GLOBAL BIOGEOGRAPHICAL PATTERNS OF *planKton* IN RESPONSE TO CLIMATE CHANGE

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Global biogeographical patterns of plankton in response to climate change

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A SMOOTH SEA
NEVER MADE
A SKILLED SAILOR

A mi madre

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Summary

The scientific evidence is overwhelming: climate change is occurring and much of the ongoing change is a direct result of human activity. Observations show that ~84% of the total heating of the Earth over the last 40 years has gone into warming the oceans, altering the many natural systems inhabiting on it. These include a strong sea temperature warming (0.11°C decade^{-1}) in the upper 75 m between 1971 and 2010, increasing wind velocity and storm frequency, changes in ocean circulation, vertical structure and nutrient loads, ocean acidification, as well as rising sea level by more than 15 cm in the last century.

Impacts of global warming are affecting the whole pelagic ecosystem from plankton to higher trophic levels. Such impacts can result in poleward movements in species distribution, shifts in phenology and changes in abundance and community structure. Observational studies have already documented shifts in plankton biogeography and community structure in several ocean basins, with changes that rank among the fastest and largest of any marine or terrestrial group. Species responses to climate change, hence, may lead to local extinction and invasions, resulting in changes in the pattern of marine species richness and trophic mismatches. In these set of species ecological responses to climate change, dispersal, through simply moving from one habitat patch to another, is a central process; it determines the potential spread rate of a population and, as the process by which genes are moved between populations, it influences the rate of adaptation to changing conditions and the potential for evolutionary rescue. Hence, the vulnerability of marine communities to climate change will depend on the species capacity to adapt and disperse, and on the degree of connectivity between them.

Understanding, predicting and managing biodiversity responses to rapid climate change demands a full consideration of species' biogeogeographical patterns, defined by its niche requirements and dispersal characteristic, and how these characteristics may themselves change under climate change. Studies of zooplankton, the ocean's core secondary producers and the main target group of this thesis, can improve existing knowledge of how marine ecosystems are coping under a changing climate. Zooplankton is particularly sensitive to short-term environmental changes, as both their population dynamics and physiological processes are influenced by temperature. Due to this sensitivity, zooplankton communities can be used as indicators to assess whole-of-ecosystem health, and variation of their distribution patterns can provide valuable information about the physical changes occurring in the global oceans.

This study aims to gain an understanding of the global biogeographical patterns of planktonic communities and its response to a changing climate. Biogeographical studies require a deep knowledge of the species ecological niche, defined here as the range of tolerance of a species when several environmental factors are considered. This thesis pretends to analyze broad scale macro-ecological patterns of plankton, from genes to community level, from coastal areas to global ocean, from historical trends to future projection. To that end we have combined global datasets and state of the art statistical tools.

The thesis is structured in two main parts and 4 chapters. Part I: Climate change and habitat modelling of plankton (Chapter 1 and 2) and Part II: Connectivity and biogeographical patterns of plankton (Chapter 3 and 4).

The main **objectives** are:

1. To test whether the zooplankton community is responding (”what changes”) to the ongoing temperature change, as well as to detect the amplitude of the responses (”by how much”) and its timing and spatial temporal scales.

2. Evaluate the impacts of future climate change on plankton using habitat modelling techniques (GAMs), and its coupling to climatic models to determine the rate of distribution and seasonal shifts and community changes of these organisms in the North Atlantic Ocean.

3. Assess global connectivity patterns of pelagic communities in relation to geographical and ecological distances at different taxonomic groups (from prokaryotes to small mesopelagic fish) based upon beta-diversity metrics.

4. Evaluate the vulnerability of marine biodiversity at global scale to climate change by analyzing the dispersal and connectivity patterns in populations of different marine ecosystems (plankton in open sea and benthic macroinvertebrates on the coast).

In the **first chapter**, we have characterized the ecological niche of zooplankton at local scale series across three time series of the North Atlantic and Mediterranean Sea, to test whether the zooplankton abundance trends keep the pace with to the observed sea surface temperature increase trends. Results reveal a response of the zooplankton to climate, with significant community changes with time due to sea warming and environmental factors. Such shift might be related to changes in sea surface temperature, because in 46% of the

species, the expected copepod abundance trends following its thermal niche agree with the observed trends. At community level, the long-term β-diversity changes were related to niche descriptors, mostly to changes in sea temperature, and environmental factors (21%), after partialling out for temporal autocorrelation.

In the **second chapter**, we scaled up in space from local time series in coastal stations (Chapter 1) to basin-wide scale at the North Atlantic (Chapter 2). Using data from Continuous Plankton Recorder (CPR), we characterized the ecological niches of a set of zooplankton assemblages by means of habitat modelling techniques to project the distribution of copepods under future climate change IPCC scenarios. According to results, the impacts of the change expected by the end of the century on copepods highlight poleward shifts (9 km/decade), earlier seasonal peak (14 days) and changes in biodiversity spatial patterns that might lead to alterations of the future North Atlantic pelagic ecosystem.

