ATLAS Deliverable 4.5

Integrated management considering connectivity patterns

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Executive Summary

Connectivity was assessed during ATLAS for a diversity of organisms, from the corals that structure Vulnerable Marine Ecosystems (VMEs) to economically important fishery species using two main pathways. Predicted connectivity patterns were obtained through simulated larval Lagrangian particle modelling, based on oceanographic data gained in WP1 and reproductive knowledge produced in WP4. Realised connectivity was inferred using population genetics on sets of samples gathered before and during ATLAS, focusing on a subset of the target species initially listed, for which enough samples could be gathered to perform comprehensive population genetics analysis.

Lagrangian modelling of larval dispersal within ATLAS unravelled the effect of long-term ocean variability (Atlantic Meridional Overturning Circulation - AMOC, subpolar gyre strength - SPG and North Atlantic Oscillation - NAO) and larval behaviour on particle transport pathways and population connectivity (Fox et al., 2016), the contribution of man-made structures to connectivity (Henry et al., 2018) and the application of these results to marine planning and the development of ecologically coherent marine protected area networks. This work has underlined the crucial need for data on reproductive and larval biology to inform these predictions (Fox et al., 2016). This proved to be even more important for deep-sea species due to the vast extent of the water column through which larvae can disperse. Very different outcomes can be expected depending not only on the timing of reproduction or the length of pelagic larval duration (PLD), but also on the behaviour of larvae remaining on the seafloor or migrating more or less along the water column. The relationship between PLD and "realised connectivity" as estimated through population genetics is far from easily predictable, despite some relationship existing (Riginos et al., 2011). This is likely to be worse in the deep sea as exemplified by recent models where extensive PLD resulted in extreme variance of predicted connectivity (Ross et al., 2019), possibly due to the importance of the third dimension (depth) in the space potentially explored by larvae. Nevertheless, the new method developed in ATLAS (Fox et al., 2019) allows a generic approach to optimise multi objectives in the design of MPAs. This showed that for highly dispersive behaviours, all the Northern Atlantic could in theory be connected with a favoured anti-clockwise dispersal along the slopes. Results also underlined that seamount populations may act as crucial stepping stones (hubs) in the broad scale connectivity, placing them in the priority list to maintain connectivity for a broad range of species. This important role of seamounts and offshore banks was also demonstrated through Lagrangian modelling based on the reef coral *Lophelia pertusa*'s reproductive and larval biology (Fox et al., 2016).

As for inferences of "realised" connectivity, population genetics and genomics allow identification of distinct management units (MUs; Palsbøll et al., 2007), i.e. populations of conspecific individuals among which the degree of connectivity is sufficiently low so that each population should be monitored and managed separately, for example along the Northeast Atlantic coasts and the Mediterranean where the majority of samples analysed within ATLAS framework could be gathered. These samples laid also the foundations for a basin-scale analysis in the coming years in collaboration with partners from the northwest Atlantic under the leadership of the EU-funded project iAtlantic (see below). Importantly, genetically differentiated populations are not only demographically independent but may also shelter singular genetic diversity, one of the three components of biodiversity in need for conservation but too long neglected by management and conservation plans (Laikre et al., 2010). This was true for VMEs species such as *Madrepora oculata*, but also the commensal polychaete *Eunice norvegica* where at least one cryptic species was identified in the Atlantic. As for *Lophelia pertusa*, homogeneity was found in the Bay of Biscay despite some hints of differentiation of SE Rockall bank (Boavida et al., 2019b). The occurrence of those distinct MUs, or even distinct evolutionary significant units (ESUs; Ryder, 1986) in the case of *Eunice* sp., is essential for conservation, for each of them should be treated as distinct diversity entities, with no demographic (Brown Kodric-Brown, 1977) interdependence. This also means in case one MU would collapse, no evolutionary (Orr Unckless, 2014; Tomasini Peischl) rescue effect can be expected from the others, which needs to be accounted for in monitoring and management plans. Fish species studied in ATLAS were chosen among the target listed at the origin of the project for both their economic interest and, likewise invertebrates, the availability of samples to allow assessing connectivity over broad scales with a sufficient number of samples. Distinct MUs were also detected in the boarfish *Capros aper*, the horse mackerel *Trachurus trachurus*, and the Norway lobster *Nephrops norvegicus*. These MUs are demographically independent populations, thus multiple stocks expected to respond independently to harvesting and management. While the MUs in the boarfish largely agreed with the areas defined by the International Council for the Exploration of the Sea (ICES) (one exception though being noticed in the southern border), uncertainties remain for the horse mackerel and clear mismatches were revealed between MUs defined with genetic data and management areas for the Norway lobster, calling for a revision of management plans.

In this report, we also develop detailed explanations of the difference between genetic and demographic independency that are essential to understand the power and limitation of population genomics, but also to account for connectivity data in management plans. We believe those explanations are essential to share with managers and stakeholders, as well as scientific colleagues

expert in fields other than population genetics who are interested in applying population genetics to management and conservation.

On the basis of the results obtained in ATLAS, guidelines could be provided for future management plans, whether through the identification of mismatch between fisheries management units and the genetic differentiation of stocks, or the identification of genetically specific and disconnected populations for benthic organisms characterising VMEs. In fact, nearly every species showed a singular spatial delineation of MUs, resulting in a mosaic of patterns illustrating the challenge of multispecies purpose MPAs. One result is to account for the most limited connectivity potential in management plans, to ensure the maintenance of exchanges. In fact accounting for very limited dispersal to include connectivity in spatial planning showed the need to design large areas and to favour contiguous prioritisation units for conservation (Combes et al., in prep.).

Remaining uncertainties in areas where no genetic differentiation was detected is also important to consider and is different among taxa. Compared to those species for which clear MUs (or even ESUs) could be recognised, there were species and areas where no genetic differentiation could be detected (such as *Lophelia pertusa* in the Bay of Biscay), or no signature of bottleneck could be encountered (as was the case for most populations studied in ATLAS), despite extensive referenced exploitation or habitat destruction. In such cases it is very difficult to disentangle the real absence of barrier to gene flow and/or bottleneck from the insufficient power of the molecular method used. As demonstrated recently through simulations (Bailleul et al., 2018), there is a time lag between the moment barriers to connectivity or bottleneck occur and their signature can be detected through population genetics. This was designed as the “grey zone effect” and its duration depends on the statistical power delivered by the set of genetic markers used, but can encompass several tens to a thousand years (see Box 2.1.1). New generation high density genome scan analysis can help increasing the statistical power to detect such events. However, these methods are very demanding in terms of DNA quality and not all collections examined in ATLAS, particularly the older ones, gave such high quality DNA. Much work was thus dedicated during ATLAS to resolving DNA extraction protocols so that important existing deep-sea sample collections could be used. First results obtained on the two reef framework-forming corals and their associated commensal polychaete (*Eunice* spp., for we now know it encompasses at least two species), as well as the coral *Dendrophyllia cornigera*. For the last two species some samples liberated high quality DNA to build libraries that are being produced, and will allow to inferring our ability to detect hitherto ignored disruption of connectivity or bottlenecks. These data will be completed, analysed and interpreted beyond ATLAS, in the framework of iAtlantic using lessons learnt from genomic issues met and circumvented during ATLAS.

Due to issues related to DNA quality, RADSeq analysis on a dozen species for which just a handful of specimens met DNA quality standards allows the provision of genomic resources to be used with protocols requiring a lower DNA quality standard. These new resources will allow optimisation of the use of old but precious specimens and DNA collections of deep-sea organisms. Along with the basin scale analysis forecast for the two main reef framework-forming corals taxa in collaboration with US partners, those are important perspectives of development beyond ATLAS, that are planned to emerge during the iAtlantic project.

1 Context and objectives

1.1 Definitions of connectivity

Connectivity, in the broadest sense, is the multiplicity of links that can be established and maintained

Box 1.1: Definitions

Dispersion, migration: According to the Oxford Dictionary of Ecology, migration is "*The movement of individuals or their propagules (seeds, spores, larvae, etc.) from one area to another. Three cases may be distinguished (a) emigration, which is outward only, (b) immigration, which is inward only and (c) migration, which in the stricter sense implies periodic movements to and from a given area and usually along well defined routes. Such migratory movement is triggered by seasonal or other periodic factors (e.g. changing day-length), and occur in many animal groups*." (Allaby, 2010). While the latter part is the most famous definition, this reports deals with migration from one cohesive group (population) to another such group, thus encompassing both (a) and (b). In the genetic literature, dispersion and migration are defined as the movement of individuals or propagules between spatially discrete populations, followed by more or less long-term settlement in the new population (adapted from Cowen Sponaugle, 2009; Lowe et al., 2010).

Metapopulation : A system of local populations interacting with each other through the migration of individuals.

Local population or *Deme:* A group of individuals of the same species relatively close genetically, which geographical distribution is restricted to a given area. Groups more or less connected to each other (with greater exchanges among them than with other groups) constitute a metapopulation.

Evolutionary trajectory of a population: Development of a population over time under the joint influence of evolutionary forces (migration, mutation, drift and selection).

Management Units: populations of conspecific individuals among which the degree of connectivity is sufficiently low so that each population should be monitored and managed separately (Taylor Dizon, 1999)

Evolutionary Significant Units: a group of conspecific populations that have substantial reproductive isolation, which has led to adaptive differences so that the populations represent a significant evolutionary component of the species (Palsbøll et al., 2007).

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between entities in a network. In geography, connectivity is the property of a network to offer alternative routes between places.

The search for greater connectivity is generally linked to the desire to reduce the vulnerability of a space's accessibility to the risk of network link failure. In ecology, connectivity refers to the non-fragmentation of environments and landscapes. Cowen et al. (2007b) define connectivity among local populations as the exchange of individuals between these populations (also called demes), geographically separated, and forming a metapopulation (see Box 1 for definitions).

Most marine species exhibit a complex life cycle with several stages presenting distinct dispersal capabilities. In the case of rather benthic marine species (c.f. holobenthic and bentho-pelagic life cycle organisms here, Box 1.2 Figure 1), population connectivity includes the dispersal phase from

Box 1.2: Life cycles of marine organisms

Palumbi (2003) proposed that "connectivity is the extent to which populations in different parts of a species range are linked by the movement of eggs, larvae or other propagules, juveniles or adults". Three main types of life cycles characterize marine organisms and determines the extent of connectivity across their distribution range:

- The bentho-pelagic life cycle concerns the vast majority of marine organisms (Figure 1). Juveniles and adults live near the bottom, while eggs and pelagic larvae develop in the water column. It is usually the pelagic phase that mediates the connectivity.
- Organisms with a holobenthic life cycle have by definition a very small or non-existent pelagic phase (*e.g.* seahorses, amphipods and some isopods) often correlated with a low dispersion.
- Other organisms qualified as pelagic can migrate at all stages of their life cycle and potentially over long distances (*e.g.* marine mammals, many finfishes or planktonic species....).

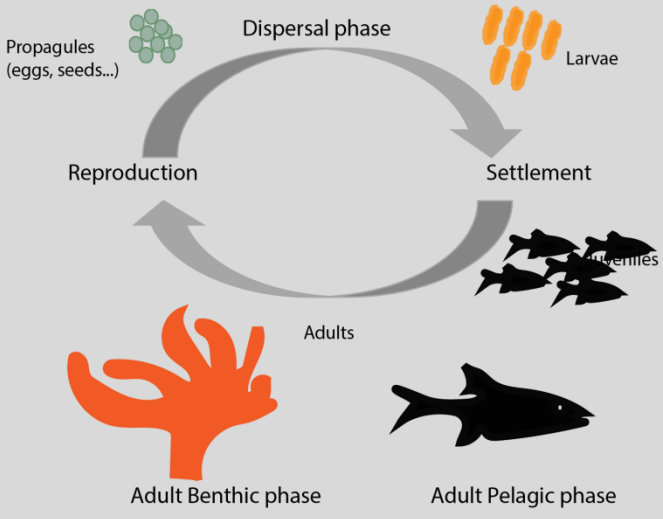


Figure 1 : Typical life cycle of marine organisms, most of them with a benthic adult stage compared to the dispersive developmental stages

reproduction to establishment of individuals (including habitat selection and metamorphosis). In the case of more pelagic species such as finfish, mammals or planktonic species, the adult stage is an additional stage during which individuals have the capacity to disperse over vast distances.

As a result, ecosystems shelter a diversity of organisms with different life histories that strongly differ as to the extent and pattern of their dispersal capacity, connectivity and levels of population structure across their distribution range. Reconciling this diversity of connectivity patterns in conservation plans is a challenge (Gaines et al., 2007; Moffitt et al., 2011). It requires the joint study of a diversity of organisms with distinct life-history traits such as those studied during ATLAS. In WP4, we studied benthic engineer species that structure habitats such as the deep-water corals *Viminella flagellum*, *Lophelia pertusa* and *Madrepora oculata*, the associated invertebrates *Eunice norvegica*, *Nephrops norvegicus* and *Cidaris cidaris*, the bentho-pelagic fish *Helicolenus dactylopterus*, but also pelagic species such as *Capros aper* and *Trachurus trachurus*).

