



## Exploring multiple stressor effects with Ecopath, Ecosim, and Ecospace: Research designs, modeling techniques, and future directions



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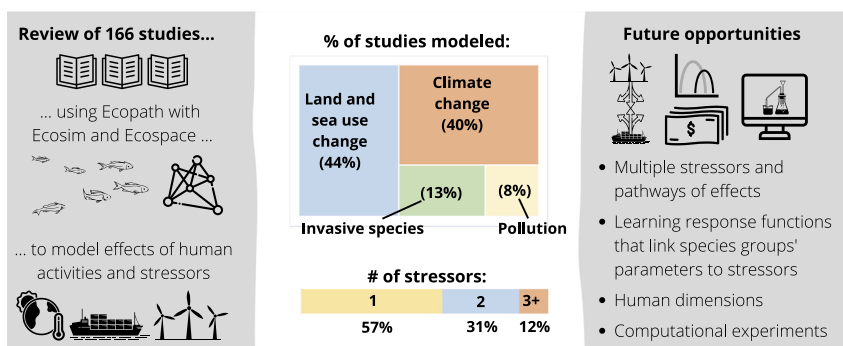
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### HIGHLIGHTS

- Review of studies modeling human stressors in Ecopath, Ecosim, Ecospace
- Encompassing climate change, land and sea use, pollution, invasive species
- Most studies investigated single stressors, only 12% three or more
- Identify four research gaps that can be filled with existing data and methods.
- Interdisciplinary framework for modeling cumulative human impacts

### GRAPHICAL ABSTRACT



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### ABSTRACT

Understanding the cumulative effects of multiple stressors is a research priority in environmental science. Ecological models are a key component of tackling this challenge because they can simulate interactions between the components of an ecosystem. Here, we ask, how has the popular modeling platform Ecopath with Ecosim (EwE) been used to model human impacts related to climate change, land and sea use, pollution, and invasive species? We conducted a literature review encompassing 166 studies covering stressors other than fishing mostly in aquatic ecosystems. The most modeled stressors were physical climate change (60 studies), species introductions (22), habitat loss (21), and eutrophication (20), using a range of modeling techniques. Despite this comprehensive coverage, we identified four gaps that must be filled to harness the potential of EwE for studying multiple stressor effects. First, only 12% of studies investigated three or more stressors, with most studies focusing on single stressors. Furthermore, many studies modeled only one of many pathways through which each stressor is known to affect ecosystems. Second, various methods have been applied to define environmental response functions representing the effects of single stressors on species groups. These functions can have a large effect on the simulated ecological changes, but best practices for deriving them are yet to emerge. Third, human dimensions of environmental change – except for fisheries – were rarely considered. Fourth, only 3% of studies used statistical research designs that allow attribution of simulated ecosystem changes to stressors' direct effects and interactions, such as factorial (computational) experiments. None made full use of the statistical

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possibilities that arise when simulations can be repeated many times with controlled changes to the inputs. We argue that all four gaps are feasibly filled by integrating ecological modeling with advances in other subfields of environmental science and in computational statistics.

## Contents

1.	Introduction . . . . .	2
2.	Methods . . . . .	3
2.1.	Identification of studies . . . . .	3
2.2.	Categorization of studies . . . . .	3
2.3.	Concepts and terminology . . . . .	4
3.	Literature summary . . . . .	4
3.1.	Overview . . . . .	4
3.2.	Linking with external models . . . . .	4
3.3.	Indicators of human impact . . . . .	4
3.4.	Research designs . . . . .	5
4.	Assessing stressor effects with static Ecopath models . . . . .	6
5.	Human activities and stressors in Ecosim and Ecospace models . . . . .	6
5.1.	Overview of modeling techniques and terminology . . . . .	6
5.2.	Overview of modeled stressors . . . . .	7
5.3.	Modeling individual stressors . . . . .	7
5.3.1.	Physical climate . . . . .	7
5.3.2.	Species introductions . . . . .	8
5.3.3.	Habitat loss and restoration . . . . .	10
5.3.4.	Eutrophication and deoxygenation . . . . .	10
5.3.5.	Aquatic contaminants . . . . .	11
5.3.6.	Aquaculture . . . . .	11
5.3.7.	Ocean acidification . . . . .	11
5.3.8.	Offshore energy . . . . .	11
5.3.9.	Underwater noise . . . . .	12
5.3.10.	Biomanipulation . . . . .	12
5.3.11.	Other infrastructure and stressors . . . . .	12
5.4.	Simplified models simulating many human activities . . . . .	12
6.	Gaps and future opportunities . . . . .	12
6.1.	Gap 1: represent multiple pathways of impact for each stressor . . . . .	12
6.2.	Gap 2: develop best practices for characterizing stressor response functions . . . . .	13
6.3.	Gap 3: relate ecological impacts to multiple human dimensions, including ecosystem services . . . . .	14
6.4.	Gap 4: employ computational experiments to disentangle multiple stressors' direct and indirect effects . . . . .	14
	Funding . . . . .	14
	CRedit authorship contribution statement . . . . .	14
	Data availability . . . . .	15
	Declaration of competing interest . . . . .	15
	Appendix A. Supplementary data . . . . .	15
	References . . . . .	15

## 1. Introduction

Many ecosystems are degraded by multiple stressors resulting from global change and local human activities (Halpern et al., 2015; Vörösmarty et al., 2010; Williams et al., 2020). Human impacts caused by these stressors pose profound risks to biodiversity and nature's contributions to people including ecosystem services (Di Marco et al., 2018; IPBES, 2019). Food web structure and functional redundancy of species and interactions can buffer against stress but may be overwhelmed by multiple stressors (Nagelkerken et al., 2020). Understanding ecosystem-scale cumulative effects of multiple stressors is consequently a research priority and one of the scientific challenges raised by the UN Ocean Decade (Mason et al., 2017; Ryabinin et al., 2019; Gissi et al., 2021). Yet multiple stressor effects are complex and characterized by non-linear ecosystem responses, stressor interactions, and feedback mechanisms (Côté et al., 2016; Crain et al., 2008; Darling and Côté, 2008; Hunsicker et al., 2016; O'Connor et al., 2021). Laboratory experiments have provided fundamental information about multiple stressor effects but cannot be directly translated into ecosystem-scale impacts in nature. In contrast, field research can reveal

human-driven changes at the ecosystem scale, but the cost of field data collection and potential for confounding from unmeasured variables limits its ability to identify causal mechanisms.

Models are therefore a necessary component of the toolkit for investigating ecosystem-level cumulative effects (Hodgson and Halpern, 2018). The most common modeling approaches are simple, for example, assuming linear ecosystem responses to stress and no interactions between stressors (Halpern et al., 2008; Korpinen and Andersen, 2016). Such simple models can yield important insights, e.g., into hotspots of anthropogenic stress, but their outputs can be highly uncertain (Gissi et al., 2017; Stock et al., 2018a; Stock and Micheli, 2016) and comparisons with field data have yielded mixed results (Clark et al., 2016; Stockbridge et al., 2021). Using models that ignore the complex interactions that characterize cumulative human impacts for decision making can underestimate impacts resulting from stressor interactions and lead to inefficient environmental management (Arrigo et al., 2020; Brown et al., 2014). Understanding, predicting, and managing cumulative human impacts at the ecosystem scale thus remains a grand challenge (Borja et al., 2020; Bundy et al., 2021).

An important step towards better modeling of multiple stressor effects and cumulative human impacts is the integration of species interactions via food web modeling (Giakoumi et al., 2015). Multi-species ecological models such as Ecopath with Ecosim and its spatial extension Ecospace (henceforth, EwE; Christensen and Walters, 2004) and Atlantis (Fulton et al., 2011) are in principle able to represent the dynamics of food webs under stress (Griffith et al., 2011; Griffith et al., 2012; Villasante et al., 2016) but have so far been limited to analyzing combinations of few stressors (Hodgson and Halpern, 2018). Here, we focus on EwE, a widely used ecosystem modeling tool that has both scientific and practical applications (Christensen and Walters, 2004; Vassilides et al., 2017a), with three core components. Ecopath is a mass-balanced food web model representing average trophic flows between functional groups consisting of one or more species as well as detritus compartments. Ecopath models incorporate estimates of known parameters such as biomass and diet composition of the functional groups and derive unknown parameters such that all energy is accounted for. Ecosim uses a balanced Ecopath model for simulations through time (e.g., showing ripple effects of fishing at high trophic levels through the food web), and Ecospace allows for spatiotemporal simulations. EwE is commonly used to address questions about fisheries and ecosystem functioning (Colléter et al., 2015). In early applications of EwE, other stressors such as climate change had to be represented by ad-hoc modifications to the model (Overholtz and Link, 2009). Yet EwE's capabilities have expanded, and many stressors and their interactions have now been investigated (Coll et al., 2015). For example, an EwE-based global model for predicting climate impacts on marine ecosystems is included in the Fisheries and Marine Ecosystem Model Intercomparison Project (Tittensor et al., 2018).

Given that EwE has limitations but also potential for cumulative impact research, we answer three questions based on a literature review. First, how have individual human activities and stressors been modeled in EwE? Second, which research designs are commonly used to investigate cumulative effects with EwE (e.g., experimental designs vs. qualitative comparison of scenarios), and which indicators of environmental change are frequently reported? Third – given that cumulative effects research must be an interdisciplinary undertaking (Hodgson et al., 2019) – how can EwE be best integrated with other approaches to cumulative effects research and computational methods? To answer these questions, we present a review of studies that simulate human activities and stressors other than fishing with EwE (because EwE is a well-documented tool for simulating fisheries, we considered studies that simulated fishing but no other human activities or stressors out of scope). This review can serve as a guide for modelers who wish to include human activities and stressors in EwE simulations and can help researchers and practitioners judge the suitability of EwE as a modeling platform for answering specific questions about cumulative effects. We also identify four research gaps in the literature and propose an interdisciplinary framework to fill them, combining EwE with methods from other research fields relevant to understanding the cumulative effects of multiple stressors on nature and people.

## 2. Methods

Below we describe the two main aspects of our comprehensive synthetic review: the identification of relevant literature, and the categorization of studies in relation to our research questions. We then briefly explain how we addressed differences in terminology between studies.

### 2.1. Identification of studies

The literature search comprised three steps: 1) an initial search using broad search terms and relevant collections of EwE-based studies; 2) a search with expanded search terms that were updated based on the studies identified in step 1; and 3) the selection of articles to include in the review based on various criteria. We first searched for literature with this procedure in autumn 2020 and repeated all steps again in January 2022 to include up-to-date publications to the extent possible.

In the first step, an initial literature base was compiled from three sources. (a) We searched the Web of Science using the search terms: (ecopath OR ecosim OR ecospace) AND (((cumulative OR combined OR synergistic OR antagonistic OR accumulating OR collective) NEAR/2 (impact\* OR effect\*)) OR (stressor\* OR activit\* OR anthropogenic)). Only titles, keywords and abstracts were included in the search. (b) We searched EcoBase, a database of EwE models, for relevant articles (Colléter et al., 2015). EcoBase contained metadata (including literature references) for 470 models at the time of search. (c) We included a collection of articles describing EwE applications compiled by one of the model's developers (co-author V. Christensen, personal communication).

In the second step, we expanded the initial literature base using a wider range of search terms that occurred in articles from the first step. This involved searching the Web of Science again for specific human activities that were modeled in the initial body of literature, using the search phrase: (Ecopath OR Ecosim OR Ecospace) AND (climate OR warming OR temperature OR acidification OR farm OR aquaculture OR mariculture OR acidification OR “offshore energy” OR eutroph\* OR “habitat loss” OR “habitat degradation” OR noise OR shipping OR dam OR hydropower OR “Freshwater diversion” OR pollut\* OR contamin\* OR invasive OR alien OR reintroduction OR rewilding OR construction OR dumping). The purpose of this search was to find articles about modeling stressors (e.g., “ocean warming”) that did not mention the general search terms (e.g., “stressor”) and were not included in EcoBase and the personal collection of articles of Step 1. We only considered literature written in English and published journal articles, except in rare cases where other document types addressed human activities, stressors, modeling techniques, or applications that were not represented in journal articles. These criteria resulted in the inclusion of one Master's thesis, one book chapter, and one proceedings article, after evaluating all documents as described in the next paragraph. After removing duplicates, this process resulted in a final collection of over 1000 documents.

In the third step, we scrutinized each document more closely to ensure that it was within scope. This step involved reading the title, abstract, and keywords for each document. We retained a document if and only if these elements mentioned at least one human activity or stressor other than fishing, yielding 322 documents for full examination. While we excluded articles that investigated effects of fishing and other forms of direct exploitation (e.g., hunting) alone, we included articles that investigated the combined effects of fishing and at least one other stressor. For these articles, we counted fishing as a separate stressor if its effects were explored (e.g., an article simulating warming and fishing scenarios was counted as modeling two stressors). After full reading, a document was included in the review if it investigated ecological or socioeconomic effects of one or more human activities or stressors by means of an EwE model (possibly in combination with other models). In addition to human stressors, we included research investigating the effects of past climate on ecosystems, because distinguishing the effects of natural and anthropogenic climate variability and trends in historical simulations is not always possible and because the modeling techniques are similar. In contrast, we excluded documents that explored environmental changes without attribution to specific human activities or stressors (e.g., Duan et al., 2009) and research that characterizes ecosystems under stress but does not explicitly investigate ecosystem change (e.g., Arbach Leloup et al., 2008; Barausse et al., 2009). After applying these selection criteria, 166 articles were analyzed in the review.

Eight studies presented several Ecosim or Ecospace models for different study areas. Such studies were counted as a single study throughout the manuscript because they investigated the same stressors with the same techniques in all cases.

### 2.2. Categorization of studies

To summarize this body of literature, we grouped individual research articles based on the human activities and stressors that they modeled, using human activity and stressor categories that emerged from the literature itself. For example, we identified a set of research articles that investigate potential impacts of offshore wind farms with similar research

questions and objectives; we therefore treated offshore energy as a separate category of human activity.

To illustrate how the emerging stressor categories fit into broader knowledge needs, we related them to five broad drivers of environmental change that have been identified as most important globally (IPBES, 2019): Land and sea use changes (e.g., agricultural expansion and habitat loss to coastal infrastructure), direct exploitation such as fishing and logging, climate change, pollution, and invasive species. We acknowledge that other groupings are possible, and that some human-driven environmental changes fit into several stressor categories. For example, models investigating the shrinking extent of sea ice were included in counts for both the climate change and the habitat loss category. Conversely, broad categories such as physical climate change and eutrophication could have been split into several stressors.

Categories of ecological indicators and research designs also emerged from the literature itself, i.e., they were defined after reading all studies included in the review based on properties that many studies shared.

Some stressors were covered in prior literature reviews. Vasslides et al. (2017a, 2017b) review modeling approaches for eutrophication, salinity changes, and habitat restoration in coastal systems. Coll and Libralato (2012) review applications of EwE in the Mediterranean Sea, including research investigating anthropogenic stressors. None of these reviews included articles beyond 2014. Hence, for studies that were covered in prior reviews, we included them in the analyses but discuss them only briefly.

### 2.3. Concepts and terminology

Broadly speaking, human activities generate one or more stressors (or pressures) which can affect vulnerable ecological components (Murray et al., 2014). Regarding multiple stressor effects, there are terminological challenges such as discrepancies in operational definitions of synergistic and antagonistic interactions (Piggott et al., 2015). The literature included in this review encompassed both human activities (e.g., aquaculture) and stressors (e.g., ocean warming). For simplicity, we use the term “stressor” in the remainder of this review to refer to either a human activity or a stressor that can cause ecological changes (including positive effects on some species, e.g., by creating artificial habitat). Furthermore, we do not distinguish strictly between “effects” and “impacts”. When summarizing literature, we use terminology such as synergism and antagonism following the respective authors, recognizing that different authors likely use these terms somewhat differently.

## 3. Literature summary

### 3.1. Overview

We identified 166 articles fulfilling the criteria for inclusion in this review. Of these articles, 21% presented spatiotemporal simulations with Ecospace and 59% presented non-spatial simulations with Ecosim. The

remaining 20% of articles used static Ecopath models to investigate ecosystem changes along stressor gradients (e.g., before and after a biological invasion). Most articles focused on marine (82% including estuaries) and freshwater systems (15%). A single article focused on a terrestrial system (Fretzer, 2015), and some articles included both terrestrial and aquatic components (2%). For example, Reyes-Martínez et al. (2015) built a food web model for a sandy beach, and Capitani et al. (2021a) modeled the loss of floodplain forest habitat. While we did not exclude any ecosystem types from this review a priori, the existing literature and therefore our results pertain mainly to aquatic systems.

Study areas covered all continents but were most concentrated in Europe and North America (Fig. 1A; this may partially reflect the exclusion of literature in languages other than English). The number of papers investigating stressors other than fishing increased over the last two decades, peaking at 27 papers in 2021 (Fig. 1B). Spatiotemporal simulations with Ecospace have become more frequent after 2015. This growth coincides with a general increase in EwE-based studies over the last decades: According to the Web of Science, the number of publications mentioning Ecopath, Ecosim or Ecospace in their title, abstract, or keywords increased from 40 in the 1990s to 325 in the 2000s and 678 in the 2010s.

The modeled food webs were detailed, containing on average 33 functional groups (median), with a minimum of 7 and a maximum of 108. In contrast, most papers investigated only few stressors: one (57%), two (31%), or three (10%; Fig. 2A). These percentages should be interpreted as coarse estimates because they depend on our classification of stressors. For example, five studies modeled sea ice loss together with other aspects of climate change; sea ice loss is caused by climate change, but we counted habitat loss and physical climate change as two separate stressors (see Section 2.2 for other effects of our classification decisions on counts). While the first multi-stressor studies appeared in the early 2000s, they have been most common since 2014 (Fig. 2B), and there is recent progress towards modeling a more comprehensive set of human activities and stressors (Section 5.4).

### 3.2. Linking with external models

About 21% of studies linked EwE with other models. These linked models largely addressed climate (to incorporate future physical conditions) and biogeochemical aspects (simulating lower-trophic level dynamics, with biomasses replacing those of the respective functional groups in the EwE models). In most cases, models were linked via external model outputs feeding into EwE, but there were some examples of two-way coupling (EwE simulations drawing on the outputs of an external model, and EwE outputs feeding back into that model; Beecham et al., 2015; Fulton, 2011; Kearney et al., 2012).

### 3.3. Indicators of human impact

Most studies reported a small number of indicators of environmental change (median 2, counting measures such as biomass that are often

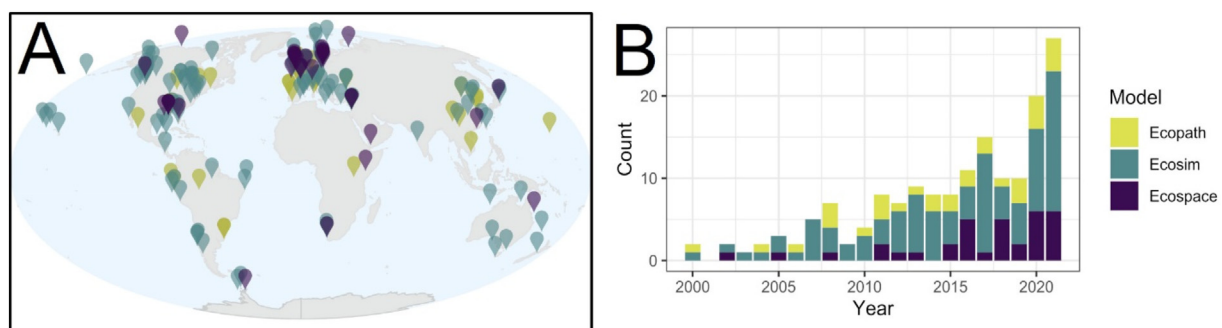
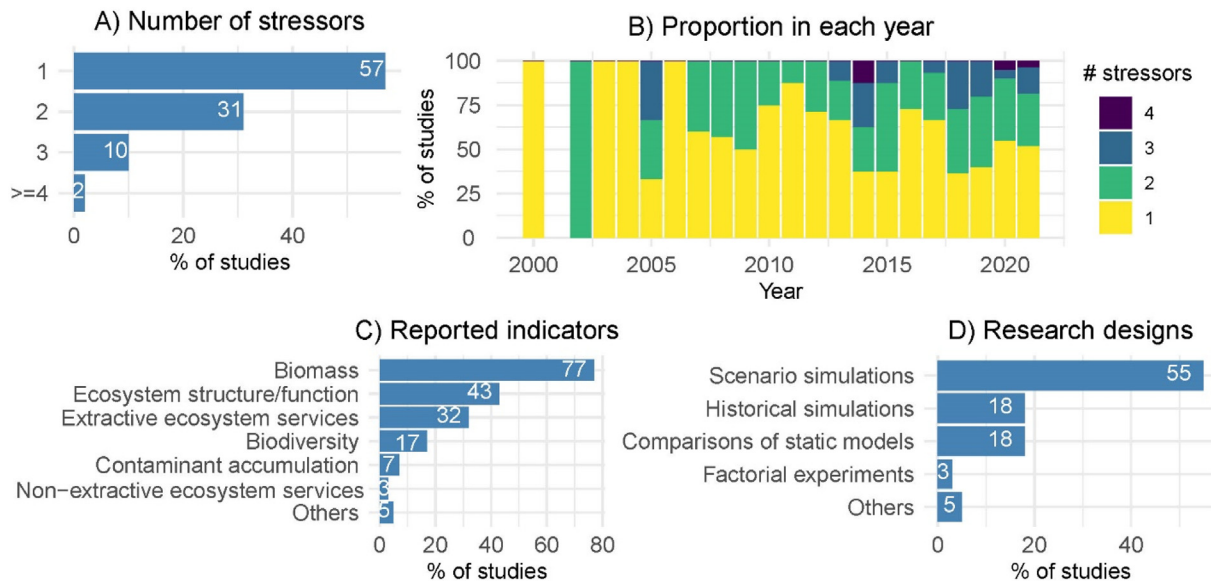


Fig. 1. Study areas of reviewed articles (A, excluding one global-scale study) and number of articles per year investigating one or more human activities or stressors other than fishing with Ecopath only, Ecosim, and Ecospace (B).