In the **third chapter**, we jumped from basin-wide scale to global scale, to analyze large-scale connectivity patterns and its relationship with the body size. Contrary to what has been focused in Chapter 1 and 2, in the Chapter 3 and 4 we also account for dispersal, which is a key proccess driving species distributions. In chapter 3 we report a global effort to identify characteristic connectivity scales and the factors driving them for pelagic organisms spanning from marine prokaryotes to mesopelagic fish. To that end, we have merged two unique datasets: (1) global estimates of timescales of ocean connectivity and (2) biological data collected globally along the Malaspina circumnavigation expedition. We show organismal body size to be a key biological trait shaping the spatial patterns of community assembly, with large-bodied plankton showing significantly lower dispersal scales compared to small-bodied plankton. We also provide evidence that shows that neutral processes, such as dispersal limitation, are much more important than the niche descriptors to connect plankton communities.

In the **fourth chapter**, we conducted a parallel analysis of biological connectivity at genetic and community levels in marine groups with different dispersal traits. We estimated dispersal distances from population genetic data and from β-diversity at the community level. Results reveal that dispersal distances ranked the biological groups in the same order at both genetic and community levels, as predicted by organism dispersal ability and seascape connectivity: macrozoobenthic species without dispersing larvae, followed by macrozoobenthic species with dispersing larvae and plankton (phyto- and zooplankton). This ranking order is associated with constraints to the movement of macrozoobenthos within the seabed compared with the pelagic habitat. We showed that dispersal limitation similarly

determines the connectivity degree of communities and populations, supporting the predictions of neutral theories in marine biodiversity patterns.

Overall, the studies developed within the framework of this PhD thesis have provided new insights into the understanding of the climate-related impacts in the present and future biogeography of the plankton communities and the processes driving species spatial patterns of community assembly. After reviewing the limitations of the niche concept, we argue that the habitat modelling techniques are a useful and rapid tool to appraise the effects of climate-induced temperature changes on zooplankton. In addition, beta-diversity metrics are also a valuable tool to explore what species are where, and why, in the global oceans.

Resumen

La evidencia científica es abrumadora: el cambio climático está ocurriendo y gran parte del cambio es un resultado directo de la actividad humana. Las observaciones demuestran que durante los últimos 40 años el 84% del total del calentamiento de la tierra ha ido a calentar los océanos, alterando así los sistemas naturales que habitan en él. Se han observado incrementos en la temperatura superficial del agua (0.11°C década^{-1}) entre 1971-2010, incrementos en la velocidad del viento y frecuencias de tormentas, cambios en la circulación oceánica, estructura vertical y aporte de nutrientes, acidificación de los océanos, así como un incremento del nivel del mar de en torno a unos 15 cm durante el último siglo.

Los impactos del cambio climático afectan a todo el ecosistema pelágico, desde el plancton hasta niveles tróficos superiores. Estos impactos generan una serie de respuestas en las especies como por ejemplo cambios latitudinales en los rangos de su distribución, cambios en los ciclos estacionales, así como cambios en la abundancia y estructura de las comunidades. Particularmente en el plancton, se ha demostrado que los cambios en la biogeografía son de los más grandes y rápidos observados hasta ahora. Por ello, el cambio climático puede dar lugar a extinciones o invasiones locales en las especies, que repercuten en los patrones de biodiversidad y causan desajustes tróficos. En esta serie de respuestas, la dispersión de las especies, con el simple hecho de desplazarse desde un hábitat a otro, es un proceso clave; determina el ritmo de extensión de una población y permite el flujo genético entre ellas, lo cual es fundamental en los procesos de adaptación a condiciones climáticas cambiantes. De este modo, la resiliencia o vulnerabilidad de las comunidades marinas frente al cambio climático dependerá de la capacidad de adaptación o dispersión de cada especie así como de su grado de conectividad.

Comprender, predecir y gestionar las respuestas de la biodiversidad al cambio climático exige una consideración completa de los patrones biogeográficos de las especies, que están definidos por su nicho ecológico y características de dispersión, y cómo estas características pueden cambiar debido al cambio climático. Los estudios sobre el zooplancton, los principales productores secundarios del océano y el principal grupo objetivo de esta tesis, pueden mejorar el conocimiento existente sobre cómo los ecosistemas marinos están respondiendo al cambio climático. El zooplancton es particularmente sensible a los cambios ambientales a corto plazo, ya que tanto su dinámica poblacional como sus procesos fisiológicos están altamente ligados a la temperatura. Debido a esta sensibilidad, las comunidades de zooplancton pueden utilizarse como indicadores para evaluar la salud de los

ecosistemas marinos, y la variación de sus patrones de distribución puede proporcionar información valiosa sobre los cambios físicos que ocurren en los océanos globales.

