Atlantic trout were caught in the upper 10 m, with char below 10 m. Most fish were concentrated in near the lake floor with few fish caught in open water.



Lake cross section



Updates/corrections

Several updates/corrections were made to the species lists for each lake such that the "lake info sheets" have slightly updated information compared to the body of the synthesis report.

These changes are as follows:

Lake Chalain
Project Lac species
Telestes souffia → *Telestes souffia souffia* [subspecies added]

Lake Murten
Previously recorded species
Telestes souffia → *Telestes souffia aggassizi* [subspecies added]

Lake Biel
Previously recorded species
Telestes souffia → *Telestes souffia aggassizi* [subspecies added]

Lake Lucerne
Previously recorded species
Telestes souffia → *Telestes souffia aggassizi* [subspecies added]
ADDED: Schwebforelle †; Salmo schiefermuelleri

Upper Lake Constance
Previously recorded species
Telestes souffia → *Telestes souffia aggassizi* [subspecies added]

Brienz
Previously recorded species
Orange-bellied char VU → Limnetic char Brienz VU
Salvelinus sp "Limnetic Thun/Brienz" → *Salvelinus* sp "Limnetic Brienz"

Maggiore
Projet Lac species
Three-spined stickleback (western) NT → Three-spined stickleback (Adriatic lineage) DD

Previously recorded species
Gobio gobio → *Gobio* sp
Gudgeon LC → Gudgeon DD

Lugano
Previously recorded species
Gobio gobio → *Gobio* sp
Gudgeon LC → Gudgeon DD
ADDED: Twaite shad †; *Alosa fallax*

Poschiavo
Previously recorded species
ADDED: Southern rudd NT, *Scardinius hesperidicus*

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