**Fig. 2.** Percentages of studies that simulated different numbers of stressors (A, see Section 3.1), the proportion of studies modeling different numbers of stressors each year (B), percentages of studies that reported one or more indicators falling into various categories (C, see Section 3.3), and percentages of studies that employed different research designs to investigate the effects of one or more stressors (D, see Section 3.4).

reported for each functional group separately as one indicator), but one reported 28. The largest number of indicators were reported by studies comparing static Ecopath models (median: 12 indicators), likely due to historical limitations of the EwE software; however, a broad set of indicators can now be easily calculated for temporal and spatiotemporal models with the ECOIND plugin (Coll and Steenbeek, 2017). Most reported indicators fell into six broad groups (Fig. 2C). First, 77% of articles reported changes in the biomass of species or functional groups, making it the most frequently reported indicator. Second, 43% of articles reported indicators describing ecosystem structure and functioning, such as total system throughput, mean trophic level, ascendancy, Finn's cycling index, and System Omnivory Index. Such indicators were especially frequent in articles comparing static Ecopath models. Third, 32% of articles reported indicators related to extractive ecosystem services, especially fishing (e.g., catch, landings). Fourth, 17% of articles reported indicators related to biodiversity like a modified Kempton index (Ainsworth and Pitcher, 2006). Because the number of species in EwE models is fixed, these indices represent species evenness, not richness. Fifth, 7% of articles reported indicators describing contaminant accumulation in biota. Sixth, only 3% of papers reported indicators representing non-extractive ecosystem services, such as carbon sequestration and recreational opportunities. Finally, 5% of papers reported indicators that did not clearly fit into one of the five categories. For example, Uusitalo et al. (2022) summarized the results of EwE and other models in a Bayesian Network estimating the risk of failing to achieve Good Environmental Status for several descriptors (sensu the European Union's Marine Strategy Framework Directive) under different climate and management scenarios.

### 3.4. Research designs

Most reviewed articles employed one of four broad research designs (logical frameworks leading from data and models to conclusions about environmental change; Fig. 2D): (1) comparisons of static Ecopath models along temporal or spatial stressor gradients; (2) historical simulations aiming to reproduce and explain past environmental changes driven by one or more stressors; (3) scenario simulations that modify stressors based on anticipated future changes (e.g., climate scenarios) or hypothetical considerations, and that compare simulation results across scenarios qualitatively; and (4) factorial experimental designs with two or more

stressors as independent variables. The following paragraphs explain these designs.

Comparisons of static Ecopath models along stressor gradients were presented in 18% of articles. This research design investigates ecological changes by constructing two or more models of the food web at different times (e.g., before and after a biological invasion; Stewart and Sprules, 2011) or along spatial gradients of stress (e.g., along a eutrophication gradient or at a sediment dumping site and a control site; Patricio and Marques, 2006; Pezy et al., 2018). Broadly speaking, this research design uses Ecopath as a tool to aggregate data from different times or locations into food web models and then compares indicators describing ecosystem-level characteristics such as nutrient recycling.

Historical simulations were presented in 18% of articles. Like comparisons of static Ecopath models, historical simulations serve to understand past ecological change. In contrast to static models, ecosystem dynamics are explicitly simulated through time. For example, testing how much the inclusion of specific time series improves model fit allows insights into which factors drive observed ecosystem changes: Bentley et al. (2020) compared simulations of the Irish Sea ecosystem with and without incorporating time series of environmental variables such as depth-integrated temperatures. This enabled them to explain a slow recovery of stocks after a reduction in fishing effort: the changes in effort coincided with changes in environmental conditions that reduced recruitment. As another example, Hoover et al. (2013a, 2013b) compared simulations for Hudson Bay incorporating time series describing hunting for marine mammals, rising temperatures, and reduced sea ice extent with simulations without hunting, warming and sea ice loss.

Scenario simulations were presented in 55% of articles. In this research design, an Ecopath model is first built with past data. Ecosim or Ecospace then simulate the ecosystems in two or more scenarios (e.g., ocean warming according to a climate scenario vs. a baseline scenario with no warming). Typically, changes in biomasses and other indicators are then compared across scenarios without quantification of individual stressor effects or stressor interactions. While scenario simulations sometimes include past time periods for model fitting and to test if the model can reproduce historical patterns, this research design serves to explore potential ecological changes that have not (yet) occurred in the real world. The investigated scenarios included simple hypothetical scenarios (e.g., varying primary production from -30% to 30% as a potential range of climate-induced

changes; Watson et al., 2013), what-if scenarios (e.g., what if sea otters had not been reintroduced on Vancouver Island; Gregr et al., 2020), and more detailed future scenarios. For example, Serpetti et al. (2017) compared simulations for a baseline scenario with current temperatures and fishing to scenarios characterized by fishing at maximum sustainable yield and temperature increases according to four IPCC Representative Concentration Pathways of atmospheric greenhouse gases. However, only two articles (Bauer et al., 2019; Hyytiäinen et al., 2021) used detailed scenarios for stressors other than climate and fishing, both building on previously developed socioeconomic trajectories for the Baltic Sea region (Zandersen et al., 2019).

Factorial experimental designs with multiple stressors as variables were presented in 3% of articles. In this research design, two or more stressors each take on discrete levels of intensity and simulations are run for all combinations of levels. For example, Kao et al. (2014) conducted simulations for a bay of Lake Huron with three levels each for three stressors: Nutrient loads and biomasses of two invasive species. In contrast to scenario simulations, this more systematic variation of stressors allows quantification of direct stressor effects and interactions, yet this possibility has rarely been exploited.

Research designs different from the four categories above were presented in 5% of articles. These included, e.g., descriptions of a serious gaming platform where Ecospace provides ecosystem responses to human activities in a marine spatial planning game (Goncalves et al., 2021; Steenbeek et al., 2020) and simulations of contaminant accumulation in the food web without consideration of specific scenarios (e.g., Tierney et al., 2018).

The following sections review in greater detail the approaches taken by articles comparing static Ecopath models (Section 4) and simulation-based research designs (historical simulations, scenario simulations, factorial experiments, and a simulation-based serious game with implications for simulating many stressors together; Section 5). In contrast to studies using static Ecopath models, the techniques available to represent stressors in simulations are different for each stressor. Therefore, Section 4 discusses all stressors together, whereas Section 5 describes modeling techniques for each stressor in a separate subsection.

#### 4. Assessing stressor effects with static Ecopath models

Thirty articles compared Ecopath models along stressor gradients in space or time, investigating a variety of human activities and stressors (Table 1).

The stressors that were most frequently studied in this way were climate, invasive species, and eutrophication, each with six studies. Studies investigating climate effects compared Ecopath models, e.g., for different ENSO phases (Jorge-Romero et al., 2021; Yin et al., 2021; Tam et al., 2008), before and after observed ecosystem changes attributed to climate change (Chevillot et al., 2019), and during multi-year periods of different sea surface temperature variability (Hernández-Padilla et al., 2021). Studies investigating the effects of invasive species compared Ecopath models for times before and after the arrival of the new species (Yin et al., 2022; Corrales et al., 2017b; Akoglu et al., 2014; Stewart and Sprules, 2011). Some studies also included Ecopath models describing the system while the new species became established (Colvin et al., 2015; Downing et al., 2012). Most studies investigating the effects of eutrophication compared Ecopath models for different times between which nutrient inputs changed or new nutrient management measures were implemented (Baeta et al., 2011; Brando et al., 2004; Watson et al., 2020; Xu et al., 2016). One study instead compared Ecopath models for the same time but constructed for different locations along a spatial eutrophication gradient (Patrício and Marques, 2006). Studies investigating other stressors compared Ecopath models, e.g., before and after the construction of a wind farm (Wang et al., 2019), for a sediment dumping site and a control site (Raoux et al., 2020), and for a heavily visited urban beach versus a nearby beach in a protected area (Reyes-Martínez et al., 2015). While most of these studies focused on single stressors, Akoglu et al. (2014) compared four Ecopath

**Table 1**

Human activities and stressors that have been investigated by comparing static Ecopath models.

Stressors	References
<b>Climate</b>	Chapman et al., 2020; Chevillot et al., 2019; Hernández-Padilla et al., 2021; Jorge-Romero et al., 2021; Tam et al., 2008; Yin et al., 2021
<b>Invasive species</b>	Akoglu et al., 2014; Colvin et al., 2015; Corrales et al., 2017b; Downing et al., 2012; Stewart and Sprules, 2011; Yin et al., 2022
<b>Land and sea use</b>	Díaz López et al., 2008; Kluger et al., 2016; Phong et al., 2010
Aquaculture	Burkhard et al., 2011; Wang et al., 2019
Offshore energy	Akoglu et al., 2014; Baeta et al., 2011; Brando et al., 2004; Patrício and Marques, 2006;
Eutrophication	Watson et al., 2020; Xu et al., 2016 Reyes-Martínez et al., 2015
Urbanization near beach	
<b>Pollution</b>	
Deepwater Horizon spill	Lewis et al., 2021
<b>Other stressors</b>	
Sediment dumping	Pezy et al., 2018; Raoux et al., 2020
Hydropower dam	Wang et al., 2017; Lima et al., 2020
Flow regulation	Yang and Chen, 2013
Freshwater discharge	Jorge-Romero et al., 2019

models for the Black Sea spanning a 50-year period including eutrophication and a subsequent reduction in nutrient inputs, fisheries collapse, and biological invasions.

Beyond analyses of past ecosystem changes, Ecopath has been used to compare results of external simulation models and scenarios. For example, Burkhard et al. (2011) simulated possible changes in bird species distributions and sedimentation effects on low-trophic level species resulting from the construction and operation of a proposed wind farm and compared Ecopath models with and without these potential future changes. Chapman et al. (2020) compared Ecopath models constructed with current data and incorporating biomass changes expected under different climate scenarios.

All studies compared the Ecopath models using combinations of various ecosystem indicators describing the food web. Specifically, these indicators described changes in the system's throughput (reported in 73% of studies), omnivory (63%), production (63%), the ratio of production and biomass (63%), cycling (Finn's index; 60%), ascendancy (53%), and the ratio of production and respiration (53%). In addition to such network indicators, many studies reported total or focal species biomass (50%) or indicators describing fisheries (33%). Other types of indicators were rarely reported. Qualitatively comparing which indicators were reported for different stressors, we found no systematic differences.

While the scope of this review is strictly on models that investigate ecosystem change, it is worth noting that mixed trophic impact or keystone indices calculated for single Ecopath models of systems with established invasive species can clarify their role in the food web (e.g., Arbach Leloup et al., 2008; Khan and Panikkar, 2009; Michailidis et al., 2019; Villanueva et al., 2008).

#### 5. Human activities and stressors in Ecosim and Ecospace models

##### 5.1. Overview of modeling techniques and terminology

Because EwE involves complex ideas and terminology, understanding how articles modeled human stressors in ecosystems requires knowledge of key capabilities of this modeling platform, and the terms used to describe those. The most used capabilities were forcing functions, environmental response functions, and mediation functions. About 80% of articles used one or more of these capabilities, and among them, forcing functions were the most common (over 60% of articles; in part reflecting that forcing functions

were available in the software earlier than environmental response functions). Less frequently used capabilities were discrete habitat types, marine protected areas, and fishing fleets used to model stressors other than fishing. The rest of this section introduces these key capabilities for readers unfamiliar with this EwE-specific terminology.

**Forcing functions** in Ecosim are time series of a multiplier to one of a functional group's biological parameters. For example, many articles investigating impacts of climate and nutrient changes used forcing functions to simulate anticipated changes in phytoplankton biomass (e.g., Österblom et al., 2007). Furthermore, forcing functions play a second, technical role in the EwE software, where they serve to provide input time series for environmental variables to which response functions (see below) are provided.

**Environmental response functions** (sometimes called preference functions) can represent the functional groups' tolerances to environmental conditions (which can include stressors such as underwater noise). They do so by making a functional group's relative foraging arena size a function of environmental conditions. For example, various recent publications include environmental response functions to water temperature for all functional groups as a mechanism to simulate effects of global warming. The environmental conditions are provided in Ecosim as time series of scalars (technically, as forcing functions, see above) and in Ecospace as (time varying) maps. Both Ecosim and Ecospace use environmental conditions and environmental response functions to calculate a species niche in the system: in Ecosim one niche value for the entire system; in Ecospace a niche value per grid cell. In the next version of the EwE software (6.7), it will be possible to modify mortality directly via environmental response functions, including in response to contaminant buildup simulated with Ecotracer (see below).

**Mediation functions** can represent indirect ecological effects, where one group's biomass has implications for other groups through non-trophic interactions (i.e., by means other than direct predation/herbivory). Thus, a group's parameters like vulnerability to predation become dependent on the biomass of one or more other groups. Mediation functions were often used to emulate changes in biogenic habitat that provides shelter for prey. For example, Alva-Basurto and Arias-González (2014) modeled coral bleaching by means of a forcing function relating mortality to temperature, and the resulting habitat loss as mediation function where coral biomass affected the vulnerabilities of small fish to predation.

**Discrete habitat types** allow modeling of functional groups' binary habitat preferences (preferred or not preferred) and were used in 5% of articles. Changes in habitat related to human activity can be explored by modifying the habitat map provided to Ecospace. For example, Alexander et al. (2016) added artificial reef habitat to represent hard substrate provided by offshore energy installations.

**Marine protected areas** (MPAs) in Ecospace represent areas where some or all types of fishing are excluded. This capability can also be used to represent conflicts between fishing and other human activities (for example, exclusion of fishing from offshore wind farms; Alexander et al., 2016). It has also been employed as a workaround to simulate species introductions from seed cells (Espinosa-Romero et al., 2011).

**Fishing fleets** in EwE can be used to simulate biomass extraction other than animals (e.g., kelp harvest; Vilas et al., 2021b), other mortality (e.g., bird collisions with wind turbines; Fretzer, 2015), and short-term mass mortality events (Fulton et al., 2018). They are also used to keep the biomass of invasive species negligible until the time of introduction (e.g., Langseth et al., 2012).

In addition to the core capabilities of the EwE software described above, there are several *plug-ins* that are directly relevant for modeling stressors, specifically pollution and habitat change. First, *Ecotracer* simulates the accumulation of contaminants in the food web (Walters and Christensen, 2018). It has been available since the early 2000s and was used in most reviewed articles modeling pollution. In *Ecotracer*, contaminants enter biomass pools through direct uptake from the environment, food, and immigration. Contaminants leave the ecosystem through decay, biomass extraction, and emigration; they move to the environment, other groups or detritus through excretion, predation, or non-fishing mortality. Second,

*Ecoengineer* is intended to represent the crucial role of ecosystem engineers, i.e., functional groups that provide biogenic habitat. It creates maps of habitat structural complexity based on the biomasses of these ecosystem engineers. These maps can then be used in combination with environmental response functions representing functional groups' reliance on structurally complex habitat (Sadchatheeswaran et al., 2021). Given its publication in 2021, *Ecoengineer* was not yet used in any other publications at the time the literature search for this review concluded.

## 5.2. Overview of modeled stressors

EwE has been used to investigate a broad collection of stressors beyond fishing (Fig. 3, Table 2). Many stressors were first included in EwE models in the 2000s, while others (e.g., underwater noise) have only recently been studied with EwE. For all stressors, at least half of the studies (often more and sometimes all) were published since 2015.

The most modeled stressor category was changes in the physical climate. This broad category encompassed various stressors such as future warming and anticipated changes in primary production due to effects on stratification and upwelling, as well as articles investigating the effects of past climate variability. Accordingly, dividing this category into more detailed stressors would have made it less dominant. The "Other infrastructure and stressors" category encompassed infrastructure such as ports and desalination plants, freshwater and sediment diversion, and general physical disturbance and pollution. A detailed breakdown of modeled stressors and summary of the applied modeling techniques are found in Section 5.3. Then, Section 5.4 summarizes progress towards an Ecospace-based simulation framework that can represent many human activities at the same time.

## 5.3. Modeling individual stressors

### 5.3.1. Physical climate

Sixty studies investigated direct and indirect effects of the physical climate such as global warming and decadal oscillations. This section summarizes research on future climate change as well as past climate variability, because many modeling techniques can be applied in both situations, and because anthropogenic change and natural variability cannot always be distinguished in historical simulations. We discuss ocean acidification separately in Section 5.3.7.

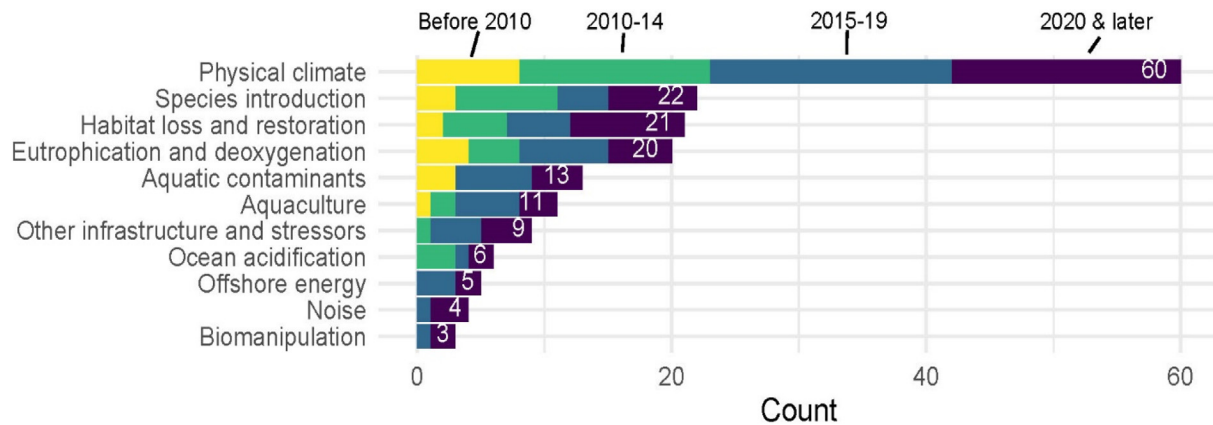
Many historical simulations modeled climate impacts using forcing functions based on time series of sea surface temperature, surface chlorophyll *a*, net primary production, or climate indices like the Pacific Decadal Oscillation Index and the Atlantic Multidecadal Oscillation Index (e.g., Arreguín-Sánchez et al., 2015; Field et al., 2006; Heymans et al., 2007; Parrish et al., 2012). Such simulations have been used to disentangle the effects of climate variations from fishing impacts, among other applications (e.g., Alms and Wolff, 2020; Shannon et al., 2008; Taylor et al., 2008a). Historical time series of biomasses obtained from field surveys and stock assessments across several ENSO cycles have also been simulated with forcing functions (Taylor et al., 2008b).

To simulate potential effects of future climate change, EwE is typically linked with climate and biogeochemical models that provide inputs describing future environmental conditions (e.g., temperature projections) or variables related to lower trophic levels, such as future primary production.

In many studies, forced primary production or phytoplankton biomass stood in for aspects of climate change that could not be modeled directly in EwE. For example, Lockerbie and Shannon (2019) represented expected changes in wind-driven upwelling in the southern Benguela Current ecosystem due to higher land-sea temperature gradients as increased primary production.