Nuestro estudio tiene como objetivo analizar los patrones biogeográficos del plancton a escala global y su respuesta frente al cambio climático. Los estudios biogeográficos requieren un profundo conocimiento del nicho ecológico de las especies, definido aquí como el rango de tolerancia de cada especie a un set de variables ambientales que limitan su distribución. Esta tesis pretende estudiar los patrones macro-ecológicos del plancton en varias escalas: desde los genes hasta las comunidades, desde zonas costeras hasta el océano global, desde tendencias históricas hasta proyecciones futuras. Para tal fin, hemos aplicado técnicas y modelización estadística en bases de datos globales.

Esta tesis se estructura en dos partes principales y cuatro capítulos. Parte I: Cambio climático y modelización del hábitat del plancton (Capítulo 1 y 2) y Parte II: Conectividad y patrones biogeográficos del plancton (Capítulo 3 y 4).

Los principales **objetivos** son:

1. Analizar si la comunidad del zooplancton está respondiendo ("que cambia") al incremento de temperatura, así como detectar la amplitud de las respuestas ("cuanto cambia") en escalas spacio-temporales.

2. Evaluar los impactos del futuro cambio climático en el plancton del Atlántico Norte utilizando técnicas de modelado de hábitats (GAMs) y su acoplamiento a modelos climáticos para determinar la tasa de migración, los cambios estacionales así como los cambios que se pueden dar en la comunidad.

3. Evaluar patrones de conectividad globales en las comunidades pelágicas en relación a la distancia geográfica y ambiental a partir de métricas de beta-diversidad. Para ello se han utilizado datos de diferentes grupos taxonómicos (desde procariotas hasta peces meso-pelágicos pequeños).

4. Evaluar la vulnerabilidad de la biodiversidad marina frente al cambio climático analizando los patrones de dispersión y conectividad en poblaciones de diferentes ecosistemas marinos (plancton en mar abierto y macro-invertebrados bentónicos en la costa) a escala global.

En el **primer capítulo**, hemos caracterizado el nicho ecológico del zooplancton en zonas costeras a través de tres series temporales del Atlántico Norte y el Mar Mediterráneo, para comprobar si las tendencias de abundancia del zooplancton se corresponden con las tendencias en el incremento de la temperatura del mar. Los resultados revelan una respuesta del zooplancton al calentamiento del mar, con cambios significativos en la comunidad en el tiempo, debido al calentamiento y a factores ambientales. Tales cambios podrían estar relacionados con cambios en la temperatura de la superficie del mar, ya que en el 46% de los casos, las tendencias esperadas de abundancia de copépodos por nicho térmico coinciden con las tendencias de abundancia observadas. A nivel de comunidad, los cambios que se han observado en la beta-diversidad son debidos a los cambios en las variables ambientales que determinan el nicho de cada especie, principalmente la temperatura (21%), después de tener en cuenta la auto-correlación temporal.

En el **segundo capítulo**, pasamos de zonas costeras (Capitulo 1) a cuencas oceánicas del Atlántico Norte (Capitulo 2). A partir de datos del Continuous Plankton Recorder (CPR), caracterizamos el nicho ecológico de las especies clave de zooplancton con técnicas de modelado del hábitat para proyectar su futura distribución utilizando escenarios de cambio climático del IPCC (Panel Intergubernamental del Cambio Climático). Los resultados revelan desplazamientos latitudinales en el rango de distribución (9 km década^{-1}), avances en los picos estacionales (14 días) y cambios en los patrones espaciales de biodiversidad que podrían alterar el ecosistema pelágico futuro del Atlántico Norte.

En el **tercer capítulo** pasamos de las cuencas oceánicas del Atlántico Norte (capitulo 2) al océano global, para analizar los patrones de conectividad del plancton y micro-necton y su relación con el tamaño. Al contrario de lo que hemos hecho en el capítulo 1 y 2, en el capítulo 3 y 4 hemos tenido en cuenta la dispersión, un proceso clave en la distribución de las especies. En el capítulo 3 hemos estimado por un lado la conectividad biológica de las poblaciones del plancton y micro-necton a partir de su escala de dispersión, y por otro lado hemos analizado los procesos ecológicos que determinan su distribución. Los grupos estudiados abarcan una amplia comunidad y tamaños, desde las procariotas hasta pequeños peces meso-pelágicos. Para ello, hemos utilizado dos set de datos únicos: (1) estimas de tiempo de conectividad a partir de corrientes con modelos de circulación general, y (2) datos biológicos obtenidos durante la expedición Malaspina. Los resultados de este estudio demuestran que el tamaño es un *rasgo* biológico fundamental que configura los patrones espaciales de las comunidades planctónicas, siendo la escala de dispersión del plancton de mayor tamaño significativamente menor que la del plancton más pequeño. También proporcionamos evidencias que demuestran que los procesos neutros, como la dispersión limitada, son mucho más importantes que los descriptores de nicho para conectar las comunidades de plancton.