The direct observation and study of migratory movements is almost impossible in the oceans due to i) the reduced potential to fully access the marine environment, ii) the often extremely large population sizes *sensu stricto*, and iii) the generally substantial migration distances, as adults or larvae. Limited prediction can be made on the migration distance based on life history traits, for no strict relationship was demonstrated between genetic differentiation and life-history traits suspected to influence dispersal potential (Riginos et al., 2011). Therefore, tracking and indirect inferences of connectivity patterns are needed. Systems allowing the direct estimates of spatial movements such as Mark-Recapture (MR) or electronic tags are at present realistic only for a very low proportion of marine species (mostly top predators and large pelagics – marine mammals, turtles, sharks, tunas and billfish). Indirect methods such as modelling of dispersal and population genetic inferences thus play a central role in the study of marine connectivity and were the two main approaches adopted in ATLAS.

1.2 Connectivity in ATLAS framework

The Atlantic is the second largest world ocean, with the Northern Atlantic representing about 11% of all Oceanic surface on Earth. It counts among the most impacted regions due to climate change and anthropogenic pressure, from commercial fishing to pollution, commercial shipping and ocean acidification (Halpern et al., 2008; Merino et al., 2014; Ramirez-Llodra et al., 2011). It also encompasses a variety of deep-sea ecosystems (Ramirez-Llodra et al., 2010) including seamounts, canyons, coral reefs, chemosynthetic ecosystems (hydrothermal vents and cold seeps) and sponge

gardens (Brooke et al., 2017; Henry et al., 2014b; Morato et al., 2013; Ramiro-Sánchez et al., 2019; van den Beld et al., 2017; Vanreusel et al., 2010). Thus far, the management of the resources and ecosystems it supports is fragmentary and incomplete. Within the Economic Exclusive Zone, conservation and management is entirely controlled by the relevant nation state. The mandate provided by the Convention for Biological Diversity is entirely dependent on national impetus to ensure that ratification is followed by action. Contrastingly, biodiversity in areas beyond national jurisdiction (BBNJ) is only protected by a very fragmentary governance framework (De Santo, 2018). Regional Fisheries Management Organizations (RFMOs) focus on the management of fisheries resources, for which the accurate delineation and management of stocks requires a better knowledge of migration routes, connectivity and population structures (Carvalho Hauser, 1994; Weiss et al., 2018). On the other hand, with the exception of some exploited resources (RFMOs for fisheries, the Authority for mining etc…), and a few regional initiatives (Rochette et al., 2014), biodiversity in areas beyond jurisdiction is thus far left without a governance framework to plan and ensure their conservation (Druel Gjerde, 2014). Agreeing on a governance framework to facilitate the development of Area Based Management Tools (ABMTs), among which are Marine Protected Areas (MPAs), is one of the four objectives of the ongoing negotiations at United Nations, triggered in 2015 (Resolution 69/292, Article 2, https://undocs.org/A/RES/69/292) after 10 years of preparatory meetings. While waiting for such legal framework to be in place, a few regional initiatives have proposed priority areas to design networks of MPAs based on scientific rationale. Both the International Union for Conservation of Nature (IUCN) and the CBD organized a series of scientific workshops to list the criteria relevant for prioritising Ecologically or Biologically Significant Areas for Conservation (EBSAs; Dunn et al., 2014). Although EBSAs are called to be constantly revised to incorporate new knowledge, it is still not entirely clear how they will translate into Marine Spatial Management (Dunn et al., 2014; Dunstan et al., 2016).

In this framework, the ATLAS teams have been contributing new knowledge on the distribution of biodiversity in the Northern Atlantic (both species and genetic diversity), habitat modelling and projections for habitat change under climate change for a handful of important VMEs and harvested species (Morato et al., 2020), and the adaptation of species to present and forecasted environmental conditions. Our findings clearly show that the design of MPAs and the management of exploited resources cannot be solely based on a static picture of the ongoing distribution of ecosystems, VMEs and harvested resources, but should integrate knowledge of its dynamics over space and time.

In this context, ATLAS aimed to gather as much information as possible on deep sea VMEs at the scale of the Northern Atlantic to feed into both biological and ecological knowledge, and also into

management plans that will develop in the forthcoming years under the intergovernmental governance framework being negotiated. In WP4, connectivity was studied to provide information to elaborate, adapt and improve 1) the conservation plans for species forming the basis of some emblematic VMEs, as well as associated species sheltered in these ecosystems, and 2) the management of fisheries resources for a set of heavily harvested species.

The four main objectives initially aimed at in ATLAS were to:

1. Identify source and stepping-stone areas that maintain meta-populations of VME indicator taxa, deep-sea fish species including those of commercial importance, and potential targets of Blue Growth fisheries.

2. Measure congruence between VIKING20/regional (Rockall Bank) models (WP1) and the realised connectivity of species (WP4) using population genomic approaches that consider phylogeographic and life history traits.

3. Understand whether fisheries and habitat loss have degraded exploited fish meta-populations.

4. Establish a new adaptive management framework that integrates meta-population genomics.

While the first three objectives were already tackled in previous deliverables, here we summarise these previously detailed results and focus on the way they apply to objective 4.

1.3 Connectivity and Conservation

Most species are discontinuously distributed across their distribution range, with groups of individuals forming populations more or less strongly connected by migration-mediated gene flow. The scale, distribution, and direction of migration-mediated gene flow are parameters defining 'connectivity'. It plays a major role in population and community dynamics both on the long and the short run (Hanski, 2005), by determining the demographic, ecological (Brown et al., 1977) and evolutionary (Orr et al., 2014; Tomasini et al., 2020) inter-dependency of populations (Armsworth, 2002; Cowen et al., 2009). Migratory movements allow the persistence of limited sized, temporarily demographically impacted (source-sink systems), or genetically impoverished (bottlenecked) populations. Dispersal capacity can also determine the ability for range shifts (Årevall et al., 2018; Huang et al., 2020; Parmesan Yohe, 2003). Connectivity thus strongly influences the species capacity to cope with spatially and temporally fluctuating environmental conditions and improves resilience. While population fragmentation is an important concern in conservation genetics of terrestrial species (Lindenmayer Fischer, 2006), the problem has long been neglected in the marine realm (Balbar Metaxas, 2019; Cowen et al., 2007a; Magris et al., 2014).

The resilience of an ecosystem is partly dependent on the connectivity that characterises the different species it supports (Cowen et al., 2007a; Kritzer Sale, 2004; McCook et al., 2009; Roberts et al., 2003). In the marine realm, the management of fisheries resources, the control and prevention of invasive species and the conservation plans for threatened species or vulnerable ecosystems thus require the knowledge of interconnection and interdependency of stocks, populations and communities constituting these ecosystems. Connectivity patterns are essential criteria to be included in marine conservation policies, both at the level of individual MPAs and at the level of national or international species conservation objectives, including the management of fisheries resources (Cowen et al., 2007a; Cowen et al., 2009; Kritzer et al., 2004).

Nevertheless, the creation of MPAs was, up to the 2000's, mainly influenced by local initiatives. In the framework of ecological coherence, the criteria of representativeness (hosting within the MPA network a representative selection of the biodiversity elements of the region under consideration) and adequacy (covering in sufficient proportion each biodiversity element to ensure their persistence) have guided efforts to deploy MPA networks. Subsequently, the establishment of MPAs was framed by the national strategies for their creation and management, and progressively incorporated, *a posteriori*, the notion of a coherent network with regard to the various targeted objectives (Andrello et al., 2013; Lagabrielle et al., 2014). However, both the way genetic diversity was distributed and thus represented in targeted area (Laikre, 2010; Laikre et al., 2010) and the spatial dynamics of biodiversity – i.e. connectivity – are still often neglected (Balbar et al., 2019; Magris et al., 2014).

Both Aichi *Target 11* and the United Nations *Sustainable Development Goal 14* (SDG14 to "conserve and sustainably use the oceans, seas and marine resources for sustainable development"), require moving from individual MPAs to regional and global MPA networks that ensure optimal coherence between both environmental and societal objectives. This is particularly relevant in the framework of ongoing negotiations on biodiversity beyond national jurisdiction (Blasiak Yagi, 2016; De Santo, 2018). Finally, the management of fisheries resources also needs to rely on improved knowledge of the stocks' delineation, dynamics and interactions, which can be provided by modelling and population genetics data (Casey et al., 2016; Ward, 2000).

The dynamic component of biodiversity should ideally integrate both the scale of generations, i.e. population connectivity, and the scale of decades, by predicting shifts in the range distribution of species (Johnson et al., 2018; Johnson and Kenchington, 2019). The possible modification of the physiology of dispersing stages under changing environmental conditions (Gerber et al., 2014), may also affect not only range distribution but also connectivity patterns. Both

generational and decadal perspectives were considered in ATLAS. First, modelled present-day habitat and forecast changes in species distribution due to climate change (D3.3; Morato et al., 2020) have been integrated in a modelling framework to design priority areas (D3.4; Combes et al., submitted), as suggested in WP7 (Johnson et al., 2018; Johnson et al., 2019).

Second, and this is the topic of the present report, connectivity was tackled in WP4 and at the interface between WP4 and WP1, by using two complementary approaches:

1. The modelling of "predicted" connectivity based on Lagrangian modelling of particles. Predicted connectivity was mostly inferred for those species showing a bentho-pelagic cycle (Box 1), in which larval dispersal is the key stage during which migration takes place, although larval movement can also be significant for pelagic species. The models developed relied on the knowledge of oceanographic dynamics synthetized and implemented in WP1, the predicted spatial distribution of species synthetized in WP3, and the knowledge of larval development (mostly duration and migration in the water column) when available (i.e. for *Lophelia pertusa*, Larsson et al., 2014; Strömberg and Larsson, 2017), to obtain more precise estimates (see D4.4). Generic approaches have also been undertaken to estimate the incidence of future climate changes on water masses and on connectivity patterns (D1.1, Fox et al., 2016), the effects of larval behaviour on dispersal and connectivity (D1.6, Gary et al., 2020), as well as the importance of human infrastructures susceptible to act as stepping stones for connectivity (Henry et al., 2018).
2. The indirect reconstruction of "realised" connectivity based on population genetics targeted two groups of species. First those species structuring VMEs, including *Lophelia pertusa*, *Madrepora oculata* (Boavida et al., 2019c) and *Dendrophyllia cornigera* or species associated to them (the polychaete *Eunice norvegica*); second, fish resources (the fishes *Helicolenus dactylopterus*, the boar fish *Capros aper* (Farrell et al., 2016), horse mackerel *Trachurus trachurus* (Farrell et al. In prep.) and the Norway lobster (Gallagher et al., 2019). These studies were initially based on microsatellites (Boavida et al., 2019c) and/or mitochondrial DNA (Gallagher et al., 2019). ATLAS partners also switched to Next Generation Sequencing (see D4.3) before or during ATLAS and by developing innovative genotyping by sequencing (GBS) using methods based on microsatellites (Carlsson et al., 2013; Vartia et al., 2016) or genetic resources based on genome scan -RAD sequencing (Boavida et al., in prep.).

Results obtained in those studies are summarised here with an attempt to emphasise the knowledge acquired both to integrate connectivity (and genetic diversity) into management plans, and to forecast future research paths to overcome the challenges discovered during the course of the project, particularly those that seem specific to the deep sea.

1.4 Objective of the present deliverable

The Deliverables have been remodeled during ATLAS, in order to adapt to the natural evolution of the project during its lifetime. The initially planned deliverables were D4.4 (Report on main life history traits and how they may affect dispersal), D4.5 (Genetic data analysis, maps illustrating network of connectivity for all species retained), D4.6 (Report on fish delimitation and demographic reconstruction) and D4.7 (Synthesis of connectivity patterns and guideline to integrate connectivity to management plans). These became D4.4 (encompassing D4.4, D4.5, D4.6 and the first half of D4.7) and the present D4.5 (Integrated management considering connectivity patterns, encompassing half the initial D4.7).

D4.5 thus relies on the synthesis of connectivity patterns provided in D4.4. Here we first provide a general summary of the crucial distinction between migration features affecting either the demography, the genetics of populations, or both. In the second part, we aim to propose a summary of the key knowledge required (already developed in D4.4), and of the challenges faced to predict (through modelling) or estimate (through population genetics, physical or chemical tagging methods) connectivity, particularly in the marine environment, with a focus on the deep sea. Finally, we summarize the knowledge acquired to define spatial areas of interest through modelling, or identify predicted (modelling) or detected (population genetics) management units and the way they are distributed in space for several species. These findings underline some relevant information for stock management, spatialized VMEs conservation measures, but also the caveats of each family of methods used to study connectivity. These results and blocking points open perspectives for future developments beyond ATLAS, some expected to emerge during the iAtlantic project.

2 Demographic and genetic connectivity: import and limitation of model predictions and genetic inferences

The two methods used by ATLAS partners to predict (hydrodynamic modelling) or estimate (population genetics) connectivity in ATLAS have different properties relative to these two kinds of connectivity. It is thus important to be able to fully understand the difference between genetic and

demographic connectivity, to interpret and combine the estimates of predicted and realized connectivity.