In some studies investigating future climate change, such anticipated changes in primary production were the only climate change effect considered. Phytoplankton biomass or production were forced, e.g., with functions that empirically relate historical chlorophyll *a* and sea surface





**Fig. 3.** Number of articles that investigated broad stressor categories in Ecosim or Ecospace simulations during different time periods (based on dates of publication). The “2020 & later category” contains studies published until early 2022.

temperature anomaly data and with future biomasses obtained from biogeochemical and oceanographic models under climate scenarios (Bell et al., 2013; Brown et al., 2010; Fulton, 2011; Fulton et al., 2018; Howell et al., 2013; Lira et al., 2021; Neira et al., 2009; Woodworth-Jefcoats et al., 2015). Other authors explored general primary production scenarios to understand the potential for bottom-up ecosystem changes under different climate conditions (Ortega-Cisneros et al., 2018; Suprenand and Ainsworth, 2017; Watson et al., 2013). Phytoplankton were often represented as a single functional group, but sometimes split into a small number of functional types or size classes.

Some studies modeled climate change by forcing or environmental response functions for consumers as well as producers (Kumar et al., 2017; Smith et al., 2021). Modeled effects on consumers included recruitment and feeding interactions (i.e., vulnerabilities; Watters et al., 2003), biomass changes of groups expected to be affected by climate and stratification changes (Griffiths et al., 2010; Li et al., 2014), and zooplankton community structure (Ainsworth et al., 2011). In many studies, one or more lower trophic level groups such as phytoplankton and krill were simulated with external, climate-driven biogeochemical models (Whitehouse et al., 2021; van Leeuwen et al., 2021). The estimated biomasses were then used to force the respective groups in Ecosim models focused on higher trophic levels and fisheries.

Ecospace models can be driven by spatiotemporal data such as satellite- or model-derived time series of primary production, temperature, and salinity maps (e.g., Christensen et al., 2015; Coll et al., 2016, 2020; Steenbeek et al., 2013). Many studies investigated ocean warming impacts by means of temperature-based forcing functions (Libralato et al., 2015) or environmental response functions derived from geographic species distributions for many functional groups (e.g., Bentley et al., 2020, 2017; Capitani et al., 2021b; Corrales et al., 2018, 2017a; Serpetti et al., 2017; Vilas et al., 2021a). Response functions to temperature were commonly obtained from global databases of species distributions like AquaMaps (Kaschner et al., 2019). Some authors adjusted such global data with the help of local experts (Corrales et al., 2017a; Corrales et al., 2018; Vilas et al., 2021b). Alternatively, environmental response functions for species groups can be constructed from literature (Coll et al., 2016) or with statistical models fitted, e.g., to local presence-absence or catch data (Hervann et al., 2020; Bourdaud et al., 2021; De Mutsert et al., 2021).

While forcing and environmental response functions were the most widespread and general modeling techniques for including physical climate change in EwE models, some studies used more application-specific approaches. For example, Booth and Zeller (2005) used Ecotracer to model the accumulation of methyl mercury in the food web and explored interactions with climate change by making metabolic rates temperature dependent. Sinnickson et al. (2021) explored the effects of river discharge, affected by droughts and other climate phenomena, on an estuarine ecosystem. Discharge and nutrient concentrations forced primary production, and

one species' foraging area was modified by a response function representing general environmental conditions (availability of mangrove habitat and rising temperatures).

A series of studies simulated the combined effects of eutrophication, fishing and climate change in the Baltic Sea (Niiranen et al., 2012, 2013; Costalago et al., 2019; Ehrnsten et al., 2019; Bauer et al., 2018; Bauer et al., 2019; Hyytiäinen et al., 2021; Uusitalo et al., 2022). We summarize these studies in Section 5.3.4 (“Eutrophication and deoxygenation”). Studies investigating sea ice loss due to global warming (Dahood et al., 2020, 2019; Hoover et al., 2013a; Pedersen et al., 2021) are summarized in Section 5.3.3 (“Habitat loss and restoration”).

### 5.3.2. Species introductions

Twenty-two studies modeled species introductions. We treat accidental and intentional species introductions as one modeling problem, because simulating potential ecological trajectories of a newly arrived species is based on the same modeling approaches in both situations. While early studies used ad-hoc workarounds – for example, Kitchell et al. (2000) emulated an invasion of quagga mussels in Lake Superior by forcing a biomass reduction of its main native competitor – more recent research has focused on direct simulations of the arrival and establishment of new species.

A first challenge in modeling species introductions in EwE is that all functional groups must be present in the initial Ecopath model. The general strategy for simulating the introduction of a new species under this constraint is to include it in the Ecopath model but prevent it from affecting other functional groups until the time of introduction. Langseth et al. (2012) compare several ways to achieve this. Most commonly, the new species is included in the initial Ecopath model with either high or very low biomass (resulting in different balanced models). The new species' biomass is then immediately reduced to near-zero by setting a high fishing mortality (Arias-González et al., 2011; Chagaris et al., 2020; Corrales et al., 2017a; Gregor et al., 2020; Haak et al., 2017; Kumar et al., 2016a, 2016b; Libralato et al., 2015; Pine and Kwak, 2007; Woodruff et al., 2021). Because of its low biomass, the new species is in practice not affecting its predators or prey. Fishing mortality is then removed at the time of introduction, allowing the new species' biomass to grow from its low level. For historical simulations, the biomass of the new species can be forced with time series (Rogers et al., 2014; Sadchatheeswaran et al., 2020). For species that are not yet established, growth can follow the EwE simulation, be forced to correspond to a theoretical model such as logistic growth (Corrales et al., 2018; Haak et al., 2017), or be forced to grow to biomass levels observed in similar systems where the new species is already established (Vilas et al., 2021b). Although somewhat ad-hoc, slow or incomplete release from initially high fishing mortality can be used to emulate non-trophic barriers to establishment, such as limited substrate availability or non-optimal temperatures (Kumar et al., 2016a, 2016b). An alternative for keeping a new species from affecting the rest of the food web until its introduction is to



**Table 2**

Overview of modeled stressors and common modeling techniques. This table is ordered by broad categories and does not follow the order of stressors listed in Fig. 3 or as described in the main text.

Stressor	References	Modeling techniques
<b>Direct exploitation</b>		
Fishing, whaling, sealing, hunting, kelp harvest, ...	EwE includes sophisticated functions for simulating fisheries and other biomass extraction. They are described in 100 s of publications and not discussed further here.	
<b>Climate change</b>		
Physical climate	Ainsworth et al., 2011; Alms and Wolff, 2020; Alva-Basurto and Arias-González, 2014; Arreguín-Sánchez et al., 2015; Bauer et al., 2019; Beecham et al., 2015; Bell et al., 2013; Bentley et al., 2020, 2017; Booth and Zeller, 2005; Bourdaud et al., 2021; Brown et al., 2010; Capitani et al., 2021a; Christensen et al., 2015; Coll et al., 2016, 2020; Corrales et al., 2018, 2017a; Costalago et al., 2019; Dahood et al., 2020, Dahood et al., 2019; de Mutsert et al., 2021; Ehrnsten et al., 2019; Field et al., 2006; Fulton, 2011; Fulton et al., 2018; Griffiths et al., 2010; Hernvann et al., 2020; Heymans et al., 2007; Hoover et al., 2013b; Howell et al., 2013; Hyytiäinen et al., 2021; Kumar et al., 2017; Li et al., 2014; Libralato et al., 2015; Lira et al., 2021; Lockerbie and Shannon, 2019; Neira et al., 2009; Niiranen et al., 2013, 2012; Ortega-Cisneros et al., 2018; Parrish et al., 2012; Pedersen et al., 2021; Serpetti et al., 2017; Shannon et al., 2008; Sinnickson et al., 2021; Smith et al., 2021; Steenbeek et al., 2013; Suprenand and Ainsworth, 2017; Taylor et al., 2008a, 2008b; Uusitalo et al., 2022; van Leeuwen et al., 2021; Vilas et al., 2021a, 2021b; Watson et al., 2013; Watters et al., 2003; Weijerman et al., 2018; Whitehouse et al., 2021; Woodworth-Jefcoats et al., 2015	<ul style="list-style-type: none"> <li>• Forcing of primary production or phytoplankton biomass</li> <li>• Forcing functions based on, e.g., temperature anomalies or climate indices</li> <li>• Environmental response functions to temperature based on geographic species distributions</li> <li>• Coral bleaching as short-term mortality events (emulated as a fishery)</li> <li>• Environmental data from historical time series (e.g., satellite-measured sea surface temperature) or future projections from earth system models</li> <li>• Related habitat changes (e.g., sea ice loss): See section “Habitat loss and restoration”</li> </ul>
Ocean acidification	Ainsworth et al., 2011; Alva-Basurto and Arias-González, 2014; Busch et al., 2013; Cornwall and Eddy, 2015; Schlenger et al., 2021; Zunino et al., 2021	<ul style="list-style-type: none"> <li>• Forcing functions for functional groups known to be sensitive to pH</li> <li>• Magnitude of effects defined based on effect sizes determined in review or meta-analyses of experiments</li> <li>• Mediation functions for loss of biogenic habitat</li> </ul>
<b>Invasive species</b>		
Species introductions	Arias-González et al., 2011; Chagaris et al., 2020; Corrales et al., 2018, 2017a; Espinosa-Romero et al., 2011; Gregor et al., 2020; Haak et al., 2017; Harvey and Kareiva, 2005; Kao et al., 2014; Kitchell et al., 2000; Kumar et al., 2016a; Langseth et al., 2012; Li et al., 2014; Libralato et al., 2015; Pine and Kwak, 2007; Pinnegar et al., 2014; Rogers et al., 2014; Sadchatheeswaran et al., 2021, 2020; Vilas et al., 2021b; Wang et al., 2021; Woodruff et al., 2021	<ul style="list-style-type: none"> <li>• Inclusion of new species in food web model, but keeping biomass too low to affect other groups until introduction via fishing mortality or forcing</li> <li>• Alternatively, forcing vulnerabilities to predation and of prey to zero to avoid affecting other functional groups until introduction</li> <li>• “Seed cells” representing locations from which newly introduced species spread in Ecospace via MPAs</li> <li>• Biomass growth of new species simulated or forced with historical data, data from similar systems where it is established, or theoretical models such as logistic growth</li> <li>• Diet and other parameters of new species based on data from systems where it is established or physiological considerations</li> <li>• Habitat changes (e.g., invasive ecosystem engineers): See section “Habitat loss and restoration”</li> </ul>
<b>Land and sea use change</b>		
Habitat loss and restoration	Alva-Basurto and Arias-González, 2014; Capitani et al., 2021a; Dahood et al., 2020, 2019; de Mutsert et al., 2021; Espinosa-Romero et al., 2011; Fretzer, 2015; Frisk et al., 2011; Goncalves et al., 2021; Gregor et al., 2020; Hoover et al., 2013a; Lewis et al., 2016; Pedersen et al., 2021; Pitcher et al., 2002; Plummer et al., 2013; Rogers and Allen, 2012; Sadchatheeswaran et al., 2021, 2020; Sayer et al., 2005; Shabtay et al., 2018; Steenbeek et al., 2020; Suprenand and Ainsworth, 2017; Zunino et al., 2021	<ul style="list-style-type: none"> <li>• Mediation functions adjusting vulnerabilities to predation or search rates of affected species (e.g., increased vulnerability if relying on lost habitat for shelter).</li> <li>• Forcing functions or environmental responses for functional groups depending on the habitat</li> <li>• Discrete habitat maps or environmental response functions/ habitat capacity model in Ecospace</li> <li>• Ecoengineer plugin</li> </ul>
Eutrophication and deoxygenation	Bauer et al., 2019, 2018; Beecham et al., 2015; Costalago et al., 2019; Daskalov, 2002; de Mutsert et al., 2016; Ehrnsten et al., 2019; Hansson et al., 2007; Hyytiäinen et al., 2021; Kao et al., 2014; Libralato et al., 2015; Ma et al., 2010; Niiranen et al., 2013; Okey et al., 2004; Österblom et al., 2007; Piroddi et al., 2021; Sakamoto and Shirakihara, 2017; Uusitalo et al., 2022; Wang et al., 2021; Zhu et al., 2020	<ul style="list-style-type: none"> <li>• Forcing functions for primary production or producer biomass (e.g., based on satellite data or biogeochemical models)</li> <li>• Shading of benthic vegetation as forced mortality (fishing)</li> <li>• Deoxygenation as forcing functions, e.g., modifying fish egg production based on water volumes with oxygen levels above a recruitment threshold</li> <li>• Oxygen concentration as habitat capacity layer in Ecospace</li> <li>• Habitat changes (e.g. loss of seagrass meadows): See section “Habitat loss and restoration”</li> </ul>
Aquaculture	Ferriss et al., 2016; Forrestal et al., 2012; Han et al., 2018, 2017; Izquierdo-Gomez et al., 2016; Li et al., 2014; Lin et al., 2009; Livne et al., 2020; Manju Lekshmi et al., 2020; Serpetti et al., 2021; Wu et al., 2016	<ul style="list-style-type: none"> <li>• Inclusion of farmed groups and of feed (as detritus) in food web model</li> <li>• Provision of habitat by mediation functions</li> <li>• Predator attraction in Ecospace via habitat suitability</li> <li>• Environmental response functions or mediation functions for modeling predator deterrent measures</li> </ul>
Offshore energy	Alexander et al., 2016; Halouani et al., 2020; Raoux et al., 2019, 2017; Serpetti et al., 2021	<ul style="list-style-type: none"> <li>• Hard substrate as Ecospace habitat or forcing biomass increase of species expected to benefit</li> <li>• Exclusion of fisheries by reducing fishing in Ecosim or by MPAs in Ecospace</li> <li>• Bird mortality from collisions as fishery</li> </ul>
Underwater noise	Goncalves et al., 2021; Harvey, 2018; Serpetti et al., 2021; Steenbeek et al., 2020	<ul style="list-style-type: none"> <li>• Environmental response functions and simple noise maps based on, e.g., shipping intensity or distance to sources of noise</li> </ul>
Biomaniipulation	Ofir et al., 2017; Peng et al., 2021; Wang et al., 2021	<ul style="list-style-type: none"> <li>• Stocking and targeted removal via forcing juvenile biomasses and fisheries</li> </ul>

(continued on next page)

Table 2 (continued)

Stressor	References	Modeling techniques
Other infrastructure and stressors	de Mutsert et al., 2021, 2017, 2012; Fretzer, 2015; Goncalves et al., 2021; Grossowicz et al., 2020; Shabtay et al., 2018; Steenbeek et al., 2020; Vassilides et al., 2017b	<ul style="list-style-type: none"> <li>• Forcing or environmental response functions for salinity changes from desalination plants or freshwater diversion</li> <li>• Built structures as artificial habitat in Ecospace</li> <li>• Fishing fleets emulating mortality from, e.g., road collisions and power plant water intake</li> <li>• Benthic and pelagic disturbance intensity modeled externally based on human activities, environmental response functions</li> </ul>
<b>Pollution</b>		
Aquatic contaminants	Booth et al., 2020; Booth and Zeller, 2005; Chagaris et al., 2020; Larsen et al., 2016; Ma and You, 2021; McGill et al., 2017; Niiranen et al., 2008; Rohal et al., 2020; Sandberg et al., 2007; Suprenand et al., 2019; Tierney et al., 2018; Walters and Christensen, 2018; Weijerman et al., 2018	<ul style="list-style-type: none"> <li>• Ecotracer plugin for accumulation in food web</li> <li>• 2D transport of contaminants in Ecospace</li> <li>• Forcing or environmental response functions to contaminant concentrations (dose-response relationships)</li> </ul>

temporarily “switch it off” as predator and as prey by forcing the respective vulnerabilities to zero (Kao et al., 2014; Langseth et al., 2012). Removal or culling of already established invasive species can be modeled as fishing mortality (Harvey and Kareiva, 2005).

The same approaches can be used in Ecospace to simulate the range expansion of introduced species. While Ecospace initially distributes a species' biomass uniformly over the study area, this can be overcome by setting a very high fishing mortality but designating one or more seed cells as “MPAs” protected from “fishing” (Espinosa-Romero et al., 2011).

A second challenge in constructing a food web model including a species that is not yet established is the estimation of the species' diet preferences and other parameters as well as potential predation. Potential diets for species in a new food web can be based on data from similar ecosystems where the species is already established (Gregr et al., 2020; Kumar et al., 2016a, 2016b). If this is not possible, there are methods to predict the potential diet composition of a species when introduced in a new food web (Link, 2004; Pinnegar et al., 2014). Alternatively, scenarios including different hypothetical diets can be explored (Li et al., 2014).

Effects of introduced species on biogenic habitat can be represented by mediation functions (Espinosa-Romero et al., 2011; Gregr et al., 2020). The effects of invasive ecosystem engineers can be simulated through mediation functions or the Ecoengineer plug-in (Sadchatheeswaran et al., 2021; see Section 5.3.3).

Several authors have explored interactions between biological invasions and other stressors. For example, Libralato et al. (2015) simulated biological invasions in various scenarios considering warming, oligotrophication, and fisheries. Warming was simulated such that the ecological niches held by native species opened as temperatures increased beyond their optimum or maximum tolerated values. Corrales et al. (2018a, 2017a) simulated different biomass trajectories for already established invasive species under different fishing policies and warming scenarios. Chagaris et al. (2020) found that a concurrent lionfish invasion slowed recovery from the Deepwater Horizon Oil Spill in the Gulf of Mexico. The representation of warming in EwE is summarized in Section 5.3.1 and of modeling oil spills and other water pollution in Section 5.3.5.

### 5.3.3. Habitat loss and restoration

Twenty-one studies modeled habitat loss or restoration. In Ecosim, changes in biogenic habitat availability are typically represented by mediating functions affecting the vulnerabilities and search rates of species associated with the habitat. This approach has been used, e.g., to simulate the loss of shelter for some species when removing unwanted patches of floating vegetation (Rogers and Allen, 2012), changes in eelgrass meadows (Plummer et al., 2013), the loss of fish habitat provided by coral reefs (Alva-Basurto and Arias-González, 2014), the effects of invasive ecosystem engineers providing substrate and shelter (Sadchatheeswaran et al., 2020), the loss of biogenic habitat to acidification (Zunino et al., 2021), the removal of oyster aquaculture racks (Lin et al., 2009), and the expansion of kelp habitat after the reintroduction of sea otters (Gregr et al., 2020; Espinosa-Romero et al., 2011).

Other studies explored the effects of habitat loss in Ecosim by forcing functions or environmental response functions for the species groups associated with the habitat proportional to the changes in habitat availability (Capitani et al., 2021a; de Mutsert et al., 2021; Frisk et al., 2011). The reduced extent of sea ice due to climate change has been modeled by forcing the primary production of ice algae (Pedersen et al., 2021; Suprenand and Ainsworth, 2017) as well as mediation functions that reduced the foraging area of polar bears and increased the vulnerability of fish that seek shelter in crevasses (Hoover et al., 2013b). Alternatively, Dahood et al. (2019) used forcing functions affecting foraging parameters of functional groups benefiting from sea-ice (e.g., krill) or open-water (e.g., seals).

Ecospace has long allowed modelers to define maps of discrete habitats and preferred habitats for functional groups. This functionality has been used, e.g., to evaluate scenarios for establishing artificial protected reefs (Pitcher et al., 2002; Sayer et al., 2005), to simulate the effects of removing floating aquatic vegetation (Rogers and Allen, 2012), to compare spatial plans for the area surrounding a coastal power plant (Shabtay et al., 2018), and to investigate the effects of habitat loss due to a hypothetical industrial area in combination with other stressors (Fretzer, 2015; see Section 5.3.10).

Ecospace's habitat capacity model and environmental response functions allow more detailed representations of habitat suitability for different functional groups (Christensen et al., 2014a). These capabilities have been used, e.g., to explore the effects of the historical loss of salt marsh edges (Lewis et al., 2016) and to simulate future sea ice, protected area, and fishing scenarios (Dahood et al., 2020). Like in applications modeling physical climate change (Section 5.3.1), the environmental response functions as well as mediation functions can be derived from in-situ data on species abundance and the spatial distribution of habitat. If response functions could not be determined empirically, some researchers explored hypothetical alternatives and selected the functions based on model fit to historical data (Lewis et al., 2016; Plummer et al., 2013). Finally, habitat changes have recently been modeled among various other human activities and stressors via environmental response functions in simplified Ecospace models designed for a serious gaming application (Goncalves et al., 2021; Steenbeek et al., 2020; see Section 5.4).