En el **cuarto capítulo**, se ha realizado un análisis paralelo de la conectividad biológica a nivel genético y de comunidad, a escala global, en grupos marinos con diferentes características de dispersión (plancton marino *vs* macro-bentos costero). Se han estimado las distancias de dispersión a partir de datos de genética de poblaciones y beta-diversidad a nivel comunitario. Los resultados revelan que las distancias de dispersión han clasificado los grupos biológicos en el mismo orden tanto a nivel genético como a nivel comunitario: de menor a mayor, (1) especies macro-bentónicas sin dispersión larvaria, (2) seguidas por especies macro-bentónicas con dispersión larvaria, y (3) plancton (fito- y zooplancton). Este orden está relacionado con las restricciones al movimiento del macro-bentos en el fondo marino, que son mucho mayores que las restricciones que tiene el plancton en el hábitat pelágico. De este modo hemos demostrado que la dispersión-limitada determina por igual el grado de conectividad de las poblaciones a nivel genético y de comunidad, de acuerdo con las predicciones de las teorías neutras en los patrones de biodiversidad marina.

En general, los estudios desarrollados en el marco de esta tesis doctoral han aportado nuevos conocimientos sobre los impactos climáticos en la biogeografía presente y futura de las comunidades de plancton, y de los procesos ecológicos que generan distribución espacial. Después de revisar las limitaciones del concepto de nicho, argumentamos que las técnicas de modelado de hábitats son una herramienta útil y rápida para evaluar los efectos de los cambios de temperatura en el zooplancton. Además, hemos demostrado que las métricas de beta-diversidad son también una valiosa herramienta para explorar qué especies están donde, y por qué, en los océanos globales.

0. General Introduction

0.1 Plankton biogeography and general concepts

The word ‘plankton’ derives from the Greek ‘planktos’ meaning to ‘drift’ or ‘wander’ and it is used to describe passively drifting organism that occur in aquatic systems (Figure 0.1). These organisms include drifting or floating bacteria, archaea, algae, protozoa and animals that inhabit in the pelagic zone of the oceans or bodies of fresh water. Plankton is primarily divided into broad functional (or trophic level) groups:

1. Phytoplankton (from Greek phyton, or plant), are autotrophic prokaryotic or eukaryotic algae that live near the water surface where there is sufficient light to support photosynthesis. Among the more important groups are the diatoms, cyanobacteria, dinoflagellates and coccolithophores.

2. Zooplankton (from Greek zoon, or animal), representing small protozoans or metazoans (e.g. crustaceans and other animals) that feed on other plankton (heterotrophic). Zooplankton can also be some of the eggs and larvae of larger animals, such as fish and crustaceans.

3. Bacterioplankton, bacteria and archaea, which play an important role in remineralising organic material down the water column.

4. Mycoplankton, fungi and fungus-like organisms, which also are significant in nutrient cycling, as bacterioplankton.

Although plankton can change their depth through active swimming and changes in buoyancy, they are mainly drift with ocean currents. Plankton varies hugely in size from viruses and bacteria only a few microns in diameter (pico-plankton) up to jellyfish weighing 10s of kg (macro-plankton).

Plankton can also be classified according to the portion of their life cycle spent as plankton. Organisms that spend their entire lifes as plankton are ‘holo-plankton’. However, many organisms that spend their adult lifes as nekton (swimmers, for example small mesopelagic fishes) or benthos (bottom dwellers, for example corals or crabs) spend their juvenile and/or larval stage as plankton. These organisms are called 'mero-plankton'.

Plankton are ubiquitously distributed across the oceans, although species compositions vary from place to place. For example, the differences in community structures between eutrophic and oligotrophic regions, respectively dominated by large and small phytoplankton cells, is a well-established general feature of our oceans[1]. The major factors that influence the biogeographical patterns of plankton are: (1) environmental conditions (e.g. temperature and nutrient concentrations), (2) interspecific relationships (i.e. predation and competition), and (3) dispersal[2]. The different plankton community structures that arise from the complex interplay of these factors determine the structure and functioning of the marine food web[3]. Therefore, detailed investigations of the mechanisms that lead to certain plankton biogeographical patterns can help us to better understand the processes that shape pelagic ecosystems and how they will likely respond to a changing environment.