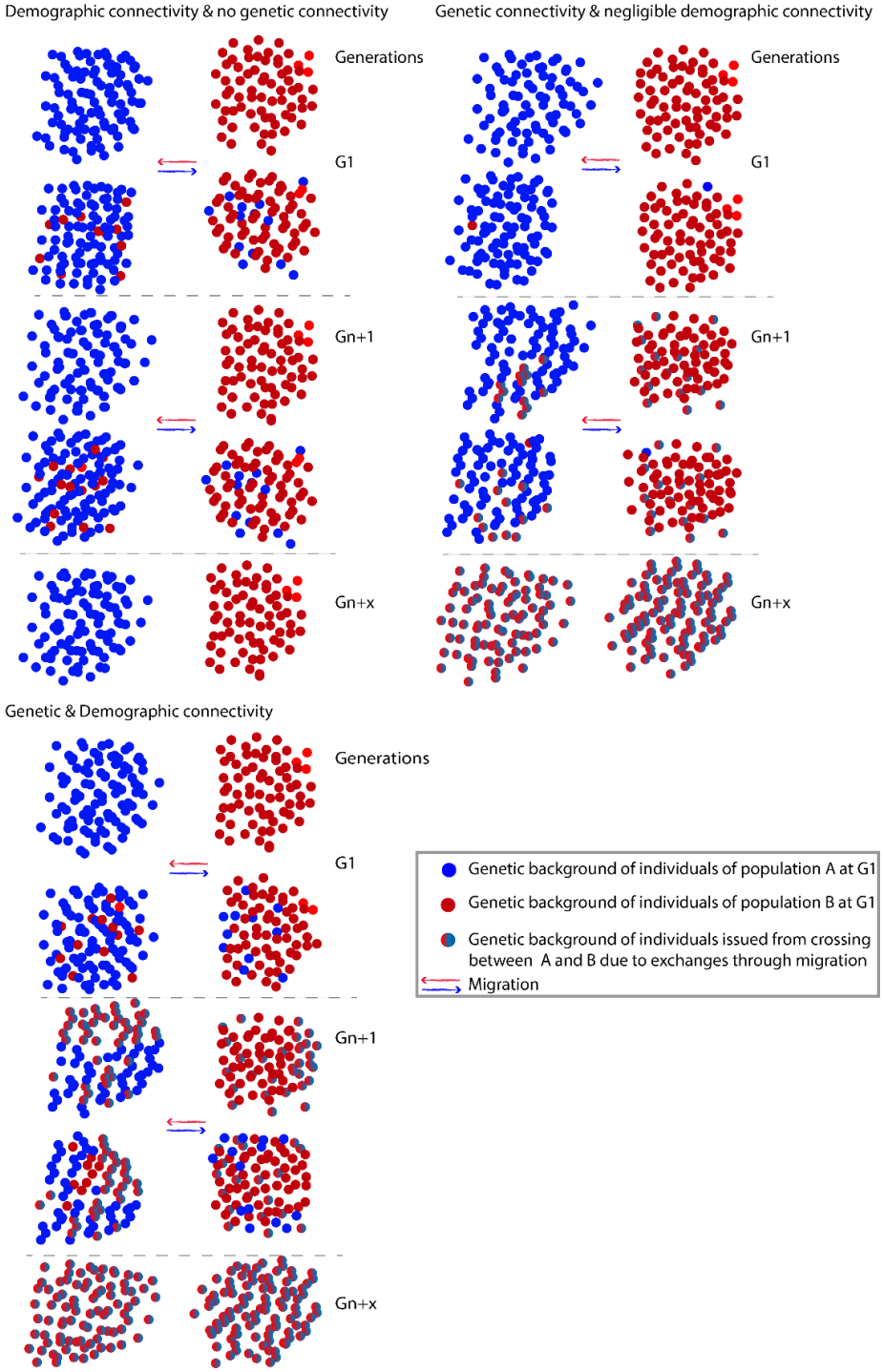
2.1 Demographic and genetic connectivity

In the marine environment, connectivity results from the movement of individuals or larvae among populations. The arrival of migrants in a new population has two coupled effects. The first effect, concomitant with the contribution of individuals to a population, is the possible modification of the dynamics of that population and is called "demographic connectivity". The second, longer-term effect occurs when migrant individuals successfully reproduce (i.e. offspring survival and retention in the host population) within the recipient population, and is called "genetic connectivity". While the first one reflects the potential for short term (demographic and ecological) rescue effect after local disturbance or depletion (Orr et al., 2014), the second is a key process for evolutionary rescue effect (Brown et al., 1977; Tomasini et al., 2020). Typically, demographic connectivity is of paramount importance to maintain critical population sizes and for facilitating exchange in metapopulation systems. Genetic connectivity is more important at longer time scales to ensure the evolutionary potential of populations and species. It influences the evolutionary trajectory of populations and increases the level of genetic variability present and maintained in the population. It also minimises the risk of inbreeding and facilitates local adaptation to environmental conditions by reducing genetic drift. Some of the methods used to assess connectivity will mostly inform on the demographic connectivity while others (such as population genetics), depending on the data obtained, can inform on the genetic and demographic connectivity. These two aspects of biological connectivity have an important role at different time scales and must be considered together in order to understand the connectivity framework of a given system in space, but also in time.

For individual contributions to influence demographics of the populations, the number of migrants must represent a significant proportion of the total number of individuals in the receiving population. Demographic connectivity can thus facilitate, or even be essential to the maintenance of a population (conservation of a sufficient density of individuals in a population to ensure that this population persists) and even guarantee the functioning of the ecosystem (maintenance of the functional role of the population, food web...). It has an instant effect at each migration event (Figure 1). It is therefore detectable on relatively short time scales. **The effect of migration on demography depends on the rate of migration**.

Genetic connectivity, contrastingly, occurs only if individuals migrate and successfully reproduce within the recipient population, hence contributing their genes to the next generation (Figure 1).

What determines genetic connectivity is not the rate of migration but the raw number of



exchanged migrants that successfully reproduce in the recipient population. It only takes a handful of successful migrants to maintain genetic connectivity (reflected in the relative homogeneity of gene pools between sub-populations) and prevent population differentiation. The observation of panmixia (i.e. lack of genetic differentiation) therefore suggests an homogeneous distribution of genetic diversity, but does not necessarily imply a sufficient input of migrants to modify the demographic dynamics of the receiving population.

Figure 1 : Illustration of the difference between demographic and genetic connectivity (adapted from Porro et al., 2019). In the first case, populations exchange a significant (10 to 15%) amount of migrants, yet those fail to reproduce in the recipient populations and each generation consists in a reset of the genetic structure of each population. In the second example, populations exchange a minimal amount (only 1 individual, less than 3% of the population size) of migrants but those reproduce successfully, leading to an homogenization of the genetic structure of populations despite the rate of migration is too low to significantly impact the demographic trend or reflect the possibility of a rescue effect. The third example combines effective dispersal (10 to 15% of allo-recruitment) and reproduction, leading to both demographic and genetic connectivity. Note that both scenario 2 and 3 lead to the same genetic outcome, making it difficult to disentangle them through population genetic analysis, unless using very powerful methods as genome scan coupled with Bayesian analysis of data.

The consequence of this discrepancy between demographic and genetic connectivity is **that the occurrence of genetic differentiation implies demographic independence of studied populations, whereas the absence of genetic differentiation (a situation called "panmixia") does not necessarily imply demographic interdependence** (Waples Gaggiotti, 2006). In fact, the latter can occur through the exchange of so few individuals that their migration does not significantly influence the demography of receiving populations, and is unlikely to counter any strong demographic event of collapse or local extinction through a "rescue effect". This situation as well as the time necessary for genetic differentiation to develop and become detectable have been called the "grey zone effect" (Bailleul et al., 2018) described on blue shark *Prionace glauca* using genetic markers (microsatellites and mitochondrial DNA). Many if not most marine populations often show such low levels of genetic differentiation due to large effective population sizes and consequently low genetic drift. In these situations, a significant amount of the genome needs to be screened to detect subtle population differentiation. It was thus suggested that Next Generation Sequencing based high-density genome scans (Box 2.1.1) be employed to detect population structure in situations where panmixia would only be apparent. At the difference of first generation population genetics relying on a handful of markers (often microsatellites and/or mitochondrial DNA), Genotyping by Sequencing (GBS, here developed on microsatellites for fishery target species to obtain several tens of microsatellites) increases the power to detect subtle differentiation. One step beyond in the density of the genome analysed, and thus the statistical power, genome scan is defined as "…genetic research method in which the entire DNA of an organism is searched systematically for locations on the chromosomes that are inherited in the same pattern as a specific trait…." ("Genome Scan," 2006). A much higher resolution is expected from those methods such as RAD-Sequencing, as they can allow detection of even low levels of genetic differentiation corresponding to demographic independence, and thus important to account for in management and conservation plans. The advantage of high density genome scans was recently confirmed on blue shark, where "DarT-RAD sequencing allowed identifying genetic differentiation initially undetected " (Bailleul et al., 2018) between Indo pacific

versus Atlantic-Mediterranean groups of samples, as well as between Northern and Southern Atlantic (Nikolic et al., in prep.).

Box 2.1.1 : Why genome scan analysis ?

Empirical population genetics started to develop in the early 90s based on the access to sequencing data, and were thus mostly based on single markers, often mitochondrial loci, for their ease of amplification and sequencing. Soon after, nuclear markers were developed, which are among the widely used microsatellites, most often analysed using up to ten or twenty markers, thus mostly targeting ten to twenty bits of the genome (loci). Early results clearly showed that the initial widespread expectation of genetic homogeneity due to large scale dispersal in the sea were mostly driven by the ignorance of the nature of barriers to gene flow (Vermeij, 1987). Over the years, however, it also became clear that populations were characterized by large size, and large scale dispersal due to the life cycle of most marine species (either pelagic or bentho pelagic, see Box 1.2). As a result, genetic differentiation could at most be extremely mild, thus requiring much more power to detect it than given by a handful of markers. In fact, the low differentiation and the time lag required to detect any disruption to gene flow leading to demographic independency was illustrated and characterized as the “grey zone effect”. This effect, analogous to the grey zone of species differentiation (de Queiroz, 2005) at the population scale , was introduced and exemplified on blue shark where panmixia (the absence of genetic differentiation) was reported at the scale of 5 oceans based on 8 microsatellites and one fragment of mitochondrial DNA (Bailleul et al., 2018). As suggested by these authors, scaling up from 9 fragments of the genome (9 loci) using first generation population genetics data to 36,000 using genome scan allowed detecting mild genetic differentiation among oceans (Nikolic et al., in prep.). Despite being mild, such genetic differentiation does imply demographic disconnection/independency that shall be accounted for in management plans (Nikolic et al., in prep.).

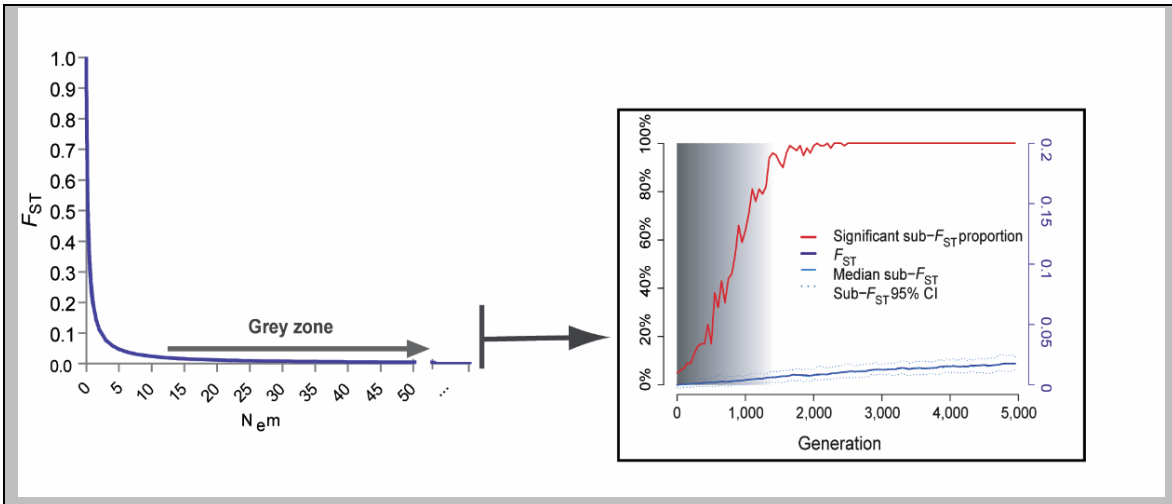


Figure 2.1.1: Illustration of the "population grey zone" adapted from Bailleul et al. (2018). On the left, the relationship between the index of genetic differentiation (F_{st}) and the raw number of migrants (N_em) exchanged between two populations, illustrating the very quick drop in F_{st} values for levels of exchange too low to ensure demographic connectivity. On the right, results of simulations for populations with effective population sizes of 100,000 and exchange of one migrant only per generation. This plot illustrates the very large number of generation necessary to capture with a high level of probability (left axis, red line) the signature of population differentiation based on F_{st} estimates (right axis, blue line with 95% confidence intervals in dotted lines) with a handful pf markers.