Beyond the core capabilities of EwE, a new plugin “Ecoengineer” calculates a measure of habitat structural complexity based on the biomasses of species that are ecosystem engineers. This complexity measure is then used as a habitat capacity layer in Ecospace. In its so far only published application, the plugin more accurately reproduced observed biomasses at the end of a historical simulation than modeling biogenic habitat changes through mediation functions (Sadchatheeswaran et al., 2021).

### 5.3.4. Eutrophication and deoxygenation

Twenty studies modeled eutrophication or deoxygenation. Eutrophication has been primarily simulated in EwE by means of forcing and mediating functions, often using external biogeochemical models to provide primary production or producer biomasses for different scenarios. EwE has also been fully coupled with a biogeochemical model simulating

nutrient dynamics (Beecham et al., 2015). The biogeochemical model provided lower-trophic level parameters to EwE, which returned predation levels and detritus in each time step.

Forcing functions are commonly used to model nutrient-driven changes in the biomass and production of phytoplankton and larger aquatic vegetation (Daskalov, 2002; Libralato et al., 2015; Ma et al., 2010; Okey, 2004; Piroddi et al., 2021; Wang et al., 2021; Zhu et al., 2020). Mediation functions can represent non-trophic effects related to eutrophication, such as the loss of seagrass meadows providing shelter (Ma et al., 2010). These two modeling approaches were reviewed in detail by Vassilides et al. (2017a). We therefore provide no further summaries of studies using forcing and mediation functions to model eutrophication. An alternative is the internal estimation of primary production in Ecosim, based on free nutrient concentrations (Kao et al., 2014). Deoxygenation has also been modeled with forcing functions. For example, Sakamoto and Shirakihara (2017) modeled effects of deoxygenation by means of a forcing function on mortality, where survival decreased linearly from a dissolved oxygen threshold specific to each functional group.

In Ecospace, eutrophication and deoxygenation can be represented using externally generated maps of nutrient, chlorophyll, or oxygen concentrations. For example, de Mutsert et al. (2016) estimated the net effect of increased primary production and hypoxia in the northern Gulf of Mexico. They used a biogeochemical model to generate monthly chlorophyll *a* and dissolved oxygen data matching an Ecospace grid and used them as forcing functions for primary production and predator search rates, respectively.

Several studies modeled eutrophication and other stressors in the Baltic Sea. In addition to modeling eutrophication through a forcing function for primary production, Österblom et al. (2007) and Hansson et al. (2007) emulated one effect of eutrophication-induced hypoxia by forcing cod reproduction proportional to changes in the water volume with sufficiently high oxygen levels for recruitment. Building on a model and forcing functions described by Tomczak et al. (2012), later studies used externally modeled time series of variables related to temperature, primary production, and oxygen conditions as environmental drivers (Niiranen et al., 2013; Costalago et al., 2019; Ehrnsten et al., 2019). In Ecospace, Bauer et al. (2018) included maps of primary production, temperature, salinity, and oxygen concentration from climate and biogeochemical models. Bauer et al. (2019) used a slightly modified model to simulate how the Baltic Sea could change over the 21st century under scenarios representing comprehensive socio-economic developments (Zandersen et al., 2019). Hyytiäinen et al. (2021) built on the same Ecospace model and scenarios to investigate differences in future ecosystem services. Uusitalo et al. (2022) embedded the same Ecospace model, coupled climate-biogeochemical models, and a fisheries economics model in a Bayesian Network to estimate probabilities of reaching environmental and economic objectives under different scenarios. This series of studies stands out by its integration of human dimensions into long-term simulations through detailed socioeconomic scenarios.

### 5.3.5. Aquatic contaminants

Thirteen studies modeled water pollution with EwE. Of these, four studies investigated ecosystem effects of pollution: Suprenand et al. (2019) created monthly maps of oil concentrations for hypothetical oil spill scenarios in the Beaufort Sea with a spill trajectory model and defined environmental responses (dose-response functions) in Ecospace. Chagaris et al. (2020) and Rohal et al. (2020) used forcing functions based on established dose-response relationships and modifying mortality and/or search rates of sensitive groups to explore impacts of the Deepwater Horizon oil spill. Weijerman et al. (2018) modeled impacts of land-based pollution on coral reefs via a simple forcing function that increased coral mortality.

The remaining nine studies focused on quantifying contaminant accumulation in the food web using Ectracer (Walters and Christensen, 2018) without modeling biological consequences. These applications investigated the accumulation of methyl mercury under different levels of fishing pressure and ocean warming (Booth and Zeller, 2005), accumulation

of contaminants leaking from dumped chemical weapons (Niiranen et al., 2008; Sandberg et al., 2007), accumulation of PAHs after a hypothetical shipping accident (Larsen et al., 2016), transport of marine PCBs and mercury into a stream by spawning salmon (McGill et al., 2017), accumulation of 127-Caesium after the Fukushima accident (Booth et al., 2020; Walters and Christensen, 2018), accumulation of Carbon-14 from normal nuclear power plants operations (Tierney et al., 2018), and accumulation of microplastics in a lake (Ma and You, 2021). In Ecospace, two-dimensional transport of contaminants can be included via velocity fields generated with hydrodynamic models (Tierney et al., 2018). As a workaround for Ecospace's lack of vertical resolution, alternative assumptions about vertical mixing have been modeled by limiting direct uptake of contaminants from seafloor sources to benthos, or alternatively, also allowing uptake by pelagic groups (Niiranen et al., 2008).

### 5.3.6. Aquaculture

Eleven studies explored ecosystem changes driven by aquaculture. The common foundation of modeling stressors related to aquaculture in EwE is to include farmed organisms as functional groups and feed as a detritus compartment (Lin et al., 2009; Livne et al., 2020; Han et al., 2017, 2018). Changes in aquaculture activities can be modeled by forcing the biomasses of these compartments (Wu et al., 2016). The following paragraph summarizes how other stressors that can be caused by aquaculture activities have been modeled in EwE.

Collection of wild-caught juveniles to raise in fish farms from the surrounding ecosystem has been simulated by adding respective fisheries (Forrestal et al., 2012; Manju Lekshmi et al., 2020). The escape of transgenic salmon from fish farms has been modeled by adding an escapee compartment to an existing model and forcing its biomass to simulate gradual or catastrophic escapes (Li et al., 2014; Izquierdo-Gomez et al., 2016). Effects of anti-predation structures have been represented by mediation functions that make the search rates of predators dependent on the biomass of farmed animals (Ferriss et al., 2016). Provision of hard substrate or structures providing shelter (such as oyster racks; Lin et al., 2009) has been modeled as mediation functions in Ecosim or as a discrete habitat in Ecospace (see also Section 5.3.3).

Some studies considered several aquaculture-related stressors together. For example, Serpetti et al. (2021) modeled the effects of a combined offshore energy – aquaculture site in Ecospace through four pathways: increased primary production, forcing detritus from the fish farm based on an external model, environmental response functions for marine mammals sensitive to noise (reduced consumption with smaller distance to the source), and an attracting effect on predators (by designating the fish farm as the most suitable habitat).

### 5.3.7. Ocean acidification

Six studies investigated ocean acidification (OA) in EwE, generally by modifying production and consumption of affected groups. Several authors modeled OA as forcing functions that decreased search rates for prey linearly with decreasing pH, with reduction rates based on literature review (Ainsworth et al., 2011; Alva-Basurto and Arias-González, 2014; Busch et al., 2013; Zunino et al., 2021). Forcing functions can be based on a quantitative analysis of published experimental results (Cornwall and Eddy, 2015). For example, Schlenger et al. (2021) based forcing functions on previously published “survival scalars” linking survival rates of various species to pH (Busch and McElhany, 2016). Loss of biogenic habitat due to acidification (e.g., seagrass meadows, coral reefs) has been modeled as mediation functions (Alva-Basurto and Arias-González, 2014; Zunino et al., 2021).

### 5.3.8. Offshore energy

Five papers simulated stressors related to offshore energy developments, building on five approaches. First, exclusion of fisheries can be represented in Ecospace via definition of protected areas (Halouani et al., 2020; Alexander et al., 2016). Second, the creation of artificial habitat can be represented as a discrete habitat (Alexander et al., 2016). Third, the creation of artificial habitat can alternatively be represented by forcing



the biomasses of species expected to benefit from such habitat (Raoux et al., 2019, 2017). Fourth, avoidance behavior by animals can be represented as an environmental response function based on distance to the installation (Serpetti et al., 2021). Fifth, while mortality from bird collisions has not been modeled for offshore installations, Fretzer (2015) emulated collisions with terrestrial wind turbines as a fishing fleet.

#### 5.3.9. Underwater noise

Four studies described Ecospace models incorporating underwater noise by means of environmental response functions relating shipping intensity and distance to acoustic deterrent devices to estimates of lost foraging time (Goncalves et al., 2021; Harvey, 2018; Steenbeek et al., 2020).

#### 5.3.10. Biomanipulation

Three studies modeled biomanipulation (stocking or removal of organisms) in lakes. Stocking can be simulated with forcing functions that increase biomasses. Removal of organisms can be modeled with fishing fleets (Ofir et al., 2017; Peng et al., 2021; Wang et al., 2021).

#### 5.3.11. Other infrastructure and stressors

Nine studies modeled stressors that did not directly fit into the prior categories; these studies were related to different kinds of coastal and marine infrastructure. These included freshwater diversion, desalination plants, coastal power plants, and industrial areas.

De Mutsert et al. (2012) investigated effects of freshwater diversion (intentional opening of Mississippi levees to resupply sediment to wetlands) by constructing salinity response functions for all compartments in an Ecosim model. The response functions were based on in-situ observations of the species and salinity and changed the feeding rates of the respective compartments in a scenario simulation with different salinity time series. De Mutsert et al. (2017, 2021) expanded this approach to spatiotemporal simulations. An external, hydrodynamic model provided maps of environmental variables (salinity, temperature, total suspended sediments, and others) for freshwater diversion scenarios for the Mississippi River. These environmental drivers were integrated into the Ecospace simulations via environmental response functions. Similarly, Grossowicz et al. (2020) simulated the effects of desalination plants by means of environmental response functions to salinity and temperature.

Fretzer (2015) explored potential effects of a hypothetical industrial area, road, and wind turbine near a terrestrial protected area in Ecospace. In addition to habitat changes due to these developments (see Section 5.3.3), mortality due to hunting and wildlife collisions with vehicles or the wind turbine was modeled via fishing fleets. Shabtay et al. (2018) compared alternative spatial plans for the area around a coastal power plant, including expansion of industrial infrastructure via habitat changes and displacement of fisheries. Vassilides et al. (2017b) modeled cooling water intake from a coastal power plant (killing organisms in the water) as a fishery. Finally, the comprehensive approaches summarized in Section 5.4 incorporate pelagic and seabed disturbance from various human activities.

While we did not review technical reports, we provide two examples illustrating the potential of EwE to support decision-making about infrastructure projects (not included in the literature statistics). First, the Vancouver Fraser Port Authority developed an Environmental Impact Statement (Port Metro Vancouver, 2015) for the Impact Assessment Agency of Canada to evaluate the potential ecological impacts of placing a container terminal in a productive estuary in British Columbia, Canada. The study used Ecospace as the key element for assessing how the resulting physical changes (wave, currents, temperature, salinity, and bottom type changes) and would affect the ecosystem and habitat area. As part of the Environmental Impact Assessment, Ecospace was also used to evaluate mortality impacts for several fish species due to construction noise, and to evaluate impacts of the proposed terminal on salmon smolt migration. Second, Lynam et al. (2017) simulated options for the decommissioning of unused marine infrastructure such as cables, pipelines, and oil and gas platforms in the North Sea.

### 5.4. Simplified models simulating many human activities

The potential of Ecospace to simulate many human activities together is demonstrated in a basic form by the “MSP Challenge”, a serious game about marine spatial planning. In this game, players negotiate and draw spatial plans for a wide range of human activities and receive maps of the resulting biomass distributions, fisheries catch and effort, and biodiversity (Goncalves et al., 2021; Santos et al., 2020; Steenbeek et al., 2020). For this purpose, 16 human activities are combined into maps of four pressures (noise, pelagic physical disturbance and pollution, seabed physical disturbance and pollution, and artificial substrate) using external software, and included as environmental drivers in Ecospace. Because the MSP Challenge focuses on planning workshops where fast model response times are needed, it currently uses models that are simplified in four ways. First, pressure maps are created by simple raster algebra conversions of human activities, as opposed to integrating more realistic models (e.g., of underwater sound propagation). Second, while Ecospace can represent conflicts between some stressors (e.g., exclusion of fisheries from wind farms), others are modeled externally (e.g., re-routing of shipping traffic to avoid wind farms). Third, environmental response functions are assumed to be linear for many stressors, in the absence of knowledge about their actual shapes. Fourth, the complexity of the food web models, and the spatial resolution, are reduced.

While these simplifications currently preclude scientific research into multiple stressor effects, the MSP challenge demonstrates the potential of Ecospace to simulate many stressors together in a unified spatiotemporal modeling framework. In this framework, human activities cause stressors that influence functional groups in the model via environmental response functions. Given the computing power available today, Section 6 discusses future research directions that can expand this modeling framework towards a tool for comprehensive investigations and management of multiple stressor effects with no consideration for computation time.

## 6. Gaps and future opportunities

We found a large and growing body of research including stressors beyond fisheries in EwE models. These stressors included many important aspects of climate change, land and sea use change, pollution, and invasive species. EwE therefore presents a strong foundation for a sophisticated examination of multiple stressor effects in aquatic ecosystems. At the core, EwE can provide the ecological simulations that can be combined with earth system models and models of functional groups' responses to stressors, and then interpreted in terms of diverse ecological and human dimensions – hence serving as a centerpiece tying different models and data together. However, current EwE applications take us only partway there. The following sections explain four gaps in the reviewed literature (Fig. 4) that can be filled by existing methods borrowed from other subdisciplines of environmental science and from data science. Accordingly, we do not consider these gaps shortcomings of existing studies, but opportunities to harness the potential of EwE as a tool for studying multiple stressor effects.

### 6.1. Gap 1: represent multiple pathways of impact for each stressor

Most studies considered only a small number of the pathways by which a stressor affects species. For example, about 30% of studies investigating future climate change considered only anticipated changes in primary production. In reality, there are many pathways by which stressors can affect different species (Bundy et al., 2021). For example, climate change affects salmon reproduction, survival, and migration through changes in stream and ocean temperatures, streamflow, and primary production (Crozier et al., 2021). While the ecosystem-scale consequences of individual impact pathways are an important research question, it is important to consider all relevant pathways when investigating potential future ecosystem changes or multiple stressor effects. For example, Brown et al. (2010) predicted increased biomass of sea turtles because of higher primary production caused



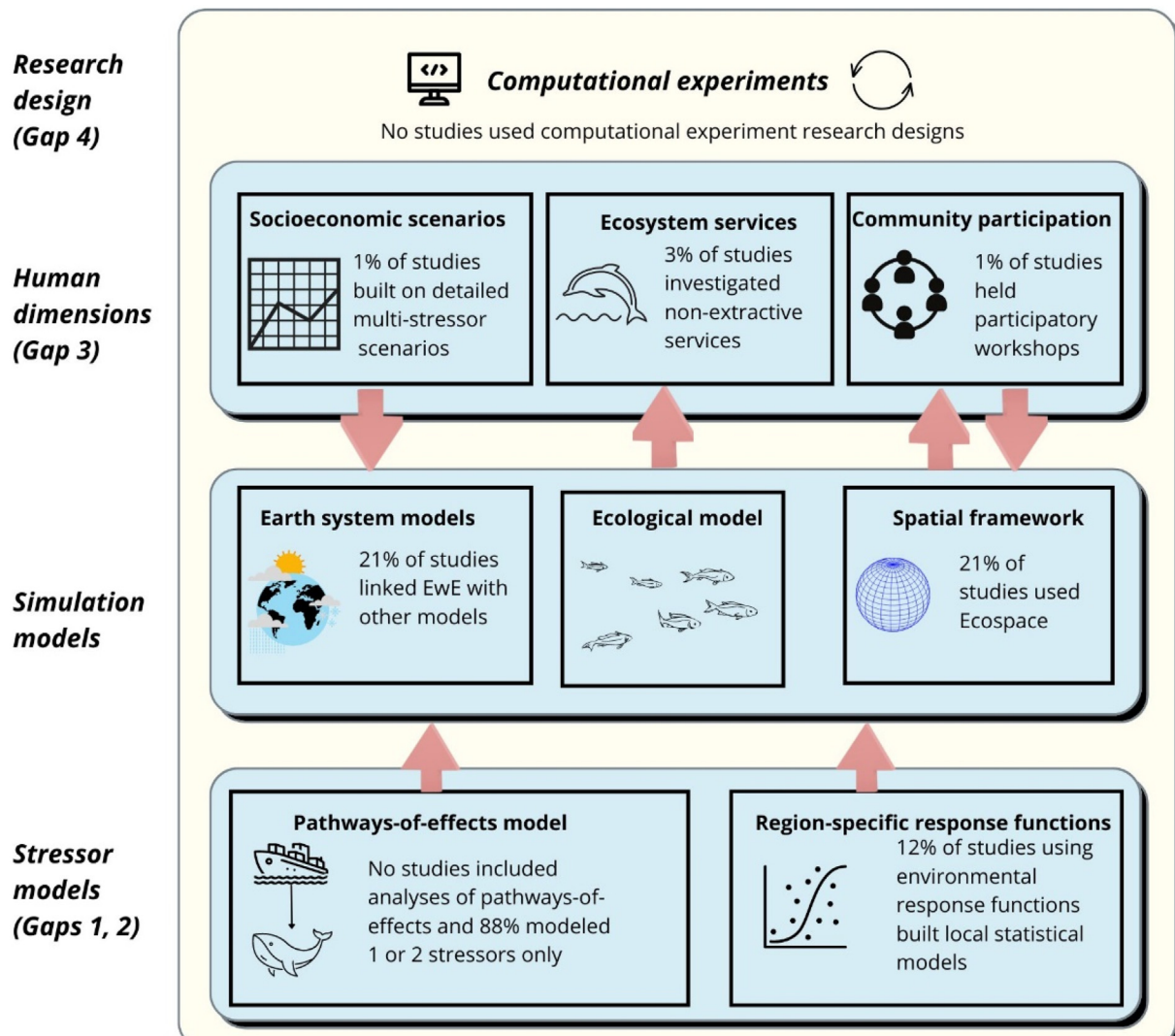


Fig. 4. Components of a modeling framework that addresses the gaps identified in this review. Arrows represent the direction of data and information flow.

by climate change. In contrast, a later modeling study predicted sea turtle populations to collapse based on the inundation of nesting beaches with rising sea levels and more frequent storms (Fulton, 2011).

Modeling of the effects of each stressor should thus be rooted in conceptual models of how each functional group is affected. One option for this step is pathways-of-effects (PoE) models. These qualitative models show the many pathways from human activities and the stressors they cause to their effects on endpoints, such as species of interest and ecosystem services. PoE models can be based on literature reviews of laboratory and field experiments or on expert workshops. They can be designed to explicitly support quantitative models. For example, Murray et al. (2021) developed a PoE model describing human impact pathways on killer whales, which then informed quantitative population viability analyses. Another useful framework for this initial, conceptual modeling step is driver-pressure-state-impact-response (DPSIR) modeling (e.g., Gari et al., 2015; Reckermann et al., 2022).

#### 6.2. Gap 2: develop best practices for characterizing stressor response functions

Representing many stressors and pathways of effects in EwE models will require the development of response functions linking changes in stressor intensity to changes in the functional groups' relevant parameters. Like choosing the shape of mediation functions (Harvey, 2014), this task can have a large influence on model outputs and conclusions but is far from

straightforward. For example, the preferred temperature range of the mussel *Mytilus californianus* according to the widely used, global-scale Aquamaps database is between 9 and 17.5 °C (Kaschner et al., 2019). In contrast, laboratory studies with animals from the coast of Washington (USA) have found optimal growth between 17 and 22 °C (Bayne et al., 1976). In addition to uncertainty in basic parameters such as temperature optima, the response curves used in published EwE studies often assume different functional forms such as trapezoid functions (Vilas et al., 2021b) and skewed Gaussian functions (Bentley et al., 2017). The latter functional form implies a much steeper initial decline of the species as one moves away from the optimum. Because many chronic stressors change gradually (e.g., global warming of 1–4 °C on average over the 21st century), such differences between response functions can have a strong effect on the timing and magnitude of impacts predicted by a model. Furthermore, even response functions based on well-established species distribution modeling techniques involve statistical decisions that can influence simulation outputs (Püts et al., 2020).