Plankton are critical to the functioning of ocean food webs because of their sheer abundance and vital ecosystem roles: (1) they provide half of the global primary production[4] (phytoplankton), (2) contribute substantially to biogeochemical cycling[5], (3) regulate the climate through the biological pump (transforming dissolved inorganic carbon into organic biomass and pumping it in particulate or dissolved form into the deep ocean), and (4) support the microbial loop[6].

The main target organism of this PhD thesis is the zooplankton. Zooplankton communities are highly diverse and thus perform a variety of ecosystem functions. Arguably, the most important role of zooplankton is to provide the principal pathway for energy from primary producers to consumers at higher trophic levels, such as fish, marine mammals, and turtles. Hence, they affect the recruitment success of larval fish[7,8], which undergoes strong inter-annual variability[9], and may have a deep impact in the economy of the local fisheries. In fact, much of the economic value of the oceans, estimated at US$21 -trillion year^{-1} globally[10], stems from critical ecosystem services, such as fishery production, nutrient cycling, and climate regulation, which is provided by zooplankton.

Figure 0.1 Plankton collected during the TARA Oceans Expedition in Shimoda Bay (Japan) in autumn with a 0.2mm mesh net. Organisms measure a maximum of 5 to 7mm. Source: http://planktonchronicles.org/en/the-project/ Photo taken by Christian Sardet, CNRS (Villefranche-sur-Mer).

0.1.1 Zooplankton as sentinels of climate change

Zooplankton can be considered excellent beacons of climate change for a host of reasons: First, physiological rates and population dynamics of zooplankton are tightly linked to temperature changes[11-13]. Second, zooplankters are ectotherms with short generation times (<1year), so there is a close coupling of climate and population dynamics[8,14-17]. Third, unlike other marine groups, such as fish and other intertidal organism, zooplankton is not commercially exploited (except krill and some jellyfish), so long term trends in response to environmental change are not generally biased with trends in exploitation. Fourth, because ocean currents provide an ideal mechanism for dispersal over large distances[18], almost all marine animals have a planktonic stage in their life cycles, hence, the alterations in the distribution of many marine groups are partially determined while floating as plankton. And fifth, zooplankton have a cosmopolitan nature as a well as a robust behaviour in the laboratory, enabling easy sampling and preservation[12,13].

Apart from being a good indicator of climate change, zooplankton plays also an important role in shaping the extent and pace of climate change. The oceans ability to act as a sink for CO_2 depends partially in the biological pump. Zooplankton is vital to the biological pump because much of the CO_2 fixed by phytoplankton is eaten by zooplankton and eventually exported to the seabed. Zooplankton also facilitate this process by moving large quantities of carbon from the ocean's surface to deeper layers when they dive each day into the ocean deep layers to avoid near-surface predatory fish[19].

0.1.2 Methods to study zooplankton distribution

Regular monitoring of plankton is essential to assess the ecosystem health of the marine environments and to establish climate-ecosystem links. There are several methods to study abundance and distributional patterns of plankton, including long-term marine monitoring programs or oceanographic campaigns.

(1) **Long-term monitoring programs** consist of a series of observations on the abundance or occurrence of the target organisms made at equal intervals over a period of time. Such time-series programs are recognized as being increasingly important in an era of accelerated global change. Statistical procedures are used to extract information and to identify trends and scales of temporal patterns in the population fluctuations. Many marine laboratories have operated coastal time-series stations at a variety of locations and for varying durations. A good example is the zooplankton time-series at Urdaibai estuary in the SE Bay of Biscay, which is an ongoing monitoring program initiated in 1997[20] with surveys carried out monthly at neap tides in the marine zone of Urdaibai. Other local time series examples include the Dove time-series off the Northumberland coast[21] and the Helgoland Roads time-series[21,22]. Such zooplankton time-series in the ICES area are reported regularly in the ICES Zooplankton Status Report[23] and on the COPEPODITE time-series network http://www.st.nmfs.noaa.gov/copepodite/. The common nets to collect plankton at the time-series are the Bongo-nets and the WP2[24], in vertical, horizontal or oblique tows at low speed, typically 1-2 knots.

(2) **Oceanographic research cruises**. These surveys run on diverse spatial scales, from basin-wide scale i.e. EURO-Basin http://www.euro-basin.eu/, to global ocean i.e. Malaspina[25] or Tara Oceans[26]. Despite its spatial coverage, they often have weak temporal resolution, especially compared to long-term monitoring programs. These

research campaigns make use more sophisticated plankton sampling techniques that allow sampling further deep in the water column and characterize the vertical structure of the communities. Sampling devices include the Multi-net, the VPR (Video Plankton Recorder)[27], the OPC-Laser (Optical Plankton Counter) and the MOCNESS[28] (Multiple Opening/Closing Net and Environmental Sensing System) or acoustics techniques[29].