In the framework of ATLAS, dealing with species exhibiting pelagic (fishes) and bentho-pelagic (corals and polychaetes) cycles, differentiation was likely to be mild; an assumption confirmed by the first studies using first generation population genetic markers (Boavida et al., 2019a; Boavida et al., 2019b; Boavida et al., in prep.-a). Therefore, UCD targeted GBS, and Ifremer teams targeted genome scan analysis in order to obtain high-resolution data and detect genetic differentiation, even in the cases it was mild, to understand the demographic independence along European coasts and inform conservation and management plans. This required development of new protocols for genome scan, but also for specimen preservation and DNA extraction, whose quality and yield has to be several order of magnitude higher than the one required thus far (see Box 4.1.3). One method to ensure microsatellite enrichment was developed at UCD (Farrell et al., 2016), leading to several hundred microsatellites loci being analysed for the boarfish *Capros aper* and the detection of several management units, and is being applied on the horse mackerel *Trachurus trachurus*. The Ifremer team developed RAD Sequencing protocols on 11 species, delivering tens of thousands of SNPs (Single Nucleotide Polymorphism) markers along their genomes (D4.3 and Boavida et al., in prep).

1. G. Vermeij, The dispersal barrier in the tropical Pacific: implications for molluscan speciation and extinction. *Evolution* **41**, 1046-1058 (1987).
2. K. de Queiroz, Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences* **102**, 6600-6607 (2005).
3. D. Bailleul *et al.*, Large-scale genetic panmixia in the blue shark (Prionace glauca): A single worldwide population, or a genetic lag-time effect of the "grey zone" of differentiation? *Evolutionary Applications* **11**, 614-630 (2018).

4. N. Nikolic *et al.*, Overcoming the grey zone effect for fisheries management: genome scan analysis reveal interoceanic differentiation in blue shark populations. (in prep.).
5. J. Boavida, R. Becheler, A. M. Addamo, F. Sylvestre, S. Arnaud-Haond, in *Past, Present and Future of Mediterranean Cold-Water Corals,* C. O. C. Jiménez, Ed. (Springer, 2019), pp. pp357-372.
6. J. Boavida *et al.*, Out of the Mediterranean? Post-glacial colonization pathways varied among cold-water coral species. *Journal of Biogeography* **46**, 915-931 (2019).
7. J. Boavida *et al.*, A taxonomic revision and an assessment of connectivity of the commensal polychaete Eunice sp. associated to cold water corals along the European margins., (in prep.).
8. E. D. Farrell, J. E. Carlsson, J. Carlsson, Next Gen Pop Gen: implementing a high-throughput approach to population genetics in boarfish (Capros aper). *R Soc Open Sci* **3**, 160651 (2016).

2.2 Inferences using genetic data

The objective of population genetics methods applied to connectivity is to delineate biological entities that are demographically independent (e.g. differentiated populations) that would correspond to distinct management units, MUs (Palsbøll et al., 2007), if existing, and to locate barriers to gene flow, or preferential pathways of migrations among those populations. In a system significantly differentiated and well sampled, further analysis could allow the assigning of migrants to their most likely population of origin (if present in the sampling) through *assignment tests* (Paetkau et al., 2004).

As mentioned above, genetic data allow for unravelling genetic differentiation and identifying the contribution of distinct subpopulations as well as barriers to gene flow. In many cases in the marine environment, the first generation (such as mitochondrial DNA and a handful of nuclear microsatellites) of molecular markers did not ensure the power needed to detect mild levels of population structure, despite these implying important demographic independence among populations (Bailleul et al., 2018; Waples et al., 2006). Advances in molecular biology have made it possible to access increasingly dense sets of markers along the genome, including protocols of genotyping by sequencing and genome "scans" such as RAD Sequencing, allowing the development of methods that provide such statistical power.

Advantage: Population genetics analysis allow an indirect assessment of movements impossible to track either through direct observation or through tagging. With high-resolution markers, it can also allow estimating the direction of dispersal, and disentangling the signature of past from present day migration. Besides connectivity, population genetic data also provide information relevant for conservation such as the distribution of genetic diversity (Laikre, 2010; Laikre et al., 2010), as well as the occurrence of cryptic species, common in the marine environment (Pante et al., 2015a; Pante et al., 2015b).

Limits: 1) Sites and individuals sampling constraints, and sample representativity. Population genetics approaches rely on the availability of a representative sampling both in terms of sites across the distribution range and of number of individuals per site, which is a challenge in the deep sea. This aspect clearly explains the strategy initially chosen by ATLAS partners, which consisted in defining *a priori* a pool of "candidate species" listed in the proposal based on their life-history and ecosystem services (engineer, common species, fisheries resources….). This strategy allowed selecting *a posteriori* the ones for which a sufficient sample pool could be secured prior to or during the first years of the project. 2) Genome sampling constraints and statistical power. Population genetics allows estimating the levels of "realized connectivity", which is the level of gene flow (implying dispersal and settlement) and genetic mixing (implying effective reproduction in the recipient population) only in the cases where genetic differentiation can be detected. In order to optimise statistical power and detect even mild genetic differentiation, the teams involved in ATLAS have developed genomic resources to allow genome scan or genome scan "like" analysis, either through massive microsatellite GBS (Carlsson et al., 2013; Vartia et al., 2016) or through RAD sequencing delivering thousands of Single Nucleotide Polymorphism (SNPs) along the genome (D4.3, Boavida et al., in prep).

2.3 Predicted *versus* realized connectivity

Well-informed particle dispersal modelling can allow predicting "potential larvae connectivity" the rate of potential self-recruitment (i.e. the recruitment of larvae in the place they were emitted) versus potential allo-recruitment (i.e. the recruitment of larvae coming from another area/population) .

Larval dispersal models (see D4.4) are used to simulate propagules (eggs and/or larvae trajectories). From these trajectories, one can quantify the amount of individuals transported from the origin sites (source/egg laying) to the destination sites (recipient/recruitment site), i.e. connectivity in the propagule phase. Larval dispersion models are generally referred to as biophysical, in the sense that they include the most important physical and biological processes of larval life: transport (advection

and diffusion) from the site of origin, growth, behaviour, survival, settlement at the settling site. These different processes involve parameters, such as the duration of the larval phase for transport, growth rate, survival rate, migration in the water column, etc.

The first step is to define the area that will be studied and modelled. For most species only the distribution range is known (at best), without a good knowledge of habitat within this area. A grid approach is performed where all grids of the distribution range have equal chances to emit propagules and the outcome only depends on current and biophysical variables affecting trajectories. Ideally, however, propagules should be emitted only from sites where the species is actually occurring, and propagule modelling should be based on habitat distribution models to define emitting areas. This approach was adopted within ATLAS for a set of species for which both predictive habitat mapping and knowledge on larval development (see below for limits) were available (*Lophelia pertusa*).

Advantage: Modelling is an exploratory method that allows, at a lower cost, prediction of the relative importance of intrinsic and extrinsic factors on dispersal and, depending on data available, the evolution of this process in time and space under changing environmental conditions. It offers the possibility to simulate dispersion for a multitude of environmental conditions and emission sites, as well as larval behaviour and development duration.

Limit: 1. Accuracy depends on habitat, reproductive and larval data available. The accuracy of habitat models is as good as the sets of observation they are built with, and the challenge to obtain observations and the extremely fragmentary nature of data in the deep sea must be acknowledged. Besides, even good knowledge of larval development in controlled conditions, which are especially challenging to obtain on deep-sea species due to their poor rate of survival outside their environment, does not necessarily accurately reflect the larval development in natural conditions. 2. Prediction is about potential movements only. Modelling cannot predict the viability of propagules in the recipient population they are susceptible to reach (i.e. will they settle and survive?). Nor does it allow prediction of their contribution to the gene pool of the recipient population and its evolutionary fate (will they successfully reproduce?). In other words, whereas a lack of connectivity through larval modelling could, provided it is based on a reliable and comprehensive set of parameters, be interpreted as a need for improvement in a network of MPAs (Andrello et al., 2013; Kenchington et al., 2019), predicted connectivity does not necessarily equate to realized connectivity. Information gaps met generally include:

- the quality and density of field observations of the distribution and range, and therefore the quality of predictive habitat mapping and thus

-the knowledge of propagule release (date, periodicity, number), behaviour, survival and the duration of the dispersal stage.

-the quality of oceanographic models along the water column down to the deepest areas.

3 Predicted connectivity knowledge for conservation and management:

Within ATLAS, Lagrangian modelling of larval dispersal has made notable contributions to five published papers (Fox et al., 2019; Fox et al., 2016; Gary et al., 2020; Henry et al., 2018; Spooner et al., 2020) and five ATLAS deliverables (4 science deliverables: D1.1, D1.6, D3.4, D4.4; one policy Deliverable D7.4). This work covers investigation of the effect of long-term ocean variability (Atlantic Meridional Overturning Circulation - AMOC, subpolar gyre strength - SPG and North Atlantic Oscillation - NAO) and larval behaviour on particle transports and population connectivity, the contribution of man-made structures to connectivity, and the application of these results to marine planning and the development of ecologically coherent marine protected area networks. Here, we briefly summarise the main results of this work, which contributed to WP4 Objectives 1, 2 and 4.

3.1 Dispersal and connectivity

Fox *et al.* (2016) showed how larval longevity and behaviour mediated dispersal and connectivity, with shorter lived and passive larvae associated with reduced connectivity, and longer-lived larvae which spend more time at the surface associated with increased connectivity. Within these behavioural categories, trajectories of *Lophelia pertusa* larvae were strongly correlated to the NAO. Variability in trajectories significantly altered network with positive phase NAO conditions producing a well-connected but asymmetrical network connected from west to east. Negative phase NAO produced reduced connectivity, but notably more larvae tracked westward-flowing currents towards coral populations on the mid-Atlantic ridge.

Henry et al. (2018) investigated the potential for anthropogenic structures in the ocean to enhance connectivity of a protected species threatened by human pressures and climate change. Biophysical dispersal models of a protected coral species simulated potential connectivity between oil and gas installations across the North Sea and naturally occurring corals downstream. These results provide the first study showing that a system of anthropogenic structures can have international conservation significance by creating connected networks and acting as paths between natural populations.

In ATLAS D1.1, we used Lagrangian tracking in the 1/20-degree Viking20 model. The Lagrangian dispersal shows large variability on seasonal to annual timescales. Much of this is due to the chaotic nature of the mesoscale eddy field, and variability on these timescales was not found to be correlated either between Case Study regions or with AMOC or NAO variability. The only Case Study region to exhibit evidence of a regular seasonal cycle in the extent of the pathways was East Mingulay, with stronger westward propagation from spring releases. At lower frequencies, some of the temporal changes in dispersal appear to be a response to decadal-scale changes in the AMOC, especially for the Case Studies in the eastern subpolar North Atlantic. These were not extreme shifts in the structure of Lagrangian pathways, rather we have found times when particles spread a little more or less compared to other times, but these changes are relatively small compared to the overall spreading envelopes. This last observation is consistent with analysis of Viking20 near-bed Kinetic Energy from an Eulerian perspective reported in ATLAS D1.2.

The core of the ATLAS modelling work on dispersal is presented in Gary *et al.* (2020), and D1.6. We hypothesise that the vertical swimming ability of deep-sea larvae, before they permanently settle at the bottom, is one way larvae can control dispersal. We test this hypothesis with more than $3x10^8$ simulated particles with a range of active swimming behaviours in the Viking20 model. Despite much stronger horizontal ocean currents, vertical swimming of simulated larvae can have an order of magnitude impact on dispersal. These strong relationships between larval dispersal, pathways, and active swimming demonstrate that lack of data on larval behaviour traits is a serious impediment to modelling deep-sea ecosystem connectivity. Such data are hard to gather and could only be obtained for a handful of species within ATLAS framework (Box 3.1). This uncertainty greatly limits our ability to develop ecologically coherent marine protected area networks. The influence of larval behaviour on predicted dispersal dominates over the relatively small changes due to AMOC or NAO described above. Larval retention in suitable habitat was predicted to be inversely proportional to dispersal area, this suggests that processes which reduce dispersal (e.g. possible weakened AMOC in the eastern subpolar North Atlantic) will increase short-range connectivity, while decreasing long-range connectivity. In meta-population studies these two scales of connectivity can be crudely considered to be proxies for habitat quality (short-range) and resilience, or the ability to recover from catastrophic damage (long-range).

Box 3.1 Challenges in obtaining data on reproductive and larvae biology of cold-water corals

Connectivity models for cold-water corals (CWCs) greatly depend on information about species reproductive strategies and larvae traits, including mode of reproduction, oocyte size and reproductive seasonality and the nature, duration and behaviour of larvae. This information is

essential to accurately select the oceanographic data to use in models in terms of season when dispersal can take place and define confidence intervals for its duration, depth of currents to be considered, and account for the ability of larvae to mitigate or enhance their influence through active dispersal.