Ideally, stressor response functions would be constructed from data specific to the study region (Hervann et al., 2020; Vilas et al., 2021a) and then adjusted where needed by local experts. Despite their importance, no widely accepted best practices for constructing response functions have emerged yet. Some response functions, e.g., small organisms' responses to warming or toxicological dose-response relationships for single species, can be derived from lab experiments. Other stressors and functional groups

(e.g., noise impacts on marine mammals related to avoidance behaviors) can only be studied in the field. Response functions can in principle be extracted from field data by means of regression models (Holon et al., 2018; Parravicini et al., 2012). However, this statistical approach involves at least two challenges. First, deriving response functions for individual stressors can be difficult because many stressors have similar spatial gradients, e.g., from land to sea (Andersen et al., 2020). Isolating an individual stressor's effect statistically is only feasible in study areas where stressors can be spatially or temporally separated (Stock et al., 2018b). Second, given the cost of data collection, many field observations are not randomly distributed in space and time and therefore lack representativeness and independence. These challenges must be addressed through sound statistical modeling and validation approaches (Gregr et al., 2019; Roberts et al., 2017; Stock, 2022).

### 6.3. Gap 3: relate ecological impacts to multiple human dimensions, including ecosystem services

Effective ecosystem-based management and nature conservation require the consideration of human dimensions (Gorenflo and Brandon, 2006; Koehn et al., 2013) because environmental change has socioeconomic drivers and consequences (Lenzen et al., 2012). Better integration of human dimensions into ecological models is hence one of the research priorities of the UN Ocean Decade (Heymans et al., 2020). While EwE has many applications encompassing sophisticated fisheries economics (e.g., Cheung and Sumaila, 2008; Christensen et al., 2014b), we identified three opportunities for the integration of human dimensions of broader environmental impacts.

First, the human drivers of environmental change should be reflected in stressor scenarios that are explored. At present, many studies exploring climate change impacts with EwE built on IPCC scenarios, yet only two studies (Bauer et al., 2019; Hyytiäinen et al., 2021) incorporated socioeconomic scenarios for a comprehensive suite of other stressors.

Second, integrating modeled environmental changes and their consequences for ecosystem services is a key challenge (Townhill et al., 2021). Only 3% of studies reported indicators of ecosystem services other than direct resource extraction such as fishing, and these indicators were often simple proxies. For example, Busch et al. (2013) and Plummer et al. (2013) reported biomasses of functional groups related to non-extractive services such as ecotourism. In addition, Plummer et al. (2013) reported biomasses of species with legal protection under the US Endangered Species Act or Marine Mammal Protection Act as a proxy for existence value. Rohal et al. (2020) reported detritus export to deep waters as a proxy for carbon sequestration. Hyytiäinen et al. (2021) used primary production as an indicator for supporting ecosystem services and the number of summer days without cyanobacterial blooms as an indicator for coastal recreation. Weijerman et al. (2018) reported fish biomass, fish biodiversity, and shark and turtle biomass as indicators of dive tourism. We found only one study that included a monetary valuation of non-extractive ecosystem services (Gregr et al., 2020). They investigated how sea otter reintroductions in British Columbia affected ecosystem services, using biomass estimates derived with EwE for scenarios with and without sea otters to provide a cost-benefit analysis considering fisheries, carbon sequestration (based on an estimate of the social cost of carbon), and tourism (based on willingness-to-pay estimated in a choice experiment).

Third, a single study reported a comprehensive social-ecological research program based on workshops linking modeled environmental changes and community concerns (van Leeuwen et al., 2021). Involving local communities in modeling studies is practically feasible: EwE has been successfully used in the context of participatory workshops in other contexts (e.g., Pitcher et al., 2004; Bentley et al., 2019). Furthermore, communicating simulation results regarding future ecosystem condition to non-scientists is simplified by new visualization capabilities (Steenbeek et al., 2021b). Taken together, there is much room for advancing the integration of human dimensions into EwE-based human impact research by integrating ecosystem modeling with the development of comprehensive

socioeconomic scenarios, environmental valuation methods, and community-based research.

### 6.4. Gap 4: employ computational experiments to disentangle multiple stressors' direct and indirect effects

Many biological experiments and several meta-analyses have investigated how two or more stressors interact (Côté et al., 2016), yet the grand challenge of understanding cumulative impacts at the ecosystem scale remains (Borja et al., 2020). There are a variety of reasons for this knowledge gap, such as marine data sets that are typically small, many confounding variables, and other issues such as spatial correlations that complicate statistical modeling (Stock et al., 2018b). EwE and other ecosystem models can partly overcome this challenge for two reasons. First, in computer simulations, researchers have perfect control over all variables. Second, the models can in principle be run 100,000 s of times – even Ecospace – while resampling inputs and hence generate “big data” about a hypothetical ecosystem. Such research is technically challenging (Steenbeek et al., 2021a), yet becoming feasible because of the unprecedented computing power available. It is facilitated by the EcoSampler plugin (Steenbeek et al., 2018), which allows resampling of biological model parameters such that the required mass balance is retained. Yet only 3% of reviewed articles used formal experimental designs suitable to disentangle the effects of multiple stressors. This small body of research already has, for example, allowed the identification of synergistic and antagonistic stressor interactions (Cornwall and Eddy, 2015). While Hodgson and Halpern (2018) pointed out that disentangling the effects of more than 2–3 stressors with ecosystem models like EwE is complicated, we argue that this is primarily a consequence of the research designs used: surprisingly, we found no studies that made use of the statistical possibilities that arise when simulations can be repeated as many times as needed and with full control over all variables.

In the future, big data consisting of model inputs and the corresponding model outputs could be fed into machine learning algorithms that can extract complicated non-linear relationships and interactions between variables describing stressors and variables describing ecosystem condition. Such data sets could also be used in global sensitivity analyses, allowing quantification of the direct and indirect contributions of model inputs describing stressors to changes of outputs describing ecosystem condition (Bracis et al., 2020; Saltelli et al., 2004). The generated data could simultaneously contribute rigorous uncertainty analyses, which are crucial for high-stakes applications in environmental policy and practice (Saltelli and Funtowicz, 2014; Steenbeek et al., 2021a). Of course, such data and analyses would describe an artificial “world in the model” (Morgan, 2012) as opposed to a real-world ecosystem – even if all relevant pathways of effects could be represented via realistic response functions. Yet ecology has a long history of experimenting with models to form hypotheses or mathematically constrain possible mechanisms acting in nature (Kingsland, 1995). Embedding EwE in computational experimental designs could continue this research tradition by harnessing the modeling techniques summarized in this review as well as the unprecedented computing power available today.

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### CRediT authorship contribution statement

**A. Stock:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing,

**Funding acquisition.** C.C. Murray: Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Supervision. E. Gregr: Conceptualization, Methodology, Writing – review & editing. J. Steenbeek: Writing – review & editing, Supervision. E. Woodburn: Formal analysis, Writing – original draft, Writing – review & editing. F. Micheli: Writing – review & editing, Supervision. V. Christensen: Conceptualization, Writing – review & editing, Supervision. K.M.A. Chan: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

## Data availability

Data tables with information about all studies analyzed in this review are provided as supplementary materials.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.161719>.

## References

- Ainsworth, C.H., Pitcher, T.J., 2006. Modifying Kempton's species diversity index for use with ecosystem simulation models. *Ecol. Indic.* 6, 623–630. <https://doi.org/10.1016/j.ecolind.2005.08.024>.
- Ainsworth, C.H., Samhouri, J.F., Busch, D.S., Cheung, W.W.L., Dunne, J., Okey, T.A., 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES J. Mar. Sci.* 68, 1217–1229. <https://doi.org/10.1093/icesjms/fsr043>.
- Akdoglu, E., Salihoglu, B., Libralato, S., Oguz, T., Solidoro, C., 2014. An indicator-based evaluation of Black Sea food web dynamics during 1960–2000. *J. Mar. Syst.* 134, 113–125. <https://doi.org/10.1016/j.jmarsys.2014.02.010>.
- Alexander, K.A., Meyjes, S.A., Heymans, J.J., 2016. Spatial ecosystem modelling of marine renewable energy installations: gauging the utility of Ecospace. *Ecol. Model.* 331, 115–128. <https://doi.org/10.1016/j.ecolmodel.2016.01.016>.
- Alms, V., Wolff, M., 2020. Identification of drivers of change of the Gulf of Nicoya ecosystem (Costa Rica). *Front. Mar. Sci.* 7. <https://doi.org/10.3389/fmars.2020.00707>.
- Alva-Basurto, J.C., Arias-González, J.E., 2014. Modelling the effects of climate change on a Caribbean coral reef food web. *Ecol. Model.* 289, 1–14. <https://doi.org/10.1016/j.ecolmodel.2014.06.014>.
- Andersen, J.H., Al-Hamdani, Z., Harvey, E.T., Kallenbach, E., Murray, C., Stock, A., 2020. Relative impacts of multiple human stressors in estuaries and coastal waters in the North Sea-Baltic Sea transition zone. *Sci. Total Environ.* 704. <https://doi.org/10.1016/j.scitotenv.2019.135316>.
- Arbach Leloup, F., Desroy, N., Le Mao, P., Pauly, D., Le Pape, O., 2008. Interactions between a natural food web, shellfish farming and exotic species: the case of the bay of Mont Saint Michel (France). *Estuar. Coast. Shelf Sci.* 76, 111–120. <https://doi.org/10.1016/j.ecss.2007.06.011>.
- Arias-González, J.E., González-Gándara, C., Luis Cabrera, J., Christensen, V., 2011. Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ. Res.* 111, 917–925. <https://doi.org/10.1016/j.envres.2011.07.008>.
- Arreguín-Sánchez, F., del Monte-Luna, P., Zetina-Rejón, M.J., 2015. Climate change effects on aquatic ecosystems and the challenge for fishery management: pink shrimp of the southern Gulf of Mexico. *Fisheries* 40, 15–19.
- Arrigo, K.R., et al., 2020. Synergistic interactions among growing stressors increase risk to an Arctic ecosystem. *Nat. Commun.* 11.
- Baeta, A., Niquil, N., Marques, J.C., Patrício, J., 2011. Modelling the effects of eutrophication, mitigation measures and an extreme flood event on estuarine benthic food webs. *Ecol. Model.* 222, 1209–1221. <https://doi.org/10.1016/j.ecolmodel.2010.12.010>.
- Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., Palmeri, L., 2009. Trophic network model of the northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. *Estuar. Coast. Shelf Sci.* 83, 577–590. <https://doi.org/10.1016/j.ecss.2009.05.003>.
- Bauer, B., Markus Meier, H.E., Casini, M., Hoff, A., Margoński, P., Orio, A., Saraiva, S., Steenbeek, J., Tomczak, M.T., 2018. Reducing eutrophication increases spatial extent of communities supporting commercial fisheries: a model case study. *ICES J. Mar. Sci.* 75, 1306–1317. <https://doi.org/10.1093/icesjms/fsy003>.
- Bauer, B., Gustafsson, B.G., Hyytiäinen, K., Meier, H.E.M., Müller-Karulis, B., Saraiva, S., Tomczak, M.T., 2019. Food web and fisheries in the future Baltic Sea. *Ambio* 48, 1337–1349. <https://doi.org/10.1007/s13280-019-01229-3>.
- Bayne, B.L., Bayne, C.J., Carefoot, T.C., Thompson, R.J., 1976. The physiological ecology of *Mytilus californianus* Conrad - I. Metabolism and energy balance. *Oecologia* 22, 211–228. <https://doi.org/10.1007/BF00344793>.
- Beecham, J.A., Bruggeman, J., Aldridge, J., Mackinson, S., 2015. An approach for coupling higher and lower levels in marine ecosystem models and its application to the North Sea. *Geosci. Model. Dev. Discuss.* 8, 5577–5618. <https://doi.org/10.5194/gmdd-8-5577-2015>.
- Bell, J.D., Ganachaud, A., Gehrke, P.C., Griffiths, S.P., Hobday, A.J., Hoegh-Guldberg, O., Johnson, J.E., Le Borgne, R., Lehodey, P., Lough, J.M., Matear, R.J., Pickering, T.D., Pratchett, M.S., Gupta, A. Sen, Senina, I., Waycott, M., 2013. Mixed responses of tropical Pacific fisheries and aquaculture to climate change. *Nat. Clim. Chang.* 3, 591–599. <https://doi.org/10.1038/ndclimate1838>.
- Bentley, J.W., Serpetti, N., Heymans, J.J., 2017. Investigating the potential impacts of ocean warming on the Norwegian and Barents seas ecosystem using a time-dynamic food-web model. *Ecol. Model.* 360, 94–107. <https://doi.org/10.1016/j.ecolmodel.2017.07.002>.
- Bentley, J.W., Hines, D.E., Borrett, S.R., Serpetti, N., Hernandez-Milian, G., Fox, C., ... Reid, D.G., 2019. Combining scientific and fishers' knowledge to co-create indicators of food web structure and function. *ICES J. Mar. Sci.* 76 (7), 2218–2234.
- Bentley, J.W., Serpetti, N., Fox, C.J., Heymans, J.J., Reid, D.G., 2020. Retrospective analysis of the influence of environmental drivers on commercial stocks and fishing opportunities in the Irish Sea. *Fish. Oceanogr.* 29, 415–435. <https://doi.org/10.1111/fog.12486>.
- Booth, S., Zeller, D., 2005. Mercury, food webs, and marine mammals: implications of diet and climate change for human health. *Environ. Health Perspect.* 113, 521–526. <https://doi.org/10.1289/ehp.7603>.
- Booth, S., Walters, W.J., Steenbeek, J., Christensen, V., Charmasson, S., 2020. An Ecopath with Ecosim model for the Pacific coast of eastern Japan: describing the marine environment and its fisheries prior to the Great East Japan earthquake. *Ecol. Model.* 428, 109087. <https://doi.org/10.1016/j.ecolmodel.2020.109087>.
- Borja, A., Andersen, J.H., Arvanitidis, C.D., Basset, A., Buhl-Mortensen, L., Carvalho, S., Dafforn, K.A., Devlin, M.J., Escobar-Briones, E.G., Grenz, C., Harder, T., Katsanevakis, S., Liu, D., Metaxas, A., Morán, X.A.G., Newton, A., Piroddi, C., Pochon, X., Queirós, A.M., Snelgrove, P.V.R., Solidoro, C., St. John, M.A., Teixeira, H., 2020. Past and future grand challenges in marine ecosystem ecology. *Front. Mar. Sci.* 7. <https://doi.org/10.3389/fmars.2020.00362>.
- Bourdaud, P., Ben Rais Lasram, F., Araignou, E., Champagnat, J., Grusd, S., Halouani, G., Hattab, T., Leroy, B., Nogués, Q., Raoux, A., Safi, G., Niquil, N., 2021. Impacts of climate change on the Bay of Seine ecosystem: forcing a spatio-temporal trophic model with predictions from an ecological niche model. *Fish. Oceanogr.* 30, 471–489. <https://doi.org/10.1111/fog.12531>.
- Bracis, C., Lehuta, S., Savina-Rolland, M., Travers-Trolet, M., Girardin, R., 2020. Improving confidence in complex ecosystem models: the sensitivity analysis of an Atlantis ecosystem model. *Ecol. Model.* 431, 109133. <https://doi.org/10.1016/j.ecolmodel.2020.109133>.
- Brando, V.E., Ceccarelli, R., Libralato, S., Ravagnan, G., 2004. Assessment of environmental management effects in a shallow water basin using mass-balance models. *Ecol. Model.* 172, 213–232. <https://doi.org/10.1016/j.ecolmodel.2003.09.008>.
- Brown, C.J., Fulton, E.A., Hobday, A.J., Matear, R.J., Possingham, H.P., Bulman, C., Christensen, V., Forrest, R.E., Gehrke, P.C., Gribble, N.A., Griffiths, S.P., Lozano-Montes, H., Martin, J.M., Metcalf, S., Okey, T.A., Watson, R., Richardson, A.J., 2010. Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Glob. Chang. Biol.* 16, 1194–1212. <https://doi.org/10.1111/j.1365-2486.2009.02046.x>.
- Brown, C.J., Saunders, M.I., Possingham, H.P., Richardson, A.J., 2014. Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Divers. Distrib.* 20, 538–546.
- Bundy, A., Renaud, P.E., Coll, M., Koenigstein, S., Niiranen, S., Pennino, M.G., ... Travers-Trolet, M., 2021. Managing for the future: challenges and approaches for disentangling the relative roles of environmental change and fishing in marine ecosystems. *Front. Mar. Sci.* 8, 753459.
- Burkhard, B., Opitz, S., Lenhart, H., Ahrendt, K., Garthe, S., Mendel, B., Windhorst, W., 2011. Ecosystem based modeling and indication of ecological integrity in the German North Sea-case study offshore wind parks. *Ecol. Indic.* 11, 168–174. <https://doi.org/10.1016/j.ecolind.2009.07.004>.
- Busch, D.S., McElhany, P., 2016. Estimates of the direct effect of seawater pH on the survival rate of species groups in the California current ecosystem. *PLoS One* 1–28. <https://doi.org/10.1371/journal.pone.0160669>.
- Busch, D.S., Harvey, C.J., McElhany, P., 2013. Potential impacts of ocean acidification on the Puget Sound food web. *ICES J. Mar. Sci.* 70, 823–833. <https://doi.org/10.2307/4451538>.
- Capitani, L., Angelini, R., Keppeler, F.W., Hallwass, G., Silvano, R.A.M., 2021a. Food web modeling indicates the potential impacts of increasing deforestation and fishing pressure in the Tapajós River, Brazilian Amazon. *Reg. Environ. Chang.* 21. <https://doi.org/10.1007/s10113-021-01777-z>.
- Capitani, L., de Araujo, J.N., Vieira, E.A., Angelini, R., Longo, G.O., 2021b. Ocean warming will reduce standing biomass in a tropical Western Atlantic reef ecosystem. *Ecosystems*. <https://doi.org/10.1007/s10021-021-00691-z>.
- Chagaris, D.D., Patterson, W.F., Allen, M.S., 2020. Relative effects of multiple stressors on reef food webs in the northern Gulf of Mexico revealed via ecosystem modeling. *Front. Mar. Sci.* 7, 1–17. <https://doi.org/10.3389/fmars.2020.00513>.
- Chapman, E.J., Byron, C.J., Lasley-Rasher, R., Lipsky, C., Stevens, J.R., Peters, R., 2020. Effects of climate change on coastal ecosystem food webs: implications for aquaculture. *Mar. Environ. Res.* 162, 105103. <https://doi.org/10.1016/j.marenvres.2020.105103>.
- Cheung, W.W.L., Sumaila, U.R., 2008. Trade-offs between conservation and socio-economic objectives in managing a tropical marine ecosystem. *Ecol. Econ.* 66, 193–210. <https://doi.org/10.1016/j.ecolecon.2007.09.001>.
- Chevillat, X., Tecchio, S., Chaalali, A., Lassalle, G., Selleslagh, J., Castelnaud, G., David, V., Bachelet, G., Niquil, N., Sautour, B., Lobry, J., 2019. Global changes jeopardize the trophic carrying capacity and functioning of estuarine ecosystems. *Ecosystems* 22, 473–495. <https://doi.org/10.1007/s10021-018-0282-9>.
- Christensen, V., Walters, C.J., 2004. Ecopath with ecosim: methods, capabilities and limitations. *Ecol. Model.* 172, 109–139. <https://doi.org/10.1016/j.ecolmodel.2003.09.003>.



- Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., Walters, C.J., 2014a. Representing variable habitat quality in a spatial food web model. *Ecosystems* 17, 1397–1412. <https://doi.org/10.1007/s10021-014-9803-3>.
- Christensen, V., De La Puente, S., Sueiro, C.J., Steenbeek, J., Majluf, P., 2014b. Valuing sea-food: the Peruvian fisheries sector. *Mar. Policy* 44, 302–311.
- Christensen, V., Coll, M., Buszowski, J., Cheung, W.W.L., Frölicher, T., Steenbeek, J., Stock, C.A., Watson, R.A., Walters, C.J., 2015. The global ocean is an ecosystem: simulating marine life and fisheries. *Glob. Ecol. Biogeogr.* 24, 507–517. <https://doi.org/10.1111/geb.12281>.
- Clark, D., Goodwin, E., Sinner, J., Ellis, J., Singh, G., 2016. Validation and limitations of a cumulative impact model for an estuary. *Ocean Coast. Manag.* 120, 88–98.
- Coll, M., Libralato, S., 2012. Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. *Fish Fish.* 13, 60–88. <https://doi.org/10.1111/j.1467-2979.2011.00420.x>.
- Coll, M., Steenbeek, J., 2017. Standardized ecological indicators to assess aquatic food webs: the ECOIND software plug-in for Ecopath with Ecosim models. *Environ. Model. Softw.* 89, 120–130.
- Coll, M., Akoglu, E., Arreguin-Sánchez, F., Fulton, E.A., Gascuel, D., Heymans, J.J., Libralato, S., Mackinson, S., Palomera, I., Piroddi, C., Shannon, L.J., Steenbeek, J., Villasante, S., Christensen, V., 2015. Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. *Rev. Fish Biol. Fish.* 25, 413–424. <https://doi.org/10.1007/s11160-015-9386-x>.
- Coll, M., Steenbeek, J., Sole, J., Palomera, I., Christensen, V., 2016. Modelling the cumulative spatial-temporal effects of environmental drivers and fishing in a NW Mediterranean marine ecosystem. *Ecol. Model.* 331, 100–114. <https://doi.org/10.1016/j.ecolmodel.2016.03.020>.
- Coll, M., Steenbeek, J., Pennino, M.G., Buszowski, J., Kaschner, K., Lotze, H.K., ... Christensen, V., 2020. Advancing global ecological modeling capabilities to simulate future trajectories of change in marine ecosystems. *Front. Mar. Sci.* 7, 567877.
- Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., Christensen, V., 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecol. Model.* 302, 42–53. <https://doi.org/10.1016/j.ecolmodel.2015.01.025>.
- Colvin, M.E., Pierce, C.L., Stewart, T.W., 2015. A food web modeling analysis of a Midwestern, USA eutrophic lake dominated by non-native common carp and Zebra mussels. *Ecol. Model.* 312, 26–40. <https://doi.org/10.1016/j.ecolmodel.2015.05.016>.
- Cornwall, C.E., Eddy, T.D., 2015. Effects of near-future ocean acidification, fishing, and marine protection on a temperate coastal ecosystem. *Conserv. Biol.* 29, 207–215. <https://doi.org/10.1111/cobi.12394>.
- Corrales, X., Coll, M., Ofir, E., Piroddi, C., Goren, M., Edelist, D., Heymans, J.J., Steenbeek, J., Christensen, V., Gal, G., 2017a. Hindcasting the dynamics of an EasternMediterranean marine ecosystem under the impacts of multiple stressors. *Mar. Ecol. Prog. Ser.* 580, 17–36. <https://doi.org/10.3354/meps12271>.
- Corrales, X., Ofir, E., Coll, M., Goren, M., Edelist, D., Heymans, J.J., Gal, G., 2017b. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. *J. Mar. Syst.* 170, 88–102. <https://doi.org/10.1016/j.jmarsys.2017.02.004>.
- Corrales, X., Coll, M., Ofir, E., Heymans, J.J., Steenbeek, J., Goren, M., Edelist, D., Gal, G., 2018. Future scenarios of marine resources and ecosystem conditions in the eastern Mediterranean under the impacts of fishing, alien species and sea warming. *Sci. Rep.* 8, 1–16. <https://doi.org/10.1038/s41598-018-32666-x>.
- Costalago, D., Bauer, B., Tomczak, M.T., Lundström, K., Winder, M., 2019. The necessity of a holistic approach when managing marine mammal–fisheries interactions: environment and fisheries impact are stronger than seal predation. *Ambio* 48, 552–564. <https://doi.org/10.1007/s13280-018-1131-y>.
- Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B Biol. Sci.* 283, 20152592.
- Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315.
- Crozier, L.G., Burke, B.J., Chasco, B.E., Widener, D.L., Zabel, R.W., 2021. Climate change threatens Chinook salmon throughout their life cycle. *Commun. Biol.* 4. <https://doi.org/10.1038/s42003-021-01734-w>.
- Dahood, A., Watters, G.M., de Mutsert, K., 2019. Using sea-ice to calibrate a dynamic trophic model for the Western Antarctic Peninsula. *PLoS ONE* 14 (4), e0214814. <https://doi.org/10.1371/journal.pone.0214814>.
- Dahood, A., de Mutsert, K., Watters, G.M., 2020. Evaluating Antarctic marine protected area scenarios using a dynamic food web model. *Biol. Conserv.* 251, 108766. <https://doi.org/10.1016/j.biocon.2020.108766>.
- Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. *Ecol. Lett.* 11, 1278–1286.
- Daskalov, G.M., 2002. Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.* 225, 53–63. <https://doi.org/10.3354/meps225053>.
- de Mutsert, K., Cowan, J.H., Walters, C.J., 2012. Using Ecopath with Ecosim to explore nekton community response to freshwater diversion into a Louisiana estuary. *Mar. Coast. Fish.* 4, 104–116. <https://doi.org/10.1080/19425120.2012.672366>.
- de Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan, J.H., Christensen, V., 2016. Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecol. Model.* 331, 142–150. <https://doi.org/10.1016/j.ecolmodel.2015.10.013>.
- de Mutsert, K., Lewis, K., Milroy, S., Buszowski, J., Steenbeek, J., 2017. Using ecosystem modeling to evaluate trade-offs in coastal management: effects of large-scale river diversions on fish and fisheries. *Ecol. Model.* 360, 14–26. <https://doi.org/10.1016/j.ecolmodel.2017.06.029>.
- de Mutsert, K., Lewis, K.A., White, E.D., Buszowski, J., 2021. End-to-end modeling reveals species-specific effects of large-scale coastal restoration on living resources facing climate change. *Front. Mar. Sci.* 8. <https://doi.org/10.3389/fmars.2021.624532>.
- Di Marco, M., Venter, O., Possingham, H.P., Watson, J.E.M., 2018. Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* 9. <https://doi.org/10.1038/s41467-018-07049-5>.
- Díaz López, B., Bunke, M., Bernal Shirai, J.A., 2008. Marine aquaculture off Sardinia Island (Italy): ecosystem effects evaluated through a trophic mass-balance model. *Ecol. Model.* 212, 292–303. <https://doi.org/10.1016/j.ecolmodel.2007.10.028>.
- Downing, A.S., Van Nes, E.H., Janse, J.H., Witte, F., Cornelissen, I.J.M., Scheffer, M., Mooij, W.M., 2012. Collapse and reorganization of a food web of Mwanza Gulf, Lake Victoria. *Ecol. Appl.* 22, 229–239. <https://doi.org/10.1890/11-0941.1>.
- Duan, L.J., Li, S.Y., Liu, Y., Moreau, J., Christensen, V., 2009. Modeling changes in the coastal ecosystem of the Pearl River Estuary from 1981 to 1998. *Ecol. Model.* 220, 2802–2818. <https://doi.org/10.1016/j.ecolmodel.2009.07.016>.
- Ehrnsten, E.S., Bauer, B., Gustafsson, B.G., 2019. Combined effects of environmental drivers on marine trophic groups - a systematic model comparison. *Front. Mar. Sci.* 6, 492. <https://doi.org/10.3389/fmars.2019.00492>.
- Espinosa-Romero, M.J., Greg, E.J., Walters, C., Christensen, V., Chan, K.M.A., 2011. Representing mediating effects and species reintroductions in Ecopath with Ecosim. *Ecol. Model.* 222, 1569–1579.
- Ferriss, B.E., Reum, J.C.P., McDonald, S., Farrell, D.M., Harvey, C.J., 2016. Evaluating trophic and non-trophic effects of shellfish aquaculture in a coastal estuarine foodweb. *ICES J. Mar. Sci.* 73, 429–440. <https://doi.org/10.2307/4451315>.
- Field, J.C., Francis, R.C., Aydin, K., 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the northern California current. *Prog. Oceanogr.* 68, 238–270. <https://doi.org/10.1016/j.pocan.2006.02.010>.
- Forrester, F., Coll, M., Die, D.J., Christensen, V., 2012. Ecosystem effects of bluefin tuna *Thunnus thynnus* thynnus aquaculture in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 456, 215–231. <https://doi.org/10.3354/meps09700>.
- Fretzer, S., 2015. Using the Ecopath approach for environmental impact assessment-a case study analysis. *Ecol. Model.* 331, 160–172. <https://doi.org/10.1016/j.ecolmodel.2015.09.022>.
- Frisk, M.G., Miller, T.J., Latour, R.J., Martell, S.J.D., 2011. Assessing biomass gains from marsh restoration in Delaware Bay using Ecopath with Ecosim. *Ecol. Model.* 222, 190–200. <https://doi.org/10.1016/j.ecolmodel.2010.08.026>.
- Fulton, E.A., 2011. Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Mar. Sci.* 68, 1329–1342. <https://doi.org/10.1093/icesjms/fsr032>.
- Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., ... Smith, D.C., 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish Fish.* 12 (2), 171–188.
- Fulton, E.A., Bulman, C.M., Pethybridge, H., Goldsworthy, S.D., 2018. Modelling the great Australian bight ecosystem. *Deep. Res. Part II Top. Stud. Oceanogr.* 157–158, 211–235. <https://doi.org/10.1016/j.dsr2.2018.11.002>.
- Gari, S.R., Newton, A., Icelly, J.D., 2015. A review of the application and evolution of the DPSIR framework with an emphasis on coastal social-ecological systems. *Ocean Coast. Manag.* 103, 63–77.
- Giakoumi, S., Halpern, B.S., Michel, L.N., Gobert, S., Sini, M., Boudouresque, C.F., Gambi, M.C., Katsanevakis, S., Lejeune, P., Montefalcone, M., Pergent, G., Pergent-Martini, C., Sanchez-Jerez, P., Velimirov, B., Vizzini, S., Abadie, A., Coll, M., Guidetti, P., Micheli, F., Possingham, H.P., 2015. Towards a framework for assessment and management of cumulative human impacts on marine food webs. *Conserv. Biol.* 29, 1228–1234. <https://doi.org/10.1111/cobi.12468>.
- Gissi, E., Menegon, S., Sarretta, A., Appiotti, F., Maragno, D., Vianello, A., Depellegrin, D., Venier, C., Barbanti, A., 2017. Addressing uncertainty in modelling cumulative impacts within maritime spatial planning in the Adriatic and Ionian region. *PLoS One* 12, e0180501.
- Gissi, E., Manea, E., Mazaris, A.D., Fraschetti, S., Alpanidou, V., Bevilacqua, S., Coll, M., Guarnieri, G., Lloret-Lloret, E., Pascual, M., Petza, D., Rilov, G., Schonwald, M., Stelzenmüller, V., Katsanevakis, S., 2021. A review of the combined effects of climate change and other local human stressors on the marine environment. *Sci. Total Environ.* 755, 142564. <https://doi.org/10.1016/j.scitotenv.2020.142564>.
- Goncalves, M., Steenbeek, J., Tomczak, M., Romagnoni, G., Puntilla, R., Karvinen, V., Santos, C., Keijser, X., Abspoel, L., Warmelink, H., Mayer, I., 2021. Food-web modeling in the maritime spatial planning challenge simulation platform: results from the Baltic Sea region. In: Wardaszko, M., Meijer, S., Lukosch, H., Kanegae, H., Kriz, W.C., Grzybowska-Brzezińska, M. (Eds.), *Simulation Gaming through Times and Disciplines*. Springer International Publishing, Cham, pp. 290–305.
- Gorenflo, L.J., Brandon, K., 2006. Key human dimensions of gaps in global biodiversity conservation. *Bioscience* 56, 723–731. [https://doi.org/10.1641/0006-3568\(2006\)56\[723:KHDGII\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[723:KHDGII]2.0.CO;2).
- Greg, E.J., Palacios, D.M., Thompson, A., Chan, K.M.A., 2019. Why less complexity produces better forecasts: an independent data evaluation of kelp habitat models. *Ecography (Cop.)* 42, 428–443.
- Greg, E.J., Christensen, V., Nichol, L., Martone, R.G., Markel, R.W., Watson, J.C., Harley, C.D.G., Pakhomov, E.A., Shurin, J.B., Chan, K.M.A., 2020. Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science* 368, 1243–1247. <https://doi.org/10.1126/science.ayy5342> (80- ).
- Griffith, G.P., Fulton, E.A., Richardson, A.J., 2011. Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. *Glob. Chang. Biol.* 17 (10), 3058–3074.
- Griffith, G.P., Fulton, E.A., Gorton, R., Richardson, A.J., 2012. Predicting interactions among fishing, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. *Conserv. Biol.* 26 (6), 1145–1152.
- Griffiths, S.P., Young, J.W., Lansdell, M.J., Campbell, R.A., Hampton, J., Hoyle, S.D., Langley, A., Bromhead, D., Hinton, M.G., 2010. Ecological effects of longline fishing and climate change on the pelagic ecosystem off eastern Australia. *Rev. Fish Biol. Fish.* 20, 239–272. <https://doi.org/10.1007/s11160-009-9157-7>.



- Grossowicz, M., Ofir, E., Shabtay, A., Wood, J., Biton, E., Belkin, N., Frid, O., Sisma-Ventura, G., Kress, N., Berman-Frank, I., Gal, G., 2020. Modeling the effects of brine outflow from desalination plants on coastal food-webs of the Levantine basin (eastern Mediterranean Sea). *Desalination* 496, 114757. <https://doi.org/10.1016/j.desal.2020.114757>.
- Haak, D.M., Fath, B.D., Forbes, V.E., Martin, D.R., Pope, K.L., 2017. Coupling ecological and social network models to assess “transmission” and “contagion” of an aquatic invasive species. *J. Environ. Manag.* 190, 243–251. <https://doi.org/10.1016/j.jenvman.2016.12.012>.
- Halouani, G., Villanueva, C.M., Raoux, A., Dauvin, J.C., Ben Rais Lasram, F., Foucher, E., Le Loc'h, F., Safi, G., Araignous, E., Robin, J.P., Niquil, N., 2020. A spatial food web model to investigate potential spillover effects of a fishery closure in an offshore wind farm. *J. Mar. Syst.* 212, 103434. <https://doi.org/10.1016/j.jmarsys.2020.103434>.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952. <https://doi.org/10.1126/science.1149345>.
- Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6, 1–7. <https://doi.org/10.1038/ncomms8615>.
- Han, D., Chen, Y., Zhang, C., Ren, Y., Xue, Y., Wan, R., 2017. Evaluating impacts of intensive shellfish aquaculture on a semi-closed marine ecosystem. *Ecol. Model.* 359, 193–200. <https://doi.org/10.1016/j.ecolmodel.2017.05.024>.
- Han, D., Chen, Y., Zhang, C., Ren, Y., Xu, B., Xue, Y., 2018. Evaluation of effects of shellfish aquaculture and capture fishery on a semi-closed bay ecosystem. *Estuar. Coast. Shelf Sci.* 207, 175–182. <https://doi.org/10.1016/j.ecss.2018.04.005>.
- Hansson, S., Hjerne, O., Harvey, C., Kitchell, J.F., Cox, S.P., Essington, T.E., 2007. Managing Baltic Sea fisheries under contrasting production and predation regimes: ecosystem model analyses. *Ambio* 36, 265–271. [https://doi.org/10.1579/0044-7447\(2007\)36\[265:MBSFUC\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[265:MBSFUC]2.0.CO;2).
- Harvey, C.J., 2014. Mediation functions in Ecopath with Ecosim: handle with care. *Can. J. Fish. Aquat. Sci.* 71 (7), 1020–1029. <https://doi.org/10.1139/cjfas-2013-0594>.
- Harvey, B.J., 2018. Exploring Impacts of Noise from Shipping and Acoustic Deterrent Devices on Cetaceans on the West Coast of Scotland using an Ecosystem Modelling Approach. University of St Andrews.
- Harvey, C.J., Kareiva, P.M., 2005. Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia River reservoir. *Biol. Invasions* 7, 651–663. <https://doi.org/10.1007/s10530-004-5854-2>.
- Hernández-Padilla, J.C., Zetina-Rejón, M.J., Arreguín-Sánchez, F., del Monte-Luna, P., Nieto-Navarro, J.T., Salcido-Guevara, L.A., 2021. Structure and function of the southeastern Gulf of California ecosystem during low and high sea surface temperature variability. *Reg. Stud. Mar. Sci.* 43, 101686. <https://doi.org/10.1016/j.rsmas.2021.101686>.
- Hervann, P.Y., Gascuel, D., Grüss, A., Druon, J.N., Kopp, D., Perez, I., Piroddi, C., Robert, M., 2020. The Celtic Sea through time and space: ecosystem modeling to unravel fishing and climate change impacts on food-web structure and dynamics. *Front. Mar. Sci.* 7, 1018. <https://doi.org/10.3389/fmars.2020.578717>.
- Heymans, J.J., Guénette, S., Christensen, V., 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. *Ecosystems* 10, 488–502. <https://doi.org/10.1007/s10021-007-9034-y>.
- Heymans, J.J., Bundy, A., Christensen, V., Coll, M., de Mutsert, K., Fulton, E.A., ... Travers-Trolet, M., 2020. The ocean decade: a true ecosystem modeling challenge. *Front. Mar. Sci.* 7, 554573.
- Hodgson, E.E., Halpern, B.S., 2018. Investigating cumulative effects across ecological scales. *Conserv. Biol.* <https://doi.org/10.1111/cobi.13125>.
- Hodgson, E.E., Halpern, B.S., Essington, T.E., 2019. Moving beyond silos in cumulative effects assessment. *Front. Ecol. Evol.* 211. <https://doi.org/10.3389/fevo.2019.00211>.
- Holon, F., Marre, G., Parravicini, V., Mouquet, N., Bockel, T., Descamp, P., Tribot, A.S., Boissery, P., Deter, J., 2018. A predictive model based on multiple coastal anthropogenic pressures explains the degradation status of a marine ecosystem: implications for management and conservation. *Biol. Conserv.* 222, 125–135. <https://doi.org/10.1016/j.biocon.2018.04.006>.
- Hoover, C., Pitcher, T., Christensen, V., 2013a. Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: I. Re-creating past changes 1970–2009. *Ecol. Model.* 264, 130–142. <https://doi.org/10.1016/j.ecolmodel.2013.02.005>.
- Hoover, C., Pitcher, T., Christensen, V., 2013b. Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: II. Ecosystem model future projections. *Ecol. Model.* 264, 143–156. <https://doi.org/10.1016/j.ecolmodel.2013.01.010>.
- Howell, E.A., Wabnitz, C.C.C., Dunne, J.P., Polovina, J.J., 2013. Climate-induced primary productivity change and fishing impacts on the Central North Pacific ecosystem and Hawaii-based pelagic longline fishery. *Clim. Chang.* 119, 79–93. <https://doi.org/10.1007/s10584-012-0597-z>.
- Hunsicker, M.E., Kappel, C.V., Selkoe, K.A., Halpern, B.S., Scarborough, C., Mease, L., Amrhein, A., 2016. Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management. *Ecol. Appl.* 26, 651–663.
- Hyttiäinen, K., Bauer, B., Bly Joyce, K., Ehrnsten, E., Eilola, K., Gustafsson, B.G., Meier, H.E.M., Norkko, A., Saraiva, S., Tomczak, M., Zandersen, M., 2021. Provision of aquatic ecosystem services as a consequence of societal changes: the case of the Baltic Sea. *Popul. Ecol.* 63, 61–74. <https://doi.org/10.1002/1438-390X.12033>.
- IPBES, 2019. Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany.
- Izquierdo-Gomez, D., Bayle-Sempere, J.T., Arreguín-Sánchez, F., Sánchez-Jerez, P., 2016. Modeling population dynamics and small-scale fisheries yields of fish farming escapes in Mediterranean coastal areas. *Ecol. Model.* 331, 56–67. <https://doi.org/10.1016/j.ecolmodel.2016.01.012>.
- Jorge-Romero, G., Lercari, D., Ortega, L., Defeo, O., 2019. Long-term ecological footprints of a man-made freshwater discharge onto a sandy beach ecosystem. *Ecol. Indic.* 96, 412–420. <https://doi.org/10.1016/j.ecolind.2018.09.024>.
- Jorge-Romero, G., Celestano, E., Lercari, D., Ortega, L., Licandro, J.A., Defeo, O., 2021. Long-term and multilevel impact assessment of the 2015–2016 El Niño on a sandy beach of the southwestern Atlantic. *Sci. Total Environ.* 775, 145689. <https://doi.org/10.1016/j.scitotenv.2021.145689>.
- Kao, Y.C., Adlerstein, S., Rutherford, E., 2014. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: an Ecopath with Ecosim analysis. *J. Great Lakes Res.* 40, 35–52. <https://doi.org/10.1016/j.jglr.2014.01.010>.
- Kaschner, K., Kesner-Reyes, K., Garilao, C., Rius-Barile, J., Rees, T., Froese, R., 2019. AquaMaps: predicted range maps for aquatic species. [WWW Document]. URL [www.aquamaps.org](http://www.aquamaps.org).
- Kearney, K.A., Stock, C., Aydin, K., Sarmiento, J.L., 2012. Coupling planktonic ecosystem and fisheries food web models for a pelagic ecosystem: description and validation for the sub-arctic Pacific. *Ecol. Model.* 237–238, 43–62. <https://doi.org/10.1016/j.ecolmodel.2012.04.006>.
- Khan, M.F., Panikkar, P., 2009. Assessment of impacts of invasive fishes on the food web structure and ecosystem properties of a tropical reservoir in India. *Ecol. Model.* 220 (18), 2281–2290. <https://doi.org/10.1016/j.ecolmodel.2009.05.020>.
- Kingsland, S.E., 1995. Modeling nature. University of Chicago Press.
- Kitchell, J.F., Cox, S.P., Harvey, C.J., Johnson, T.B., Mason, D.M., Schoen, K.K., Aydin, K., Bronte, C., Ebner, M., Hansen, M., Hoff, M., Schram, S., Schreiner, D., Walters, C.J., 2000. Sustainability of the Lake Superior fish community: interactions in a food web context. *Ecosystems* 3, 545–560. <https://doi.org/10.1007/s100210000048>.
- Kluger, L.C., Taylor, M.H., Rivera, E.B., Silva, E.T., Wolff, M., 2016. Assessing the ecosystem impact of scallop bottom culture through a community analysis and trophic modelling approach. *Mar. Ecol. Prog. Ser.* 547, 121–135. <https://doi.org/10.3354/meps11652>.
- Koehn, J.Z., Reineken, D.R., Kittinger, J.N., 2013. Progress and promise in spatial human dimensions research for ecosystem-based ocean planning. *Mar. Policy* 42, 31–38. <https://doi.org/10.1016/j.marpol.2013.01.015>.
- Korpinen, S., Andersen, J.H., 2016. A global review of cumulative pressure and impact assessments in marine environments. *Front. Mar. Sci.* 3, 153.
- Kumar, R., Pitcher, T.J., Varkey, D., Lam, D., Ainsworth, C., Pakhomov, E., 2016a. An ecosystem model of the ocean around Haida Gwaii, northern British Columbia: ecopath, ecosim and ecospace. *Univ. Br. Columbia Fish. Cent. Res. Reports* 24, 1–76.
- Kumar, Rajeev, Varkey, D., Pitcher, T., 2016b. Simulation of zebra mussels (*Dreissena polymorpha*) invasion and evaluation of impacts on Mille Lacs Lake, Minnesota: an ecosystem model. *Ecol. Model.* 331, 68–76. <https://doi.org/10.1016/j.ecolmodel.2016.01.019>.
- Kumar, R., Pitcher, T.J., Varkey, D.A., 2017. Ecosystem approach to fisheries: exploring environmental and trophic effects on maximum sustainable yield (MSY) reference point estimates. *PLoS One* 12, 1–19. <https://doi.org/10.1371/journal.pone.0185575>.
- Langseth, B.J., Rogers, M., Zhang, H., 2012. Modeling species invasions in Ecopath with Ecosim: an evaluation using Laurentian Great Lakes models. *Ecol. Model.* 247, 251–261. <https://doi.org/10.1016/j.ecolmodel.2012.08.015>.
- Larsen, L.H., Sagerup, K., Ramsvatn, S., 2016. The mussel path - using the contaminant tracer, Ecotracer, in Ecopath to model the spread of pollutants in an Arctic marine food web. *Ecol. Model.* 331, 77–85. <https://doi.org/10.1016/j.ecolmodel.2015.10.011>.
- Lenzen, M., Moran, D., Kanemoto, K., Foran, B., Lobefaro, L., Geschke, A., 2012. International trade drives biodiversity threats in developing nations. *Nature* 486, 109–112. <https://doi.org/10.1038/nature11145>.
- Lewis, K.A., de Mutsert, K., Steenbeek, J., Peele, H., Cowan, J.H., Buszowski, J., 2016. Employing ecosystem models and geographic information systems (GIS) to investigate the response of changing marsh edge on historical biomass of estuarine nekton in Barataria Bay, Louisiana, USA. *Ecol. Modell.* 331, 129–141. <https://doi.org/10.1016/j.ecolmodel.2016.01.017>.
- Lewis, K.A., Christian, R.R., Martin, C.W., Allen, K.L., McDonald, A.M., Roberts, V.M., Shaffer, M.N., Valentine, J.F., 2021. Complexities of disturbance response in a marine food web. *Limnol. Oceanogr.* 1–13. <https://doi.org/10.1002/lno.11790>.
- Li, L., Pitcher, T.J., Devlin, R.H., 2014. Potential risks of trophic impacts by escaped transgenic salmon in marine environments. *Environ. Conserv.* 760, 152–161. <https://doi.org/10.1017/S0376892914000319>.
- Libralato, S., Caccin, A., Pranovi, F., 2015. Modeling species invasions using thermal and trophic niche dynamics under climate change. *Front. Mar. Sci.* 2. <https://doi.org/10.3389/fmars.2015.00029>.
- Lima, M.A.L., Doria, C.R., Carvalho, A.R., Angelini, R., 2020. Fisheries and trophic structure of a large tropical river under impoundment. *Ecol. Indic.* 113, 106162.
- Lin, H.J., Shao, K.T., Hsieh, H.L., Lo, W.T., Dai, X.X., 2009. The effects of system-scale removal of oyster-culture racks from Tapong Bay, southwestern Taiwan: model exploration and comparison with field observations. *ICES J. Mar. Sci.* 66, 797–810. <https://doi.org/10.1093/icesjms/fsp078>.
- Link, J.S., 2004. A general model of selectivity for fish feeding: a rank proportion algorithm. *Trans. Am. Fish. Soc.* 133, 655–673. <https://doi.org/10.1577/t02-142.1>.
- Lira, A.S., Lucena-Frédou, F., Le Loc'h, F., 2021. How the fishing effort control and environmental changes affect the sustainability of a tropical shrimp small scale fishery. *Fish. Res.* 235. <https://doi.org/10.1016/j.fishres.2020.105824>.
- Livne, L., Grossowicz, M., Tchermov, D., Ayalon, O., 2020. Predicting impacts of offshore monoculture farm expansion in ultra-oligotrophic waters of the Levantine Basin. *Front. Mar. Sci.* 7, 1–9. <https://doi.org/10.3389/fmars.2020.00556>.
- Lockerbie, E.M., Shannon, L., 2019. Toward exploring possible future states of the southern Benguela. *Front. Mar. Sci.* 6. <https://doi.org/10.3389/fmars.2019.00380>.
- Lynam, C., Steenbeek, J., Mackinson, S., Garcia, C., Wright, S.R., Posen, P., Lincoln, S., Kirby, M., 2017. Investigating food web effects due to man-made structures using Coupled Spatial Modelling. Technical Report from CEFAS, UK, p. 38.