(3) There are **other long-term monitoring programs** with large spatial and temporal coverage. A good example is the Continuous Plankton Recorder (CPR)[30]. The CPR survey is the longest series of consistent observations on a basin scale and has been instrumental in identifying important climate-related changes in the planktons of the North Atlantic Ocean[31,32]. In the Pacific Ocean, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) is another long-term marine monitoring program, gathering hydrographic and biological data collected on cruises since 1949[33-35]. The advent of the Joint Global Ocean Flux Study (JGOFS) program[36] led to the establishment of important open ocean time-series stations in both oceans, off Hawaii [Hawaii Ocean Time series (HOT)] and off Bermuda [Bermuda Atlantic Time-series study (BATS)]. In other regions of the global ocean, the Long Term Ecological Research (LTER) program has fostered time-series in a variety of ecosystems, e.g. the Southern Ocean[37].

0.2 Species Ecological Niche

0.2.1 Niche-theory

Why do species live where they live? What determines the abundance and diversity of species in a given area? What role do species play in the functioning of entire ecosystems? The understanding of what determines species' ranges is fundamental to biogeography and all of these questions share a core concept - the ecological niche. Among the different definitions of the ecological niche of a species that have been proposed during the first half of the 20th century (e.g. Grinnell[38], Elton[39]), the one from Hutchinson[40] has been the most influential. Hutchinson[40] defined the ecological niche as a series of independent environmental variables with simple ranges of suitable conditions defining an 'n-dimensional hyperspace' within which the species can survive and reproduce. As point out by Colwell[41], Grisemer[42] and Schoener[43], Hutchinson[40] used the word niche to refer to the environmental requirements of a species, whereas earlier authors, especially Grinnell[38] and Elton[39], had used the term niche to refer to a place in the environment that has the potential to support a species. Contrary to the definition proposed by Grinnell[38], according to Hutchinson, the niche is a property of a species, not a property of the environment[44]. Hutchison also distinguished "fundamental" from "realized" niches, to demarcate the conditions that species could survive from those where they actually live, respectively: (1) the fundamental niche represents the response of all species' physiological processes to the effects of environmental factors in the absence of negative interactions (e.g. competition, predation or parasitism), and (2) the realized niche, in turn, is the part of the fundamental niche actually occupied by the species including factors such as dispersal that increase niche breath or competition that tighten it. As a result of competitive exclusion[45], the realized niche can be smaller than the fundamental niche, and a species may frequently be absent from portions of its fundamental niche because of competition with other species. More recently, Pulliam[46] also agreed with Hutchinson in that the realized niche can be smaller when factors reducing survival are predominant, however, he also provide evidence that the realized niche can be greater than the fundamental niche when dispersal is high. According to Pulliam[46], the notion of Hutchinson is simple and represents a rigorous, yet operational way of assessing the niche of a species. Within this context, Hutchinson went one step further and viewed the species' realized niche reflected in the geographical space[47], a property that allows to make major questions about the interface between the ecological requirements and broad-scale patterns of species distributions[48,49]. This also helped scientist exploring processes such as diversity gradients, the assembly of ecological communities, trait evolution and speciation, species invasiveness, and responses to global climate changes (see, e.g. Wiens & Donoghue[50], Pearman et al.[51], Wiens et al.[52]). A core point of the Niche-theory is that it assumes that differences in species composition among communities is caused by heterogeneity in the environment or limiting resources[45]. In niche-based models, species are able to coexist by avoiding competition through resource and environmental partitioning[45,53]. These recent reconsiderations of the niche concept in relation to species distribution have inspired contemporary modelers to include other important parameters, such as dispersal[54-56] and population dynamics[57], or both[58], to predict present and future biogeographical patterns.

Assumptions about the shape of the response of species to an environmental variable are central for modelling. In fact, the Niche-theory, together with most current theories and analytical models, assumes that the response of the species to a given environmental gradient to be a unimodal, symmetric bell-shaped curve (Figure 0.2). Niche-theory is based on this assumption and additionally makes several others:

a. Both the fundamental and realized niches of a species are bell-shaped symmetric curves.
b. Maximum abundance occurs at the optimum for the fundamental niche. Only optimum conditions generate high abundances and allow for successful reproduction. Towards the niche extremities, energy taken from the environment is used for maintenance, towards the niche center, energy is allocated for reproduction, growth and feeding. When the environment becomes less favorable, offspring production, growth and feeding will be hampered. Extreme conditions become critical and may eventually affect survival[59].
c. Competition restricts niche breadth.
d. Species maxima are equally spaced along the gradient and are of equal amplitude.
e. There is equilibrium between species distribution and the climate. Species are said to be at equilibrium with climate if they occur in all climatically suitable areas whilst being absent from all unsuitable ones (*sensu* Araújo & Pearson[60]). Failure to colonize suitable areas is related to the dispersal ability of species and to biotic interactions.
f. Collective properties of species, e.g. species richness, dominance or stand abundance show no patterns of response along the environmental gradient.