Nevertheless, information on the reproductive and larvae biology of CWCs is scarce with reproduction studies published for 20 species, and larvae biology known for only 6 species (summarized in D4.4). This is related to different factors, including: (1) remoteness of deep-sea communities and complicated logistics associated to their sampling; (2) uneven sampling through seasons for reproductive seasonality (most samples are collected during summer when weather is good); (3) time and expertise requirements for histological techniques applied to reproduction studies. In CWCs there is often no sexual dimorphism, therefore, gametes can only be observed after fixation and decalcification and through histological processing. Moreover, even after processing, collection of reproductive data is not guaranteed, as samples might come from reproductively immature or inactive colonies. Larvae biology studies are also challenged by difficulties in inducing spawning, fertilization and rearing cold-water coral larvae at atmospheric pressure in aquaria (Orejas et al., 2019). Methods used for some shallow water species, e.g. marking and recapture of larvae, are not possible to use in the deep sea and sampling of material for e.g. genetic structuring is logistically difficult and very expensive.

Despite these difficulties, ATLAS partners characterized the reproductive biology and gametogenic cycle of four CWC species that form important Vulnerable Marine Ecosystems in the Mediterranean (*Dendrophyllia cornigera* and *D. ramea*) and the Azores (*Dentomuricea* aff. *meteor* and *Viminella flagellum*), for which no reproductive studies had been previously conducted. The studies used samples collected over several years during scientific expeditions financed by different projects or as by-catch from commercial deep-sea bottom longline fisheries (in Azores), highlighting the great effort necessary to collect enough sampling material for reproductive studies.

During ATLAS, we have also successfully induced spawning and reared larvae of the octocoral *Viminella flagellum* under aquaria conditions in the Azores. This was the first time that the larvae biology of a deep-sea octocoral has been studied and data produced used in connectivity modelling studies. Model results showed how the shorter pelagic larvae duration of *V. flagellum* in comparison with the well-studied *Lophelia pertusa,* can decrease the dispersal ability of species, emphasizing the need to better study larvae biology of a broad range of species.

Advances in ocean technology, including autonomous methods for biological sampling at the deep seafloor (e.g. Brandt et al., 2016) and improved aquaria methods and conditions for larvae rearing (Orejas et al., 2019) will accelerate knowledge on life history of deep-sea species in the near future.

Brandt, A., Gutt, J., Hildebrandt, M., Pawlowski, J., Schwendner, J., Soltwedel, T., & Thomsen, L. (2016). Cutting the umbilical: new technological perspectives in benthic deep-sea research. *Journal of Marine Science and Engineering* , *4* (2), 36;

Orejas C et al (2019). Cold-Water Coral in Aquaria: Advances and Challenges. A Focus on the Mediterranean. In Covadonga Orejas & C. Jiménez (Eds.), Mediterranean Cold-Water Corals: Past, Present and Future. Coral Reefs of the World, vol 9. Springer, Cham.

Recognising the serious impediment to modelling deep-sea connectivity presented by these new results on larval dispersal, an ATLAS workshop, including international invited participants from outwith ATLAS, was convened in January 2019 to identify species of interest within ATLAS for which

we had enough information on life history traits and habitat distribution to usefully model connectivity for ATLAS D4.4. The workshop identified only 3 species with enough information to model: Scleractinian CWC *Lophelia pertusa*, Octocoral *Viminella flagellum,* and fish *Helicolenus dactylopterus.* Present conditions were modelled for all three and future conditions – using Viking20 dispersal estimates but predictions of habitat in 2081-2100 (see ATLAS D4.4 for details) – for *L. pertusa* and *H. dactylopterus.* With severe caveats around larval behaviours and basin-scale habitat maps, the results suggested that for widespread species, with larvae drifting higher in the water column, a 60-day PLD is sufficient to keep the whole meta-population strongly connected, and could allow recolonisation of the whole basin from any single refugia anywhere in the basin. But for species with shorter PLD – less than about three weeks with drifting throughout the water column – connectivity appears much weaker with potentially isolated populations.

3.2 Management and decision-maker assistance

Fox *et al.* (2019) developed an efficient connectivity-based method for multi-objective optimisation applicable to the design of marine protected area networks. Multi-objective network optimisation highlighted previously unreported step changes in the structure of optimal subnetworks for protection associated with minimal changes in cost or benefit functions. This emphasises the desirability of performing a full, unconstrained, multi-objective optimisation for marine spatial planning. A metaheuristic method based around Markov Chain Monte Carlo methods is described which searches for the set of Pareto optimal networks given two separate objective functions. The shape of the Pareto front provides useful information for decision-makers, which is typically not available from more local target-driven optimisation methods. The optimisation and search methods are independent of the choice of objective. Results using network average shortest path as a proxy for population resilience and gene flow within the network support the use of a conservation strategy based around highly connected clusters of sites.

4 “Realised” connectivity as estimated through population genetics

Within ATLAS, population genetics has made several contributions with 5 published articles (Boavida et al., 2019b; Farrell et al., 2016; Gallagher et al., 2019; Puerta et al., 2020; Taylor Roterman, 2017), one book chapter (Boavida et al., 2019a) and contributions to D4.2, D4.3 (Boavida et al., in prep.-b) and D4.4 (Boavida et al., in prep.-a). These works allowed the investigation of population differentiation of fisheries resources and species structuring VMEs along the Mediterranean and

Northeastern Atlantic coasts, underlining the lack of population genetics data in the deep sea, developing genomic resources for a dozen deep-sea species. One also confirmed the influence of environmental changes in the present-day distribution of reef building species and associated invertebrates, a result accounted for in D3.4 also being prepared as an article (Combes et al., in prep.). These contributed to the objectives 1, 3 and 4 initially listed for WP4.

4.1 Benthic species with movements limited to the larval phase

First results published are based on first generation population genetics data on *Madrepora oculata* and *Lophelia pertusa* as well as on *Eunice norvegica* (see D4.4 and Boavida et al., 2019a; Boavida et al., 2019b). Among the most important findings relevant to conservation are detailed here below.

4.1.1 Past climatic changes have strongly affected the distribution range of both reef building species.

For both species, the genetic differentiation supported the hypothesis (De Mol et al., 2011; Frank et al., 2011) of post-glacial recolonization of the North East Atlantic from glacial refugees, at a depth suggesting the Mediterranean Outflow Water may have acted as a conveyor belt (Boavida et al., 2019b; Henry et al., 2014a).

This finding supports the need to account for climate change forecast in the habitat mapping predictions (which was done in ATLAS publication from Morato et al., 2020), and the possible physiological changes in the dispersal stage (Álvarez-Romero et al., 2018; Munday et al., 2009; O'Connor et al., 2007) for modelling predicted connectivity (also accounted for in ATLAS publication from Fox et al., 2016). These changes were included in the prioritisation of conservation areas (D3.4; Combes et al., in prep.), showing that integrating connectivity leads to favour the selection of pairs of Priorized Units (PUs) with high connectivity between them, maximising the retention of larvae in the prioritized network (Figure 4.1.1). One of the main conclusions of this work was that substantial network improvement could be achieved in the North Atlantic by extending MPAs to enhance self-recruitment, or creating new ones in adjacent zones that are likely sources or recipients of recruits for benthic species, to enhance the within-network exchanges and hence the overall resilience (Kenchington et al., 2019; Ross et al., 2017).

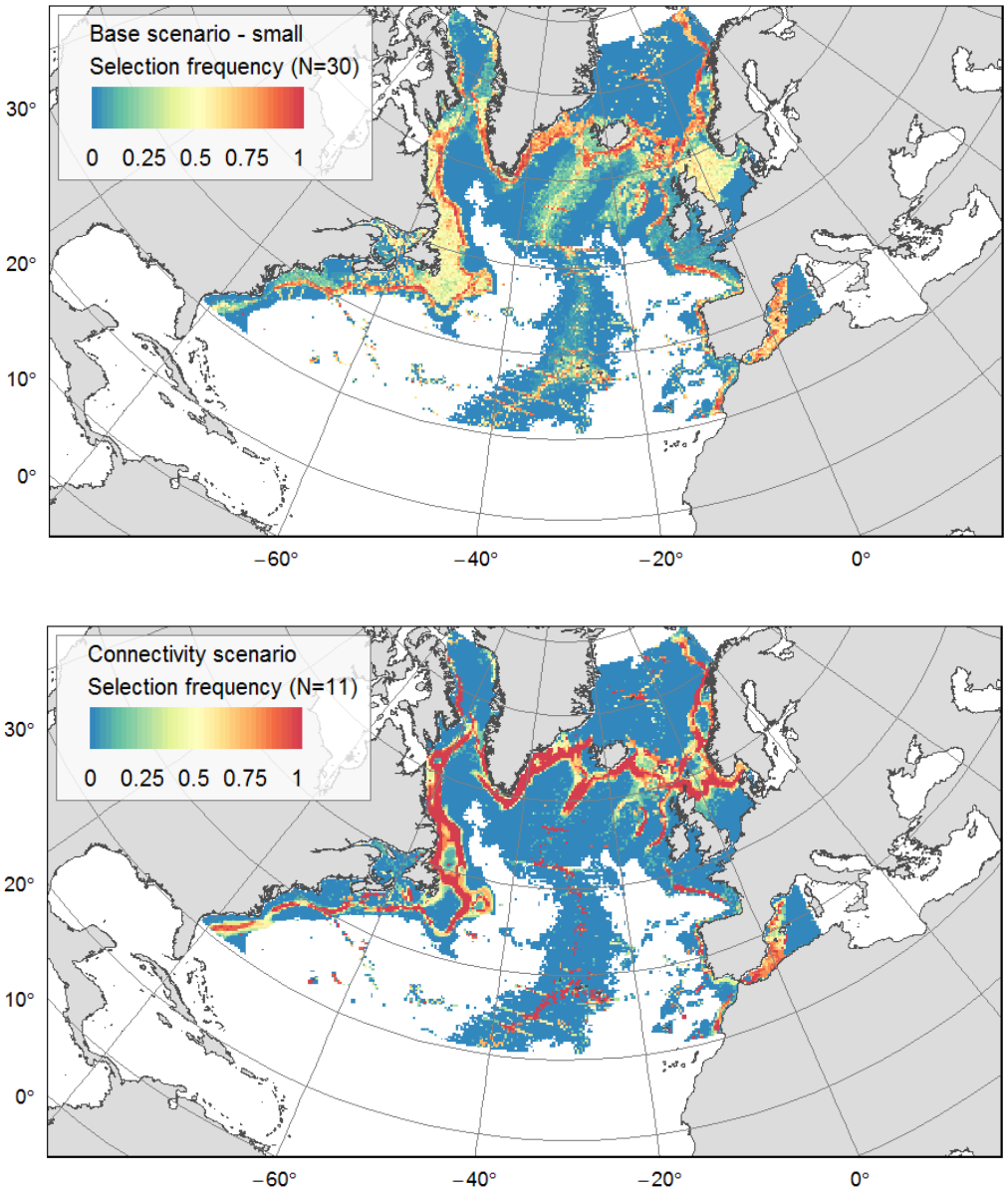


Figure 4.1.1. Output of scenarios not accounting for (upper panel) or accounting for (lower panel) connectivity: map of PU selection frequency across the N solutions, illustrating the preferential selection, when accounting for connectivity assuming a rather conservative Pelagic Larval Duration of 20 days, of pairs of PUs with high connectivity between them, maximising the retention of larvae in the prioritized network.

4.1.2 Differentiation between the Atlantic and the Mediterranean

For all species, the Mediterranean and Atlantic populations exhibit a high level of differentiation supporting the existence of distinct Management Units in the Atlantic and the Mediterranean, with no rescue effect to be expected from one another in case of local extinction. This is particularly strong for *Eunice sp.* where a cryptic species have been detected, *E. norvegica* being present in the Mediterranean and Norway, and also but sporadically in Ireland and Iceland,

while a second, likely still undescribed, species is spanning all Atlantic coasts from the Bay of Biscay to Iceland (Boavida et al., in prep.-a).