- Ma, Y., You, X., 2021. Modelling the accumulation of microplastics through food webs with the example Baiyangdian Lake, China. *Sci. Total Environ.* 762, 144110. <https://doi.org/10.1016/j.scitotenv.2020.144110>.
- Ma, H., Townsend, H., Zhang, X., Sigrist, M., Christensen, V., 2010. Using a fisheries ecosystem model with a water quality model to explore trophic and habitat impacts on a fisheries stock: a case study of the blue crab population in the Chesapeake Bay. *Ecol. Model.* 221, 997–1004. <https://doi.org/10.1016/j.ecolmodel.2009.01.026>.
- Manju Lekshmi, N., Sreekanth, G.B., Singh, N.P., Vennila, A., Ratheesh Kumar, R., Pandey, P.K., 2020. Ecopath modelling approach for the impact assessment of a small-scale coastal aquaculture system in Goa, India. *Indian J. Fish.* 67, 39–51. <https://doi.org/10.21077/ijf.2020.67.3.88300-05>.
- Mason, J.G., Rudd, M.A., Crowder, L.B., 2017. Ocean research priorities: similarities and differences among scientists, policymakers, and fishermen in the United States. *Bioscience* 67, 418–428. <https://doi.org/10.1093/biosci/biw172>.
- McGill, L.M., Gerig, B.S., Chaloner, D.T., Lambert, G.A., 2017. An ecosystem model for evaluating the effects of introduced Pacific salmon on contaminant burdens of stream-resident fish. *Ecol. Model.* 355, 39–48. <https://doi.org/10.1016/j.ecolmodel.2017.03.027>.
- Michailidis, N., Corrales, X., Karachle, P.K., Chartosia, N., Katsanevakis, S., Sfenthourakis, S., 2019. Modelling the role of alien species and fisheries in an Eastern Mediterranean insular shelf ecosystem. *Ocean Coast. Manag.* 175, 152–171. <https://doi.org/10.1016/j.ocecoaman.2019.04.006>.
- Morgan, M.S., 2012. *The World in the Model: How Economists Work and Think*. Cambridge University Press.
- Murray, C.C., Mach, M.E., Martone, R.G., 2014. *Cumulative Effects in Marine Ecosystems: Scientific Perspectives on its Challenges and Solutions*.
- Murray, C.C., Hannah, L.C., Doniol-Valcroze, T., Wright, B.M., Stredulinsky, E.H., Nelson, J.C., Locke, A., Lacy, R.C., 2021. A cumulative effects model for population trajectories of resident killer whales in the Northeast Pacific. *Biol. Conserv.* 257, 109124. <https://doi.org/10.1016/j.biocon.2021.109124>.
- Nagelkerken, I., Goldenberger, S.U., Ferreir, C.M., Ullah, H., Conne, S.D., 2020. Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. *Science* 80-. J. 369, 829–832. <https://doi.org/10.1126/science.aax0621>.
- Neira, S., Moloney, C.L., Cury, P., Mullon, C., Christensen, V., 2009. Mechanisms affecting recovery in an upwelling food web: the case of the southern Humboldt. *Prog. Oceanogr.* 83, 404–416. <https://doi.org/10.1016/j.poccean.2009.07.007>.
- Niiranen, S., Stipa, T., Hirvonen, A., Paakkonen, J.-P., Norkko, A., 2008. *Modelled bioaccumulation of chemical warfare agents within the Baltic Sea food web*. 2008 IEEE/OES US/EU-Baltic International Symposium. IEEE, pp. 1–10.
- Niiranen, S., Blenckner, T., Hjerne, O., Tomczak, M.T., 2012. Uncertainties in a Baltic Sea food-web model reveal challenges for future projections. *Ambio* 41, 613–625. <https://doi.org/10.1007/s12380-012-0324-z>.
- Niiranen, S., Yletyinen, J., Tomczak, M.T., Blenckner, T., Hjerne, O., Mackenzie, B.R., Müller-Karulis, B., Neumann, T., Meier, H.E.M., 2013. Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Glob. Chang. Biol.* 19, 3327–3342. <https://doi.org/10.1111/gcb.12309>.
- O'Connor, M.I., Mori, A.S., Gonzalez, A., Dee, L.E., Loreau, M., Avolio, M., Byrnes, J.E.K., Cheung, W., Cowles, J., Clark, A.T., Hautier, Y., Hector, A., Komatsu, K., Newbold, T., Outhwaite, C.L., Reich, P.B., Seabloom, E., Williams, L., Wright, A., Isbell, F., 2021. Grand challenges in biodiversity-ecosystem functioning research in the era of science-policy platforms require explicit consideration of feedbacks. *Proc. R. Soc. B Biol. Sci.* 288. <https://doi.org/10.1098/rspb.2021.0783>.
- Ofir, E., Heymans, J.J., Shapiro, J., Goren, M., Spanier, E., Gal, G., 2017. Predicting the impact of Lake biomanipulation based on food-web modeling—Lake Kinneret as a case study. *Ecol. Model.* 348, 14–24. <https://doi.org/10.1016/j.ecolmodel.2016.12.019>.
- Okey, T. a, 2004. *Shifted Community States in Four Marine Ecosystems: Some Potential Mechanisms*. Thesis Dr, UBC, p. 173.
- Okey, T.A., Vargo, G.A., MacKinson, S., Vasconcellos, M., Mahmoudi, B., Meyer, C.A., 2004. Simulating community effects of sea floor shading by plankton blooms over the West Florida Shelf. *Ecol. Model.* 172, 339–359. <https://doi.org/10.1016/j.ecolmodel.2003.09.015>.
- Ortega-Cisneros, K., Shannon, L., Cochrane, K., Fulton, E.A., Shin, Y.J., 2018. Evaluating the specificity of ecosystem indicators to fishing in a changing environment: a model comparison study for the southern Benguela ecosystem. *Ecol. Indic.* 95, 85–98. <https://doi.org/10.1016/j.ecolind.2018.07.021>.
- Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10, 877–889. <https://doi.org/10.1007/s10021-007-9069-0>.
- Overholtz, W., Link, J., 2009. A simulation model to explore the response of the Gulf of Maine food web to large-scale environmental and ecological changes. *Ecol. Model.* 220, 2491–2502. <https://doi.org/10.1016/j.ecolmodel.2009.06.034>.
- Parravicini, V., Rovere, A., Vassallo, P., Micheli, F., Montefalcone, M., Morri, C., Paoli, C., Albertelli, G., Fabiano, M., Bianchi, C.N., 2012. Understanding relationships between conflicting human uses and coastal ecosystems status: a geospatial modeling approach. *Ecol. Indic.* 19, 253–263. <https://doi.org/10.1016/j.ecolind.2011.07.027>.
- Parrish, F.A., Howell, E.A., Antonelis, G.A., Iverson, S.J., Littnan, C.L., Parrish, J.D., Polovina, J.J., 2012. Estimating the carrying capacity of French Frigate Shoals for the endangered Hawaiian monk seal using Ecopath with Ecosim. *Mar. Mammal Sci.* 28, 522–541. <https://doi.org/10.1111/j.1748-7692.2011.00502.x>.
- Patrício, J., Marques, J.C., 2006. Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the Mondego estuary (Portugal). *Ecol. Model.* 197, 21–34. <https://doi.org/10.1016/j.ecolmodel.2006.03.008>.
- Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P.E., Nascimento, M.C., Blanchet, M.A., Ellingsen, I.H., Jørgensen, L.L., Blanchet, H., 2021. Overexploitation, recovery, and warming of the Barents Sea ecosystem during 1950–2013. *Front. Mar. Sci.* 8, 1–22. <https://doi.org/10.3389/fmars.2021.732637>.
- Peng, G., Zhou, X., Xie, B., Huang, C., Uddin, M.M., Chen, X., Huang, L., 2021. Ecosystem stability and water quality improvement in a eutrophic shallow lake via long-term integrated biomanipulation in Southeast China. *Ecol. Eng.* 159, 106119. <https://doi.org/10.1016/j.ecoleng.2020.106119>.
- Pezy, J.P., Raoux, A., Marmin, S., Balay, P., Dauvin, J.C., 2018. What are the most suitable indices to detect the structural and functional changes of benthic community after a local and short-term disturbance? *Ecol. Indic.* 91, 232–240. <https://doi.org/10.1016/j.ecolind.2018.04.009>.
- Phong, L.T., van Dam, A.A., Udo, H.M.J., van Mensvoort, M.E.F., Tri, L.Q., Steenstra, F.A., van der Zijpp, A.J., 2010. An agro-ecological evaluation of aquaculture integration into farming systems of the Mekong Delta. *Agric. Ecosyst. Environ.* 138, 232–241. <https://doi.org/10.1016/j.agee.2010.05.004>.
- Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Reconceptualizing synergism and antagonism among multiple stressors. *Ecol. Evol.* 5, 1538–1547. <https://doi.org/10.1002/ece3.1465>.
- Pine, W.E., Kwak, T.J., 2007. Modeling management scenarios and the effects of an introduced apex predator on a coastal riverine fish community. *Trans. Am. Fish. Soc.* 136, 105–120. <https://doi.org/10.1577/T05-249.1>.
- Pinnegar, J.K., Tomczak, M.T., Link, J.S., 2014. How to determine the likely indirect food-web consequences of a newly introduced non-native species: a worked example. *Ecol. Model.* 272, 379–387. <https://doi.org/10.1016/j.ecolmodel.2013.09.027>.
- Piroddi, C., Akoglu, E., Andonegi, E., Bentley, J.W., Celić, I., Coll, M., ... Tsikiras, A.C., 2021. Effects of nutrient management scenarios on marine food webs: a Pan-European assessment in support of the marine strategy framework directive. *Front. Mar. Sci.* 8, 179.
- Pitcher, T.J., Buchary, E.A., Hutton, T., 2002. Forecasting the benefits of no-take human-made reefs using spatial ecosystem simulation. *ICES J. Mar. Sci.* 59, S17–S26. <https://doi.org/10.1006/jmsc.2002.1185>.
- Pitcher, T.J., Heymans, J.J., Forrest, R., Stanford, R., Martell, S., Ainsworth, C., Orchard, T., Mackie, Q., Simeone, B., 2004. *Back to the future: advances in methodology for modelling and evaluating past ecosystems as future policy goals*. *Fish. Cent. Res. Reports* 12 158pp.
- Plummer, M.L., Harvey, C.J., Anderson, L.E., Guerry, A.D., Ruckelshaus, M.H., 2013. The role of eelgrass in marine community interactions and ecosystem services: results from ecosystem-scale food web models. *Ecosystems* 16, 237–251. <https://doi.org/10.1007/s10021-012-9609-0>.
- Port Metro Vancouver, 2015. *Roberts Bank Terminal 2 Project - Environmental Impact Statement*.
- Püts, M., et al., 2020. Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea. *Ecol. Model.* 431, 109189.
- Raoux, A., Tecchio, S., Pezy, J.P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., Ernande, B., Le Guen, C., Haraldsson, M., Grangeré, K., Le Loc'h, F., Dauvin, J.C., Niquil, N., 2017. Benthic and fish aggregation inside an offshore wind farm: which effects on the trophic web functioning? *Ecol. Indic.* 72, 33–46. <https://doi.org/10.1016/j.ecolind.2016.07.037>.
- Raoux, A., Lassalle, G., Pezy, J.P., Tecchio, S., Safi, G., Ernande, B., Mazé, C., Le Loc'h, F., Lequesne, J., Girardin, V., Dauvin, J.C., Niquil, N., 2019. Measuring sensitivity of two OSPAR indicators for a coastal food web model under offshore wind farm construction. *Ecol. Indic.* 96, 728–738. <https://doi.org/10.1016/j.ecolind.2018.07.014>.
- Raoux, A., Baux, N., Pezy, J.P., Balay, P., Lesourd, S., Dauvin, J.C., 2020. Evaluating ecosystem functioning of a long-term dumping site in the Bay of Seine (English Channel). *Ecol. Indic.* 115, 106381. <https://doi.org/10.1016/j.ecolind.2020.106381>.
- Reckermann, M., Omstedt, A., Soomere, T., Aigars, J., Akhtar, N., Beldowska, M., ... Zorita, E., 2022. Human impacts and their interactions in the Baltic Sea region. *Earth Syst. Dynam.* 13 (1), 1–80. <https://doi.org/10.5194/esd-13-1-2022>.
- Reyes-Martínez, M.J., Lercari, D., Ruiz-Delgado, M.C., Sánchez-Moyano, J.E., Jiménez-Rodríguez, A., Pérez-Hurtado, A., García-García, F.J., 2015. Human pressure on sandy beaches: implications for trophic functioning. *Estuar. Coasts* 38, 1782–1796. <https://doi.org/10.1007/s12237-014-9910-6>.
- Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillerro-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F., Dormann, C.F., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography (Cop.)* 40, 913–929. <https://doi.org/10.1111/ecog.02881>.
- Rogers, M.W., Allen, M.S., 2012. An ecosystem model for exploring lake restoration effects on fish communities and fisheries in Florida. *Restor. Ecol.* 20, 612–622. <https://doi.org/10.1111/j.1526-100X.2011.00819.x>.
- Rogers, M.W., Bunnell, D.B., Madenjian, C.P., Warner, D.M., 2014. Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. *Can. J. Fish. Aquat. Sci.* 71, 1072–1086. <https://doi.org/10.1139/cjfas-2013-0514>.
- Rohal, M., Ainsworth, C., Lupher, B., Montagna, P.A., Paris, C.B., Perlin, N., Suprenand, P.M., Yoskowitz, D., 2020. The effect of the Deepwater Horizon oil spill on two ecosystem services in the Northern Gulf of Mexico. *Environ. Model. Softw.* 133, 104793. <https://doi.org/10.1016/j.envsoft.2020.104793>.
- Ryabinin, V., Barbière, J., Haugan, P., Kullenberg, G., Smith, N., McLean, C., Troisi, A., Fischer, A., Aricò, S., Aarup, T., Pissierssens, P., 2019. The UN Decade of Ocean Science for Sustainable Development. *Front. Mar. Sci.* 6. <https://doi.org/10.3389/fmars.2019.00470>.
- Sadchatheeswaran, S., Branch, G.M., Shannon, L.J., Moloney, C.L., Coll, M., Robinson, T.B., 2020. Modelling changes in trophic and structural impacts of alien ecosystem engineers on a rocky-shore island. *Ecol. Model.* 433, 109227. <https://doi.org/10.1016/j.ecolmodel.2020.109227>.
- Sadchatheeswaran, S., Branch, G.M., Shannon, L.J., Coll, M., Steenbeek, J., 2021. A novel approach to explicitly model the spatiotemporal impacts of structural complexity created by alien ecosystem engineers in a marine benthic environment. *Ecol. Model.* 459, 109731. <https://doi.org/10.1016/j.ecolmodel.2021.109731>.