Some authors drew attention to the lack of evidence for these belly-shape response curve assumption, because it can happen, often, that interactions between species and extreme environmental stress may cause skewed responses (e.g. Austin[61], Oksanen & Minchin[62]).

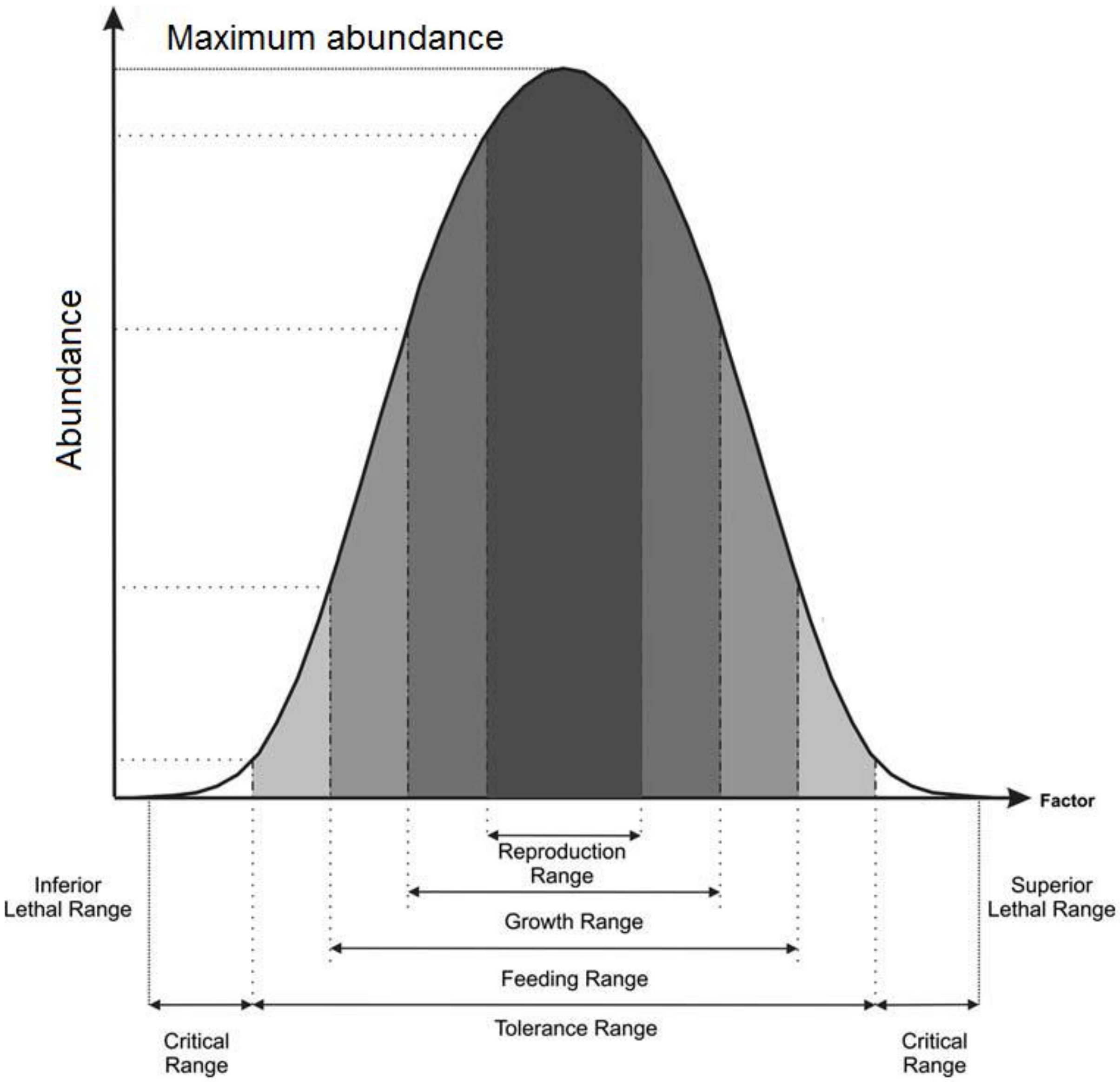


Figure 0.2 Hypothetical one-dimensional niche showing how environmental conditions may affect the species. Note that the niche may not always be Gaussian. Source: Modified from Helaouet and Beaugrand[63].