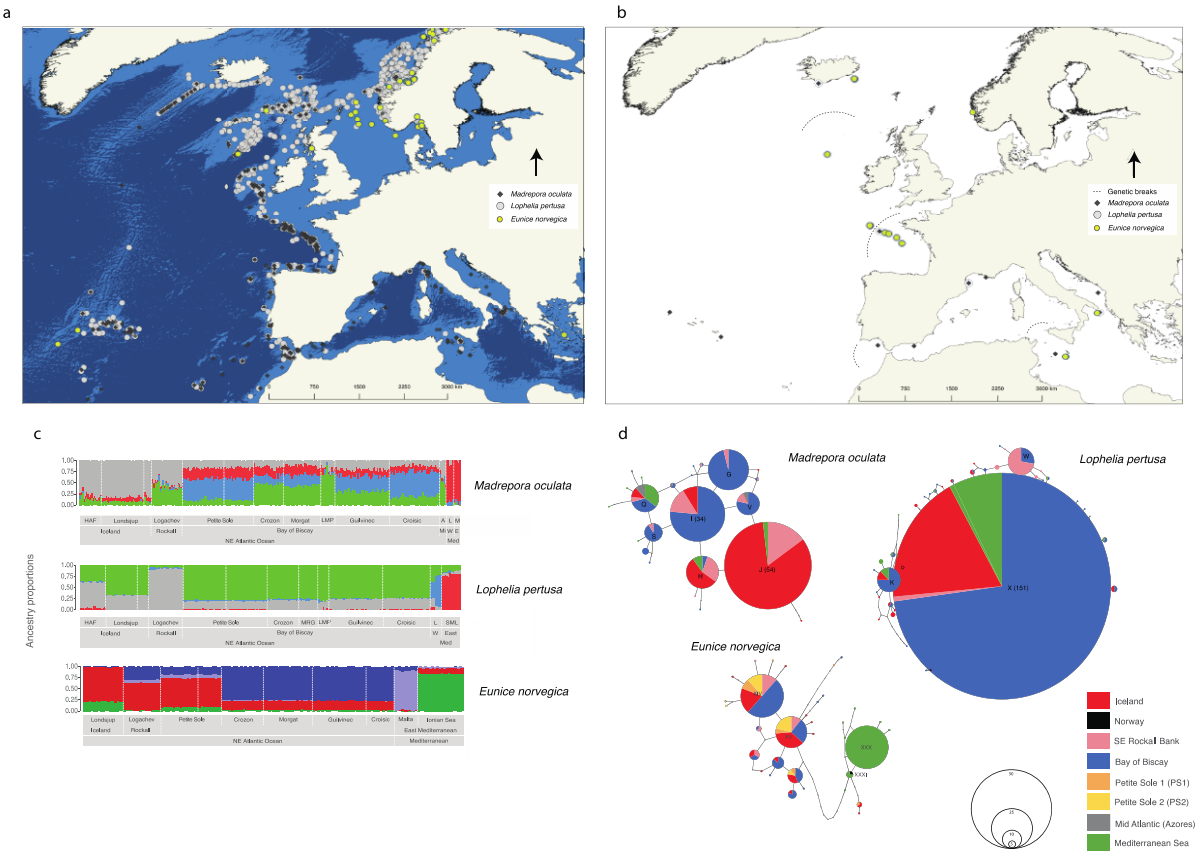


Figure 4.1.2: a) Contemporary distribution of the cold-water corals Madrepora oculata *(black diamonds),* Lophelia pertusa *(grey circles) and their commensal polychaete* Eunice norvegica *(yellow circles) in the NE Atlantic (data from 2017 UNEP database; http://data.unep-wcmc.org and 2019 GBIF https://doi.org/10.15468/dl.1rk01w); b) Sampling sites; c) Bayesian clustering showing the ancestry proportion of each species along the NE Atlantic Ocean, for K=4 genetic groups estimated by cross-validation with tess3r package based on 6-8 microsatellite loci; each vertical bar corresponds to one individual's genetic ancestry; four colour-coded genetic ancestries are shown; d) Statistical parsimony networks estimated on TCS with internal transcribed spacer sequences for* M. oculata *(1,124 base pairs) and* L. pertusa *(1,130 bp), and mitochondrial cytochrome oxydase I sequences for* E. norvegica *(499 575 bp). Abbreviations as follow: HAF - Hafadsjup, LMP - Lampaul canyon, L - Lacaze-Duthiers canyon (Gulf of Lion), W / E - Western / Eastern Mediterranean Sea, A - Azores, M - Montenegro (Adriatic Sea), Mi - Mid Atlantic, SML - Santa Maria di Leuca reef Atlantis (Ionian Sea). *Mediterranean sea - all Mediterranean samples were pooled together in M. oculata and L. pertusa network analyses. Maps created on QGIS with Mollweide's equal area projection. c) and d) adapted from Boavida et al. (2019a).*

At the scale of the Atlantic and the Mediterranean contrasted patterns of genetic differentiation emerge with *L. pertusa* exhibiting genetic panmixia (lack of detectable population structure) in the Bay of Biscay, except for reefs of the Irish Sea, while *M. oculata* shows distinct genetic backgrounds at the within basin scale (Figure 4.1.1). While the results for *M. oculata* do suggest demographic independence of populations distributed in the Mediterranean, Bay of Biscay, Ireland and Iceland, that should be treated as independent units for conservation and management,

L. pertusa show a typical grey zone effect (Bailleul et al., 2018) along the Bay of Biscay, from which demographic inter (in)dependence cannot be inferred. For the two coral species, genome scan data are therefore needed to ensure the taxonomic status of *M. oculata* (and test for the existence of cryptic species that is suggested by the co-occurrence of distinct genetic background in some canyons). They may also provide statistical power to detect genetic differentiation of *L. pertusa* at the scale of the Bay of Biscay, if existing.

Similarly to the deep-water corals, the Norway lobster *Nephrops norvegicus* have a planktonic larvae phase with the adults showing limited dispersal capacity. Further, the adults require specific soft bottom habits for settling that is patchily distributed. Hence, the management of this harvested species has been focused on small patches of habitat without taking larvae mediated connectivity into account. The ATLAS team analysed *Nephrops norvegicus* sampled throughout the distribution using both mitochondrial DNA sequences and GBS of nuclear DNA microsatellite markers. Results illustrated a clear cut between the Mediterranean and Atlantic populations, with further population structure within the Atlantic range. There was a clear mismatch between current small-scale management and the genetic based structure with population units occupying much larger geographical areas that encompass several management units. While the current management is based on adults as the individual patches of suitable habitats are clustered into small management units, the genetic data takes into account the larvae mediated gene flow and demonstrated that several current management units should be combined to allow for management on population scales. The larger geographical spread of the population based management units can also explain the lack of genetic bottlenecks in the analysed samples as each population includes more individuals than the previous management units would indicate (Figure 4.1.2).

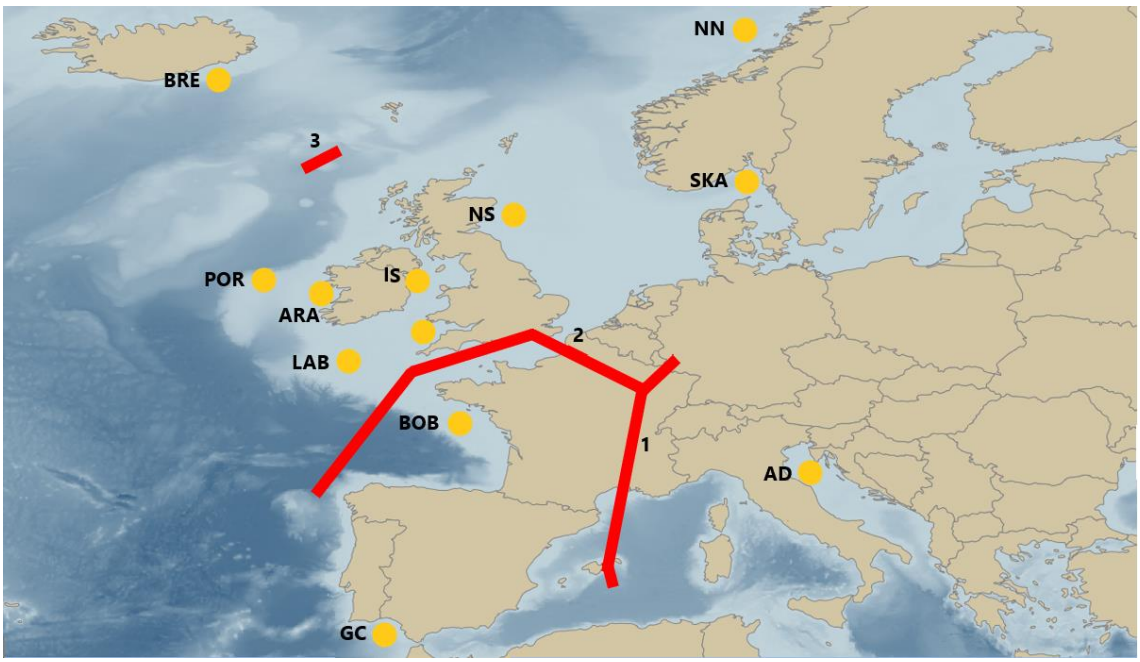


Figure 4.1.2: Potential genetic barriers to gene flow detected using microsatellites for Nephrops norvegicus *detected with a bootstrap support over 70. Sample sizes: AD 86, ARA 95, BOB 95, BRE 96, GC 87, IS 87, LAB 95, NN 95, NS 91, POR 96, SKA 88, SMA 96*

4.2 Pelagic fish species

The boarfish (*Capros aper*) is a small marine pelagic shoaling commercially important species distributed in Atlantic shelf waters from Norway to Senegal, including the Mediterranean. In the northeast Atlantic, boarfish have historically been considered a low abundance species that show periodical fluctuations in abundance with increases in the Bay of Biscay, the Galician continental shelf and the Celtic Sea between the 1980s and 2000 (Blanchard & Vandermeirsch, 2005; Fariña et al., 1997). The increases in abundance have been tentatively attributed to enhanced adult growth and recruitment as a result of climate-related changes in environmental conditions (Blanchard & Vandermeirsch, 2005; Coad et al., 2014). The UCD ATLAS team (Farrell et al., 2016) developed a *de novo* panel of microsatellite markers for boarfish to be implemented using a genotyping by sequencing approach to assess the genetic population structure of boarfish across the species' range, and investigate if purported recent increases in abundance in the northeast Atlantic area are the results of an immigration of boarfish from other regions or caused by a population expansion.

These results indicated, based on a range of genetic statistical analyses, that boarfish could be divided into at least seven populations throughout the sampled geographical range (Fig. 4.2). Further, the analyses indicated that the increased abundances in the northern distribution are better explained by demographic expansion with the regions rather than immigration from southern region.

Analyses for rapid declines of effective population sizes that could have been caused by overfishing did not detect any indication of recent bottlenecks in any sample. The presence of structure in the Atlantic likely indicates low levels of gene flow mediated through either adults or larvae and that the increase in abundances were likely caused by improved survival in the norther areas of the distribution.

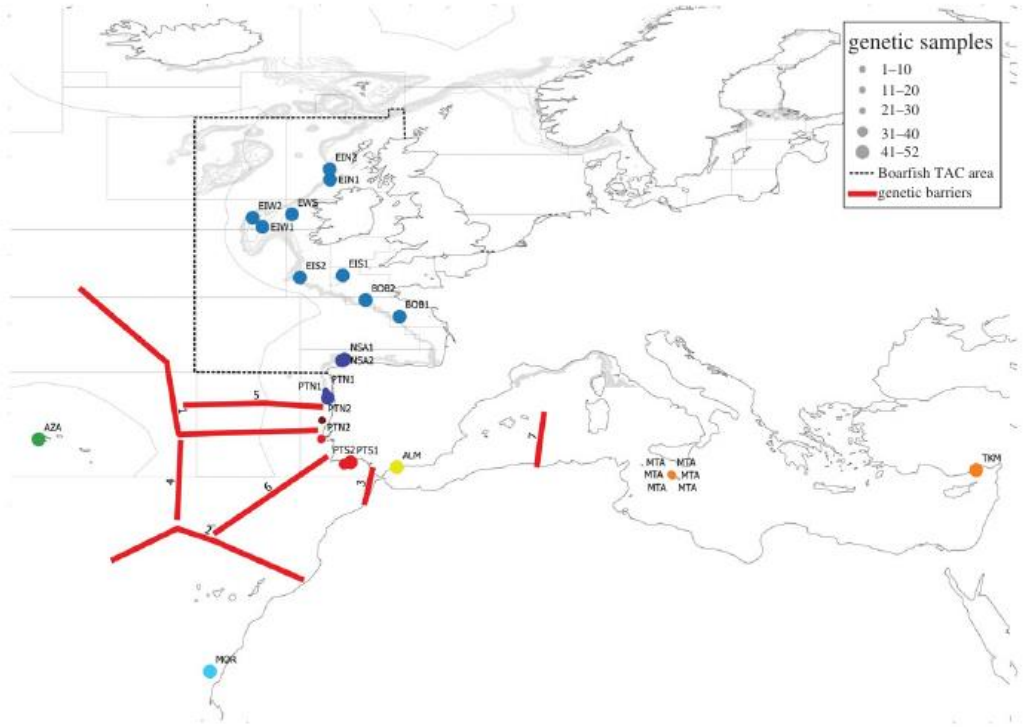


Figure 4.2: (from Farrell et al. 2016). Map of sampled locations. Location colour is in accordance with Structure analysis cluster. Red lines indicate genetic barriers and the dotted line indicates current management areas for boarfish.