- Sakamoto, A., Shirakihara, K., 2017. Ecosystem dynamics in Tokyo Bay with a focus on high trophic levels using Ecopath with Ecosim. *J. Mar. Sci. Technol.* 22, 1–10. <https://doi.org/10.1007/s00773-016-0388-8>.
- Saltelli, A., Funtowicz, S., 2014. When all models are wrong. *Issues Sci. Technol.* 30, 79–85.
- Saltelli, A., Tarantola, S., Campolongo, F., Ratto, M., 2004. *Sensitivity Analysis in Practice: A Guide to Assessing Scientific Models*. Wiley, New York, NY.
- Sandberg, J., Kumbblad, L., Kautsky, U., 2007. Can ECOPATH with ECOSIM enhance models of radionuclide flows in food webs? - an example for <sup>14</sup>C in a coastal food web in the Baltic Sea. *J. Environ. Radioact.* 92, 96–111. <https://doi.org/10.1016/j.jenvrad.2006.09.010>.
- Santos, C.P., Warmelink, H., Boode, W., de Groot, P., Hutchinson, K., Gancalves, M., Steenbeek, J., Mayer, I., 2020. A digital game-based simulation platform for integrated maritime spatial planning: design challenges and technical innovations. *J. Ocean Technol.* 15, 80–100.
- Sayer, M.D.J., Magill, S.H., Pitcher, T.J., Morissette, L., Ainsworth, C., 2005. Simulation-based investigations of fishery changes as affected by the scale and design of artificial habitats. *J. Fish Biol.* 67, 1–26. <https://doi.org/10.1111/j.1095-8649.2005.00928.x>.
- Schlenger, A.J., Beas-Luna, R., Ambrose, R.F., 2021. Forecasting ocean acidification impacts on kelp forest ecosystems. *PLoS One* 16, 1–24. <https://doi.org/10.1371/journal.pone.0236218>.
- Serpetti, N., Baudron, A.R., Burrows, M.T., Payne, B.L., Helaoui, P., Fernandes, P.G., Heymans, J.J., 2017. Impact of ocean warming on sustainable fisheries management informs the ecosystem approach to fisheries. *Sci. Rep.* 7, 1–15. <https://doi.org/10.1038/s41598-017-13220-7>.
- Serpetti, N., Benjamins, S., Brain, S., Collu, M., Harvey, B.J., Heymans, J.J., Hughes, A.D., Risch, D., Rosinski, S., Waggit, J.J., Wilson, B., 2021. Modeling small scale impacts of multi-purpose platforms: an ecosystem approach. *Front. Mar. Sci.* 8. <https://doi.org/10.3389/fmars.2021.694013>.
- Shabtay, A., Portman, M.E., Ofir, E., Carmel, Y., Gal, G., 2018. Using ecological modelling in marine spatial planning to enhance ecosystem-based management. *Mar. Policy* 95, 14–23. <https://doi.org/10.1016/j.marpol.2018.06.018>.
- Shannon, L.J., Nelra, S., Taylor, M., 2008. Comparing internal and external drivers in the southern Benguela and the southern and northern Humboldt upwelling ecosystems. *Afr. J. Mar. Sci.* 30, 63–84. <https://doi.org/10.2989/AJMS.2008.30.1.7.457>.
- Sinnickson, D., Chagaris, D., Allen, M., 2021. Exploring impacts of river discharge on forage fish and predators using ecopath with ecosim. *Front. Mar. Sci.* 8, 1–17. <https://doi.org/10.3389/fmars.2021.689950>.
- Smith, M., Chagaris, D., Paperno, R., Markwith, S., 2021. Ecosystem structure and resilience of the Florida bay estuary: an original ecosystem model with implications for everglades restoration. *Mar. Freshw. Res.* 72, 563–583. <https://doi.org/10.1071/MF20125>.
- Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J., Christensen, V., 2013. Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial-temporal data. *Ecol. Model.* 263, 139–151. <https://doi.org/10.1016/j.ecolmodel.2013.04.027>.
- Steenbeek, J., Corrales, X., Platts, M., Coll, M., 2018. Ecosampler: a new approach to assessing parameter uncertainty in Ecopath with Ecosim. *SoftwareX* 7, 198–204. <https://doi.org/10.1016/j.softx.2018.06.004>.
- Steenbeek, J., Romagnoni, G., Bentley, J.W., Heymans, J.J., Serpetti, N., Gonçalves, M., Santos, C., Warmelink, H., Mayer, I., Keijser, X., Fairgrieve, R., Abspoel, L., 2020. Combining ecosystem modeling with serious gaming in support of transboundary maritime spatial planning. *Ecol. Soc.* 25, 1–24. <https://doi.org/10.5751/ES-11580-250221>.
- Steenbeek, J., Buszowski, J., Chagaris, D., Christensen, V., Coll, M., Fulton, E.A., Katsanevakis, S., Lewis, K.A., Mazaris, A.D., Macias, D., De Mutsert, K., Oldford, G., Grazia, M., Piroddi, C., Romagnoni, G., Serpetti, N., Shin, Y., Spence, M.A., Stelzenmüller, V., 2021a. Making spatial-temporal marine ecosystem modelling better – a perspective. *Environ. Model. Softw.* 145, 105209. <https://doi.org/10.1016/j.envsoft.2021.105209>.
- Steenbeek, J., Felinto, D., Pan, M., Buszowski, J., Christensen, V., 2021b. Using gaming technology to explore and visualize management impacts on marine ecosystems. *Front. Mar. Sci.* 8. <https://doi.org/10.3389/fmars.2021.619541>.
- Stewart, T.J., Sprules, W.G., 2011. Carbon-based balanced trophic structure and flows in the offshore Lake Ontario food web before (1987–1991) and after (2001–2005) invasion-induced ecosystem change. *Ecol. Model.* 222, 692–708. <https://doi.org/10.1016/j.ecolmodel.2010.10.024>.
- Stock, A., 2022. Spatiotemporal distribution of labeled data can bias the validation and selection of supervised learning algorithms: a marine remote sensing example. *ISPRS J. Photogramm. Remote Sens.* 187, 46–60.
- Stock, A., Micheli, F., 2016. Effects of model assumptions and data quality on spatial cumulative human impact assessments. *Glob. Ecol. Biogeogr.* 25. <https://doi.org/10.1111/geb.12493>.
- Stock, A., Crowder, L.B., Halpern, B.S., Micheli, F., 2018a. Uncertainty analysis and robust areas of high and low modeled human impact on the global oceans. *Conserv. Biol.* 32, 1368–1379. <https://doi.org/10.1111/cobi.13141>.
- Stock, A., Haupt, A.J., Mach, M.E., Micheli, F., 2018b. Mapping ecological indicators of human impact with statistical and machine learning methods: tests on the California coast. *Ecol. Inform.* 48. <https://doi.org/10.1016/j.ecoinf.2018.07.007>.
- Stockbridge, J., Jones, A.R., Gaylard, S.G., Nelson, M.J., Gillanders, B.M., 2021. Evaluation of a popular spatial cumulative impact assessment method for marine systems: a seagrass case study. *Sci. Total Environ.* 780, 146401.
- Suprenand, P.M., Ainsworth, C.H., 2017. Trophodynamic effects of climate change-induced alterations to primary production along the western Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* 569, 37–54.
- Suprenand, P.M., Hoover, C., Ainsworth, C.H., Dornberger, L.N., Johnson, C.J., 2019. Preparing for the inevitable: ecological and indigenous community impacts of oil spill-related mortality in the United States' Arctic marine ecosystem. In: Gilbert, S., Hollander, D.J., Paris, C.B., Schlüter, M., Wetzel, D.L. (Eds.), *Ainsworth, C.H. Scenarios and Responses to Future Deep Oil Spills*, Springer Nature, pp. 470–493. <https://doi.org/10.1007/978-3-030-12963-7>.
- Tam, J., Taylor, M.H., Blaskovic, V., Espinoza, P., Michael Ballón, R., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L., Gutiérrez, D., Goya, E., Ochoa, N., Wolff, M., 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: comparing trophic linkages under La Niña and El Niño conditions. *Prog. Oceanogr.* 79, 352–365. <https://doi.org/10.1016/j.pocean.2008.10.007>.
- Taylor, M.H., Tam, J., Blaskovic, V., Espinoza, P., Michael Ballón, R., Wosnitza-Mendo, C., Argüelles, J., Díaz, E., Purca, S., Ochoa, N., Ayón, P., Goya, E., Gutiérrez, D., Quipuzcoa, L., Wolff, M., 2008a. Trophic modeling of the Northern Humboldt Current Ecosystem, Part II: Elucidating ecosystem dynamics from 1995 to 2004 with a focus on the impact of ENSO. *Prog. Oceanogr.* 79, 366–378. <https://doi.org/10.1016/j.pocean.2008.10.008>.
- Taylor, M.H., Wolff, M., Mendo, J., Yamashiro, C., 2008b. Changes in trophic flow structure of Independence Bay (Peru) over an ENSO cycle. *Prog. Oceanogr.* 79, 336–351. <https://doi.org/10.1016/j.pocean.2008.10.006>.
- Tierney, K.M., et al., 2018. Modelling marine trophic transfer of radiocarbon (<sup>14</sup>C) from a nuclear facility. *Environ. Model. Softw.* 102, 138–154.
- Tittensor, D.P., Eddy, T.D., Lotze, H.K., Galbraith, E.D., Cheung, W., Barange, M., ... Walker, N.D., 2018. A protocol for the intercomparison of marine fishery and ecosystem models: fish-MIP v1.0. *Geosci. Model Dev.* 11 (4), 1421–1442.
- Tomczak, M.T., Niiranen, S., Hjerne, O., Blenckner, T., 2012. Ecosystem flow dynamics in the Baltic proper using a multi-trophic dataset as a basis for food-web modelling. *Ecol. Model.* 230, 123–147. <https://doi.org/10.1016/j.ecolmodel.2011.12.014>.
- Townhill, B.L., Reppas-Chrysovitinos, E., Sühring, R., Halsall, C.J., Mollu, E., Sanders, T., Dähnke, K., Crabeck, O., Kaiser, J., Birchenough, S.N.R., 2021. Pollution in the Arctic Ocean: an overview of multiple pressures and implications for ecosystem services. *Ambio* 471–483. <https://doi.org/10.1007/s13280-021-01657-0>.
- Uusitalo, L., Blenckner, T., Puntilla-Dodd, R., Skyttä, A., Jernberg, S., Voss, R., Müller-Karulis, B., Tomczak, M.T., Möllmann, C., Peltonen, H., 2022. Integrating diverse model results into decision support for good environmental status and blue growth. *Sci. Total Environ.* 806. <https://doi.org/10.1016/j.scitotenv.2021.150450>.
- van Leeuwen, S., Salgado, H., Bailey, J., Beecham, J., Iriarte, J., García-García, L., Thorpe, R., 2021. Climate change, marine resources and a small Chilean community: making the connections. *Mar. Ecol. Prog. Ser.* 680, 223–246. <https://doi.org/10.3354/meps13934>.
- Vassilides, J.M., de Mutsert, K., Christensen, V., Townsend, H., 2017a. Using the Ecopath with Ecosim modeling approach to understand the effects of watershed-based management actions in coastal ecosystems. *Coast. Manag.* 45, 44–55. <https://doi.org/10.1080/08920753.2017.1237241>.
- Vassilides, J.M., Townsend, H., Belton, T., Jensen, O.P., 2017b. Modeling the effects of a power plant decommissioning on an estuarine food web. *Estuar. Coasts* 40, 604–616. <https://doi.org/10.1007/s12237-016-0151-8>.
- Vilas, D., Coll, M., Corrales, X., Steenbeek, J., Piroddi, C., Macias, D., Ligas, A., Sartor, P., Claudet, J., 2021a. Current and potential contributions of the Gulf of Lion Fisheries Restricted Area to fisheries sustainability in the NW Mediterranean Sea. *Mar. Policy* 123, 104296. <https://doi.org/10.1016/j.marpol.2020.104296>.
- Vilas, D., Coll, M., Pedersen, T., Corrales, X., Filbee-Dexter, K., Wernberg, T., 2021b. Future trajectories of change for an Arctic deep-sea ecosystem connected to coastal kelp forests. *Restor. Ecol.* 29. <https://doi.org/10.1111/rec.13327>.
- Villanueva, M.C.S., Isumbisho, M., Kaningini, B., Moreau, J., Micha, J.C., 2008. Modeling trophic interactions in Lake Kivu: what roles do exotics play? *Ecol. Model.* 212 (3–4), 422–438. <https://doi.org/10.1016/j.ecolmodel.2007.10.047>.
- Villasante, S., Arreguín-Sánchez, F., Heymans, J.J., Libralato, S., Piroddi, C., Christensen, V., Coll, M., 2016. Modelling marine ecosystems using the Ecopath with Ecosim food web approach: new insights to address complex dynamics after 30 years of development. *Ecol. Model.* 331, 1–4.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. *Nature* 467, 555–561. <https://doi.org/10.1038/nature09440>.
- Walters, W.J., Christensen, V., 2018. Ecotracer: analyzing concentration of contaminants and radioisotopes in an aquatic spatial-dynamic food web model. *J. Environ. Radioact.* 181, 118–127. <https://doi.org/10.1016/j.jenvrad.2017.11.008>.
- Wang, X.X., Peng, L., Su, C.J., Cheng, G.W., 2017. Impact of hydropower dam development on river ecosystems: Ecopath model application on the red river in China as an example. *Pol. J. Environ. Stud.* 26, 2811–2822. <https://doi.org/10.15244/pjoes/73805>.
- Wang, J., Zou, X., Yu, W., Zhang, D., Wang, T., 2019. Effects of established offshore wind farms on energy flow of coastal ecosystems: a case study of the Rudong offshore wind farms in China. *Ocean Coast. Manag.* 171, 111–118. <https://doi.org/10.1016/j.ocecoaman.2019.01.016>.
- Wang, S.C., Liu, X., Liu, Y., Wang, H., 2021. Disentangling effects of multiple stressors on matter flow in a lake food web. *Ecol. Evol.* 11, 9652–9664. <https://doi.org/10.1002/ece3.7789>.
- Watson, R.A., Nowara, G.B., Tracey, S.R., Fulton, E.A., Bulman, C.M., Edgar, G.J., Barrett, N.S., Lyle, J.M., Frusher, S.D., Buxton, C.D., 2013. Ecosystem model of Tasmanian waters explores impacts of climate-change induced changes in primary productivity. *Ecol. Model.* 264, 115–129. <https://doi.org/10.1016/j.ecolmodel.2012.05.008>.
- Watson, S.C.L., Beaumont, N.J., Widdicombe, S., Paterson, D.M., 2020. Comparing the network structure and resilience of two benthic estuarine systems following the implementation of nutrient mitigation actions. *Estuar. Coast. Shelf Sci.* 244, 106059. <https://doi.org/10.1016/j.ecss.2018.12.016>.
- Watters, G.M., Olson, R.J., Francis, R.C., Fiedler, P.C., Polovina, J.J., Reilly, S.B., Aydin, K.Y., Boggs, C.H., Essington, T.E., Walters, C.J., Kitchell, J.F., 2003. Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO-scale and global-warming climate drivers. *Can. J. Fish. Aquat. Sci.* 60, 1161–1175. <https://doi.org/10.1139/f03-100>.

- Weijerman, M., Gove, J.M., Williams, I.D., Walsh, W.J., Minton, D., Polovina, J.J., 2018. Evaluating management strategies to optimise coral reef ecosystem services. *J. Appl. Ecol.* 55, 1823–1833. <https://doi.org/10.1111/1365-2664.13105>.
- Whitehouse, G.A., Aydin, K.Y., Hollowed, A.B., Holsman, K.K., Cheng, W., Faig, A., Haynie, A.C., Hermann, A.J., Kearney, K.A., Punt, A.E., Essington, T.E., 2021. Bottom-up impacts of forecasted climate change on the eastern Bering Sea food web. *Front. Mar. Sci.* 8, 1–20. <https://doi.org/10.3389/fmars.2021.624301>.
- Williams, B.A., Venter, O., Allan, J.R., Atkinson, S.C., Rehbein, J.A., Ward, M., Di Marco, M., Grantham, H.S., Ervin, J., Goetz, S.J., Hansen, A.J., Jantz, P., Pillay, R., Rodríguez-Buritica, S., Supples, C., Virnig, A.L.S., Watson, J.E.M., 2020. Change in terrestrial human footprint drives continued loss of intact ecosystems. *One Earth* 3, 371–382. <https://doi.org/10.1016/j.oneear.2020.08.009>.
- Woodruff, P., van Poorten, B.T., Walters, C.J., Christensen, V., 2021. Potential effects of invasive dreissenid mussels on a pelagic freshwater ecosystem: using an ecosystem model to simulate mussel invasion in a sockeye lake. *Aquat. Invasions* 16, 129–146.
- Woodworth-Jefcoats, P.A., Polovina, J.J., Howell, E.A., Blanchard, J.L., 2015. Two takes on the ecosystem impacts of climate change and fishing: comparing a size-based and a species-based ecosystem model in the central North Pacific. *Prog. Oceanogr.* 138, 533–545. <https://doi.org/10.1016/j.pocean.2015.04.004>.
- Wu, Z., Zhang, X., Lozano-Montes, H.M., Loneragan, N.R., 2016. Trophic flows, kelp culture and fisheries in the marine ecosystem of an artificial reef zone in the Yellow Sea. *Estuar. Coast. Shelf Sci.* 182, 86–97. <https://doi.org/10.1016/j.ecss.2016.08.021>.
- Xu, D., Cai, Y., Jiang, H., Wu, X., Leng, X., An, S., 2016. Variations of food web structure and energy availability of shallow Lake with long-term eutrophication: a case study from Lake Taihu, China. *Clean - Soil, Air, Water* 44, 1306–1314. <https://doi.org/10.1002/clen.201300837>.
- Yang, Y., Chen, H., 2013. Assessing impacts of flow regulation on trophic interactions in a wetland ecosystem. *J. Environ. Inform.* 21, 63–71. <https://doi.org/10.3808/jei.201300233>.
- Yin, J., Xu, J., Xue, Y., Xu, B., Zhang, C., Li, Y., Ren, Y., 2021. Evaluating the impacts of El Niño events on a marine bay ecosystem based on selected ecological network indicators. *Sci. Total Environ.* 763, 144205. <https://doi.org/10.1016/j.scitotenv.2020.144205>.
- Yin, C., Gong, L., Chen, Y., Ni, L., Pitcher, T.J., Kang, B., Guo, L., 2022. Modeling ecosystem impacts of the invasive Japanese smelt *Hypomesus nipponensis* in Lake Erhai, southwestern China. *Ecol. Inform.* 67, 101488. <https://doi.org/10.1016/j.ecoinf.2021.101488>.
- Zandersen, M., Hyttiäinen, K., Meier, H.E.M., Tomczak, M.T., Bauer, B., Haapasaari, P.E., Olesen, J.E., Gustafsson, B.G., Refsgaard, J.C., Fridell, E., Pihlainen, S., Le Tissier, M.D.A., Kosenius, A.K., Van Vuuren, D.P., 2019. Shared socio-economic pathways extended for the Baltic Sea: exploring long-term environmental problems. *Reg. Environ. Chang.* 19, 1073–1086. <https://doi.org/10.1007/s10113-018-1453-0>.
- Zhu, K., Wu, Y., Li, C., Xu, J., Zhang, M., 2020. Ecosystem-based restoration to mitigate eutrophication: a case study in a shallow Lake Konghao. *Water* 12.
- Zunino, S., Libralato, S., Melaku Canu, D., Prato, G., Solidoro, C., 2021. Impact of ocean acidification on ecosystem functioning and services in habitat-forming species and marine ecosystems. *Ecosystems* 24, 1561–1575. <https://doi.org/10.1007/s10021-021-00601-3>.