The horse mackerel, *Trachurus trachurus* is distributed throughout the East Atlantic from Norway in the north to West Africa in the south and the Mediterranean Sea in the east. It is a pelagic shoaling species often targeted by commercial fisheries on the continental shelf and is a widely distributed species in shelf waters. Horse mackerel in the northeast Atlantic region are managed as three stocks; the Western, the North Sea and the Southern. The accuracy of alignment of these stocks with biological populations is uncertain. In an effort to resolve these uncertainties we undertook in collaboration with industry and the ATLAS project the largest and most comprehensive population genetic study undertaken on Atlantic horse mackerel. Atlantic samples were provided by industry and sampling was conducted over three consecutive years and three spawning seasons and

covered a large area of the distribution of the species including the Western, North Sea and Southern stock areas and also West African waters. Further samples from the Mediterranean (c. 100 individuals), provided by ATLAS partners, were analysed. In total 33 samples, comprising 2,295 individual fish were collected between 2015 to 2017 across the study area. Total genomic DNA was successfully extracted from 2208 of these specimens. To ensure that individual samples were all *Trachurus trachurus*, the COI section of the mitochondrial genome was sequenced using approaches developed by Farrell et al. (unpublished). It was clear that the samples from West African waters contained a high level of species misidentification while only one individual was misidentified in samples from the Mediterranean. Individuals in spawning condition were analysed with a panel 37 microsatellite markers (Farrell et al. In prep.) and population genetic statistical analyses indicated that horse mackerel in the northeast Atlantic region does not represent a single biological unit. On the highest level there are mixed species catches in African waters and to a smaller extent in the Mediterranean. Further, there is a clear separation of the southern North Sea from other regions and further, less pronounced, structure along the northeast Atlantic continental shelf. In contrast to studies of many other marine species, the Mediterranean samples did not show the strongest level of genetic differentiation. Again, these results showed the genetic differentiation does not align with fisheries management units. There were no indications of genetic bottlenecks in any population.

4.3 Ongoing improvements of genomic data

Despite all the results obtained, the important technical challenges faced by ATLAS team (and their transatlantic partners in US) with the DNA extraction from corals delayed several aspects of the genome scan work initially planned, as mentioned in previous WP4 deliverable and milestone reports (see Box 4.1.3).

As a consequence, and considering the additional delays due to the present Covid-19 situation during which no sequencing took place, despite most DNA being sent to subcontracting companies, no complete RAD dataset could be analysed for the present report. Data are available for *Madrepora oculata*, *Eunice norvegica* and *Cidaris cidaris*, half data are available for *Lophelia pertusa*. Those data were obtained late and are thus still being analysed bioinformatically. High quality DNA has been obtained for *Dendrophyllia cornigera* and *Helicolenus dactylopterus*. As soon as the partner laboratory subcontracted to build libraries reopens, libraries will be constructed and genotypes produced in an expected delay of 4 to 6 months after sending DNA to obtain analysed data.

These data, produced within ATLAS, will lead to publication likely after the end of the project, and feed transatlantic collaborations planned in iAtlantic to analyse *M. oculata* and *L. pertusa* at basin scale. Special attention will be given to the importance of results for future management plans, as results may provide more detailed patterns of connectivity and genetic diversity distribution for those species.

Box 4.1.3 The challenge of obtaining DNA for deep-sea genomic analysis: new protocols for tissue preservation and DNA extraction

The marine environment includes the majority of the Earths' phyla and classes, but nearly all the marine taxonomic groups are understudied particularly for genomics (Taylor et al., 2017). Long-standing barriers remain - access to specimens, securing long-term preservation techniques for specimen's tissue at optimal conditions to preserve DNA, and fine-tuning DNA extraction protocols. During the ATLAS project all of these barriers were encountered, but the most challenging was finding a DNA extraction protocol to obtain large quantities of high-quality DNA for high-throughput sequencing. Using first generation population genetics markers (such as mitochondrial DNA and microsatellites), very few DNA used to be needed and low molecular weight was usually enough to gather population genetics datasets. Now, new generation molecular protocols for genome scan such as RAD-Sequencing (Miller et al., 2007) require high molecular weight DNA with a high quality standard, very difficult to achieve (Graham et al., 2015; Guo et al., 2018). In our case, difficulties arose particularly with specimens preserved in Ethanol at room temperature (rather than frozen). This happened to be the case for most collections so far, and the problem tends to worsen as ethanol grade decreased (from EtOH 96° to 70°, the two main standards for tissue preservation). Marine organisms, invertebrates in particular, present high polysaccharide contents, polyphenols and other secondary metabolites that degrade DNA or inhibit downstream DNA library preparations. Protocols developed for vertebrates or plants thus do not always succeed with marine invertebrates. Such challenge proved to be even more important for corals than most other invertebrates tested thus far. At the beginning of ATLAS, WP4 teams started working on the large collections from previous projects and numerous oceanographic expeditions, on the basis of which WP4 work was planned. Neither DNA collection nor usual extraction protocols applied to tissue collections could solve the problem. At Ifremer, WP4 team tested and optimised several DNA extraction protocols for 11 deep-sea taxa (four hard corals, one soft coral, three vesicomyd bivalves, one gastropod and one crustacean), to provide sufficient DNA quality and yield for *de novo* genome sequencing and genome scan projects (D4.3; Boavida et al., in prep.).

After two years of this effort, guidelines for long-term storage (i.e. either -80°C or EtOH 96° stored at +4°C, the former giving surprisingly better results for Scleractinian corals at least) and two extraction protocols emerged. Those allowed us to start new, longer-term collections, and to rescue part of the older stored samples, to perform the genome scan analysis planned in ATLAS. We tested different variants of three commercial kits, alongside a traditional CTAB DNA extraction protocol (Doyle and Doyle, 1988) and, at last, CTAB-Phenol Chloroform extraction. After protocol optimisation, the best performing protocols in terms of DNA yield and quality were 1) a modified version of the commercial kit MN NucleoSpin Plant II that worked for most taxa, including *Madrepora oculata* and *Eunice norvegica*, and 2) A CTAB-Phenol Chloroform extraction that showed the best rate of success for Scleractinians, particularly *Lophelia pertusa* and *Dendrophyllia cornigera*. For Scleractinians, the quality and yield of the extractions were higher if samples were stored in ETOH 96 (or if preserved at -80°C, soaked in ETOH 96° before extraction). Based on those protocols, during the third year of ATLAS, the first sets of tissues (*M. occulata, E. norvegica*) were prepared and libraries built to be sequenced, and the second set is still being processed (several libraries sequenced, other being prepared).

1. M. L. Taylor, C. N. Roterman, Invertebrate population genetics across Earth's largest habitat: The deep-sea floor. Mol Ecol 26, 4872-4896 (2017). 2. M. R. Miller, J. P. Dunham, A. Amores, W. A. Cresko, E. A. Johnson, Rapid and cost-effective polymorphism identification and genotyping using restriction site associated DNA (RAD) markers. Genome Res. 17, 240-248 (2007). 3. C. F. Graham et al., Impacts of degraded DNA on restriction enzyme associated DNA sequencing (RADSeq). Mol Ecol Resour 15, 1304-1315 (2015). 4. Y. Guo, G. Yang, Y. Chen, D. Li, Z. Guo, A comparison of different methods for preserving plant molecular materials and the effect of degraded DNA on ddRAD sequencing. Plant Divers 40, 106-116 (2018)

5 Conclusion: what have we learnt for integrative management and where do we go from there?

Spatial planning is supposed to protect biodiversity, and thus account for a diversity of life history traits, habitat requirement and connectivity matrices. In this work package, the objective was to identify areas of special importance for conservation and management because they would shelter populations more or less demographically independent, and specific genetic or even species diversity, in which case population genetics is expected to reveal the occurrence of MUs or ESUs. Results obtained during ATLAS in terms of predicted and realised connectivity, on a limited amount of species considering the biodiversity sheltered in VMEs, already exemplified the known challenge of accommodating conservation measures for species with distinct histories and dispersal pattern (Gaines et al., 2007; Moffitt et al., 2011). Here some benthic species (*Lophelia pertusa*) showed more apparent (recent or contemporary) dispersal and genetic exchange at the basin scale than some pelagic fishes such as *Capros aper*.

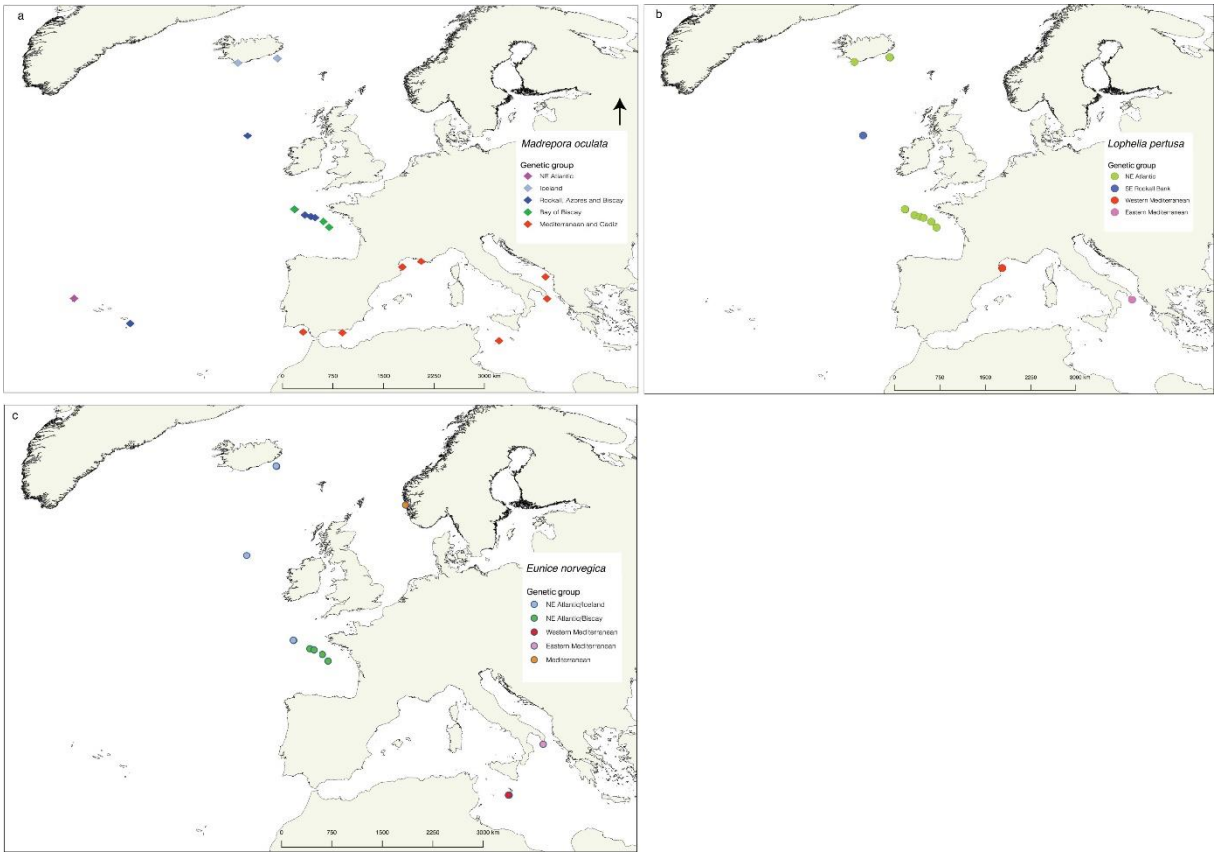


Figure 5.1: *Geographic distribution of genetic groups of cold-water coral.* Lophelia pertusa *and* Madrepora occulata*, and the associated polychaete* Eunice norvegica*. Colours refer to each genetic group (referred to in the text as population). Maps created on QGIS with Mollweide's equal area projection.*

Distinct MUs or ESUs (Palsbøll et al., 2007; Ryder, 1986) were detected for most species along the Mediterranean and Northeast Atlantic slopes, emphasising the need to compartment conservation measures in distinct areas such as the Mediterranean, the Bay of Biscay, the Mid Atlantic Ridge and the North Sea. However, within each of those areas, distinct MUs or ESUs were also found with different spatial distribution depending on taxa, calling for a fine-tuning of conservation approaches depending on the target.

The management of exploited species allows a distinct perspective on the population genetics data, particularly because species studied here (*Nephrops norvegicus, Capros aper* and *Trachurus trachurus*) do show genetic differentiation across their distribution range, allowing the identification of conservation units that should be considered for fisheries management (Figure 5.2). Norway lobsters are managed as "functional units" that are correlated to suitable habitats with a cluster of suitable habitats make up a functional unit. We analysed Norway lobster individuals throughout the range and identified large-scale population clusters while there was no evidence of fine scale clusters as represented by the functional units. Hence, there is a mismatch between biological units (populations) and current management. Our data suggest that management measures should focus on larger regions, as management of an individual functional unit will affect other functional units and functional units are not independent.

Boarfish are managed in accordance to TAC (total allowed catch) areas by ICES. Our data largely agreed with the current management areas, with the exception of the location of the southern border for the northeast Atlantic stock that should be shifted further south. Similar to Norway lobster, the Mediterranean samples showed strong genetic differentiation as compared to the Atlantic samples. In addition our analyses indicate that the recent increase in abundance of the species in the northeast Atlantic is likely caused by demographic expansion rather than range expansion and influx of individuals form the south.

Horse mackerel are managed as a western, southern and North Sea stock in the Northeast Atlantic. Our data showed a clear separation of the southern North Sea from all other stocks while a less pronounced separation was detected along the northeast Atlantic continental shelf. Unlike most other marine species that have been analysed there was no clear separation of the Mediterranean samples from those in the Atlantic. While the reason for the low level of differentiation is unclear it is possible that there is significant connectivity between the Atlantic and the Mediterranean for this species. The alignment of current management of the North Sea stock should take into account the strong genetic differences observed for the southern North Sea samples to better reflect the population structure.

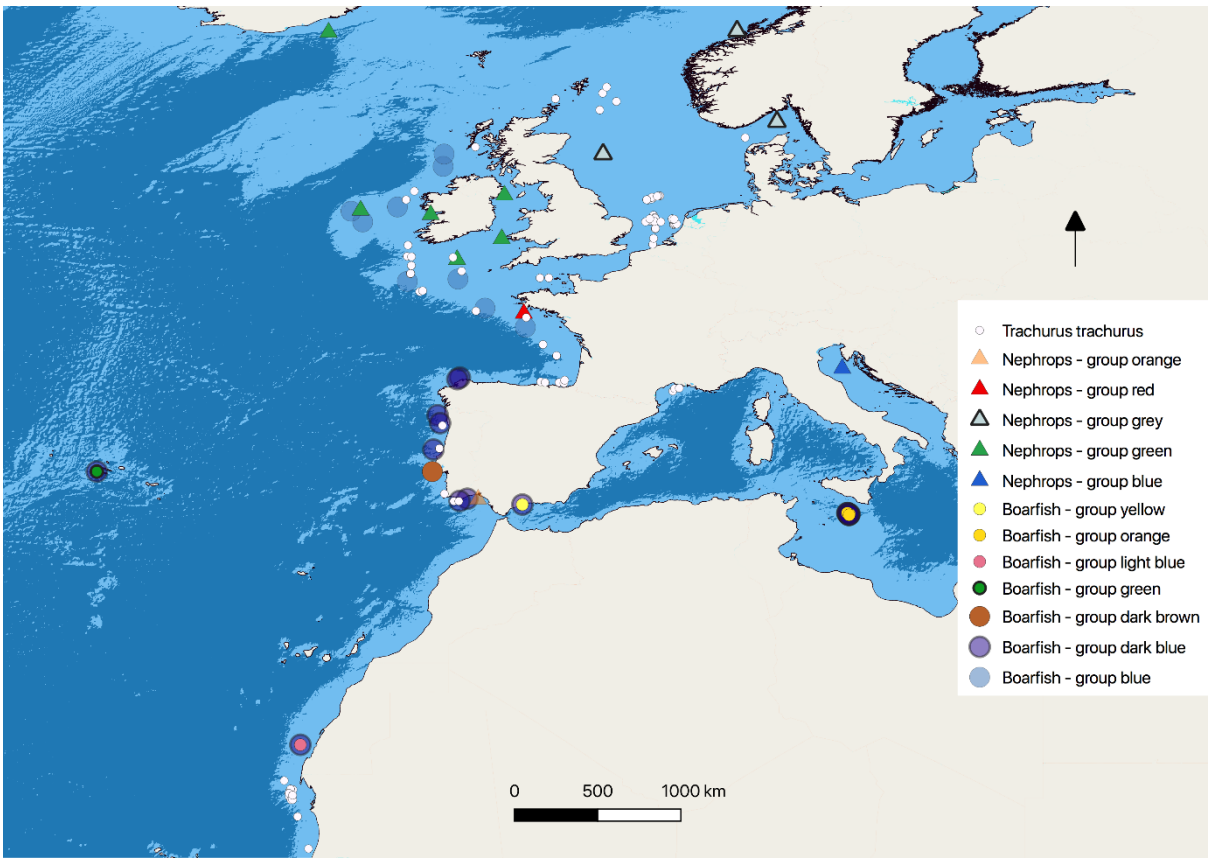


Figure 5.1: *Geographic distribution of genetic groups of harvested species associated to cold-water coral.* Trachurus trachurus - *Atlantic horse mackerel; Nephrops* - Nephrops norvegicus*, Norway lobster; Boarfish* - Capros aper. *Colours refer to each genetic group (referred to in the text as population). Maps created on QGIS with Mollweide's equal area projection.*

In none of those three cases did our data show any indication of recent genetic bottlenecks, despite well-recognized fisheries pressure. This may reveal a lack of bottleneck but it is notoriously difficult to detect in many if not most marine organisms due to their large population (and effective population) sizes. It would take very dramatic changes in population size to leave genetically detectable changes at the scale of human generation time (Figure 5.3; Bailleul et al., 2018) and it is much more likely that traditional survey techniques are better adapted to assess changes in abundances than genetic methods.

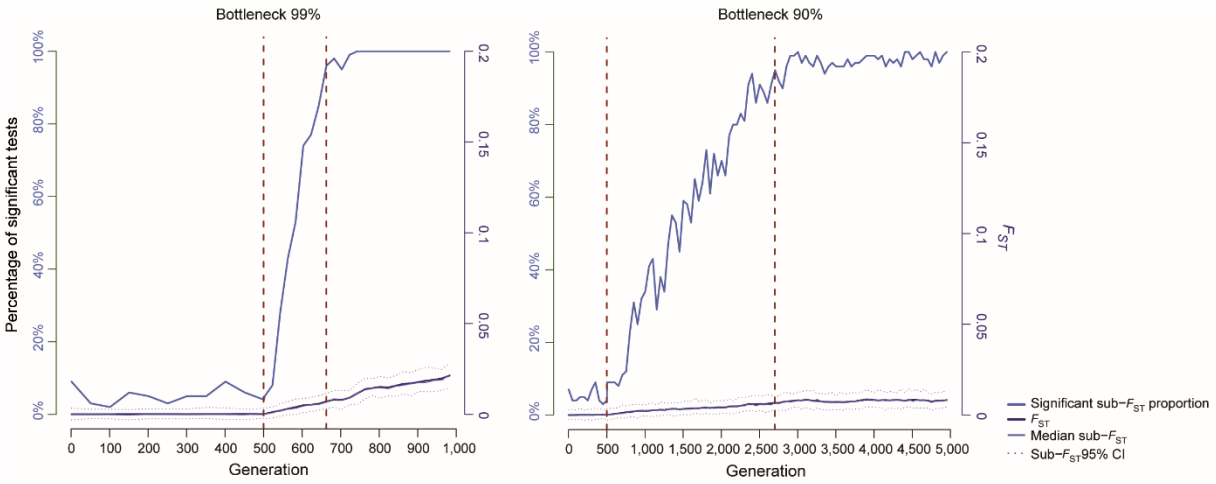


Figure 5.3: *Illustration of the impact of extreme bottlenecks with data from simulations of splits among populations adapted from Bailleul et al. (2018). Simulated population separation process with initial effective population size Ne = 1,000,000 and migration rate m = 0.0001. After 500 generations (first dashed red line), each population was reduced by 90% and 99%. The detection of significant index of genetic differentiation (sub-FST) above 95% is indicated by the second dashed red line. For each plot, the x-axis represents the number of generations since the divergence, the right y-axis the FST values (blue lines, full for the median value and dashed for the 95% envelope) and the left y-axis the percentage of significant FST values (light blue lines).*

The findings presented here on commercially important fisheries species could not have been achieved without genetic methods. Further, the difference in importance of larvae mediated connectivity compared to connectivity based on adults is clear from the findings of Norway lobster. Hence, knowledge of life history of all life-stages is, here also, crucial for developing appropriate management and conservation actions.

It may be that, in the same way that genome scans are expected to shed light on more genetic differentiation than hitherto detected for some species such as *L. pertusa*, the statistical power they deliver could also allow better detection of recent changes in population sizes (i.e. bottleneck or expansion) associated with anthropogenic activities (Bailleul et al., 2018). The RAD sequencing data being produced by ATLAS teams for *Lophelia pertusa*, *Madrepora oculata*, *Eunice norvegica* and *Helicolenus dactylopterus* may allow us to answer that question. Importantly for the conservation of deep reefs at basin scale, the collaboration developed before and reinforced during ATLAS with US teams studying the two reef building *L. pertusa* and *M. oculata* allowed standardising approaches to obtain a basin scale analysis. On both sides of the Atlantic, RAD Sequencing libraries have been and are being sequenced, and the merging of datasets is planned in the framework of iAtlantic to allow a basin scale connectivity map.

Developing appropriate management and conservation actions accommodating contrasting results obtained on those species for which we have enough knowledge to develop well-informed modelling

or obtain high-resolution genomic data remains a challenge. Several solutions have been proposed. The one consisting of focusing on those engineer species that structure the habitat already shows its limit here with *Madrepora oculata* and *Lophelia pertusa* equally building reefs along the Mediterranean and North Eastern Atlantic coasts (Arnaud-Haond et al., 2017) but showing dramatically different patterns of "realised" connectivity. A Marxan-based approach adopted in ATLAS (Combes et al., in prep.) is to use predicted connectivity using a conservative estimate of 20-day Pelagic Larval Dispersal (PLD) (Hilario et al., 2015). Though even the 20 days PLD is unlikely to be conservative enough for some sponge species (Kenchington et al., 2019). This caveat in mind, the results underlined the need to enlarge conservation areas in order to allow for self-recruitment of low dispersers while still maintaining larger scale recruitment.

One of the central objectives of ATLAS is adaptive management planning accounting for changing climate, with an emphasis on changes to/weakening of AMOC. Changing AMOC has the potential to change demographic connectivity via two main mechanisms: direct changes to advective dispersal, extent and pathways; and indirect AMOC-driven changes to local water-mass properties affecting habitat distribution and hence connectivity. The hydrodynamic modelling, Lagrangian particle tracking and analysis of observational datasets conducted for ATLAS suggests that the direct effects of AMOC weakening on demographic connectivity will be small, perhaps an order of magnitude less than either the present-day monthly variability in AMOC (Lozier et al., 2019) or the uncertainty in connectivity due to uncertainties in life history traits. So management, which accounts for this uncertainty should also account for the direct effects of changing AMOC. However, analysis of water-mass properties at the bed in the North Atlantic in both the Viking20 model and EN4 dataset (D1.2), show large-scale, coherent changes in near-bed temperature and salinity associated with AMOC variability. It appears that the more likely AMOC-related driver of changes in demographic connectivity in the deep sea is movement of habitat due to decadal-scale changes in near-bed properties (temperature, salinity, acidity, food supply, etc.).

We are navigating in a sea of uncertainties as to the diversity of life history traits of the numerous taxa inhabiting deep-sea ecosystems, and which condition their habitat distribution and dispersal, as well as the way genetic diversity is distributed under the influence of historical and contemporary factors. One of the main conclusions that could be driven from our experience is the need, as underlined in D7.4, to move from a paradigm of MPAs within an exploited ocean to a network of exploited areas within a connected, protected ocean.

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7 Appendix:

Samples exploited in ATLAS, collected within ATLAS actions (in bold) or in previous projects, or cruises of the network of ATLAS partners.

Species	Project/cruise/partner	Year	Atlantic	Mediterranean	UK	Platforms
Lophelia pertusa						
	Previous projects	2011	334	68		
	ATLAS-Medwaves	**2016**				
	ATLAS- Platforms	**2017-2018**				**88**
	Ifremer cruise (Caladu)	2019		9		
	Tjärno Station	**2017-2018**	**31**			
	Oxford - UK- NERC DeepLinks JC136	2016			316	
Madrepora oculata						
	Previous projects	2011	321	53		
	ATLAS-Medwaves	**2016**	**25**	**21**		
	Ifremer cruise (Videocor)	2017		21		
	Ifremer cruise (Caladu)	2019		27		
	Oxford - NERC DeepLinks JC136	2016			302	
Eunice norvegica						
	Previous projects	2011	247	86		
	ATLAS-Medwaves	**2016**				
	ATLAS- Platforms	**2017**				**1**
	Ifremer cruise (Caladu)	2019		8		
	Tjärno Station	**2018**	**3**			
	Oxford - UK- NERC DeepLinks JC136	2016			194	
	NHM - SponGES (H2020)	**2017**	**27**			
Dendrophyllia cornigera						
	Previous projects	2016	40			
	IEO	2016	10	2		
	IEO	2017	12			
Helicolenus dactylopterus						
	Previous projects		40			
	Ifremer cruises (EVOHE & MEDITS)	2017-2018	97	30		
	IEO cruise (MEDITS)	2017-2018	42	40		
	UAzores cruises	2018	44			
Cidaris spp.						
	Oxford - UK- NERC DeepLinks JC136	2016			266	
	Plymouth - SeaRover 2017 Survey (Ireland)	**2017**	**32**			
	Smithsonian Institution	2018	94			
	ATLAS - Medwaves	**2016**		**11**		
	Senckenberg Research Institute	2017	5			
Stereocidaris cf. ingolfiana						
	Oxford - UK- NERC DeepLinks JC136	2016			70	
	Iceland (MFRI)	2017	42			

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Dissemination level	x	PU Public, fully open, e.g. web		
		CO Confidential restricted under conditions set out in Model Grant Agreement		
		CI Classified, information as referred to in Commission Decision 2001/844/EC		

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