0.2.2 Species Distribution Models

Species Distribution Models (SDMs), also named habitat suitability models or ecological niche models, are statistical tools that model a species realized niche by relating their occurrence or abundance to environmental conditions[64]. The strategy of most SDMs distribution models is to characterize the environmental conditions which are suitable for the species to occur and derive spatially explicit predictions of environmental suitability. The identification of the suitable environmental conditions can be undertaken applying either correlative or mechanistic approaches. Statistical (or correlative) models relate species distribution or abundance to spatially explicit abiotic constraints[65]. Mechanistic models, on the other hand, incorporate additional information on species eco-physiology or population dynamics[66] The vast majority of the studies today have been correlative. The correlative modelling approach, for example, allows one to investigate spatial patterns on thousands of species, without requiring sophisticated and time-consuming mechanistic models that depend heavily on detailed knowledge of processes for each species, which are likely to be lacking for all but a few species.

The SDMs applied in this PhD thesis (Chapter 1 and Chapter 2) are correlative, because we aim to study climate-related zooplankton distributional patterns and characterize its ecological niche in the North Atlantic Ocean and Mediterranean Sea.

Steps to build a Species Distribution Model

The principal steps required to build and validate these models are outlined below (Figure 0.3).

1. **Input data.** It is a key challenge to gather a reliable[67], complete[68] non-biased[69,70] dataset on both, species distribution (presence-absence, presence only or abundance) and the environmental variables limiting the distribution of the target organism[71,72].

2. **Model selection**. Modeling methods differ in the underlying scientific question and the data type available. Known that, it is easier to do an adequate selection of the algorithm[73]. Species data can be (1) simple presence, (2) presence–absence or (3) abundance observations based on random or stratified field sampling, or observations obtained opportunistically, such as those in natural history collections[74] or fishing catches. When quantitative data are available, regression techniques such as Generalized Linear Models (GLMs; McCullagh & Nelder[75]) or

Generalized Additive Models (GAMs; Hastie & Tibshirani[76]), or neural networks have been frequently used[65,72]. When only binary (presence-absence) data are available there are far fewer techniques that can be applied, although regression techniques such as GAMs can still be used. When presence-only data is only available, other statistical techniques, which are based upon Principal Component Analysis (PCA), the principle of maximum entropy or the Mahalanobis distance algorithm (MD)[77], can be used – e.g. Ecological Niche Factor Analysis (ENFA)[78], BIOCLIM[79], MAXENT[80] and the Non-Parametric Probabilistic Ecological Niche (NPPEN) model[81]. In addition to these strict presence-only approaches, there is another way to model species distribution when only presence data is available, for example with MAXENT. These alternative approach is based on the application of presence-absence techniques and the generation pseudo-absences, points that are taken as absences but may not all be true absences, which are used for model validation[82].

In this thesis, the GAMs SDM have been used (Chapter 2) with the presence-absence data from the CPR time series in the North Atlantic, to project future zooplankton range distributions under a climate change IPCC (Intergovernmental Pannel of Climate Change) scenario.

3. **Model fitting, variable selection**. Model fitting is the process of constructing a model or mathematical function that has the best fit to a series of data points or observations[83]. Model fitting can involve either interpolation, where an exact fit to the data is required, or smoothing, in which a "smooth" function is constructed that approximately fits the data[84]. Whichever the model selected, this is a step common to all methods. During the model calibration, the most important environmental variables limiting the target organism distribution are selected. This is done by testing the contribution of each environmental driver to model variance and by ranking the predictive power or accuracy of the model, usually with the model quality indicators, such as Akaike information criterion (AIC), or by adding and removing terms and noting the change in deviance or gain in a forward stepwise procedure.

4. **Habitat-suitability maps**. Model results are represented in the geographical space i.e. the habitat-suitability map. In the SDM framework, two types of model output are common: binary results where sites are classified as presence or absence; and continuous results where each site is given a probability of species

presence (probability of occurrence). Conversion from continuous to categorical prediction is done applying an optimized probability threshold[85] (i.e. the probability value above which the habitat is considered suitable).

5. **Model evaluation**. The assessment of the utility of selected models requires an evaluation of the performance or accuracy of them. This is a critical element of model-building[64]. Measures of model reliability can be distinguished in two groups: (1) threshold-independent measures, which are used to evaluate the performance of continuous probability maps and (2) threshold-dependent measures, used to evaluated categorical binary prediction maps[71]. The latter rely on an confusion matrix yielding outputs of correctly identified of presence and absence to have an overall accuracy estimate of model performance[85]. In addition, model evaluation requires an independent dataset to avoid overfitting[86]. There are two main methods to address model evaluation[87]: (1) data-partitioning, where an independent dataset is used to evaluate the model (e.g bootstrap, cross-validation Jackniffe[64]) and (2) external validation, where the model is applied to a geographically or temporally independent dataset.

6. **Model projection.** SDM can be extrapolated in time and space to assess, for instance, the future species' biogeographical ranges under climate change scenarios[88-90] or to reconstruct the historical population distributions[91]. Model transferability, despite its limitations, is considered an appropriate tool for obtaining rapid impact assessments[64].

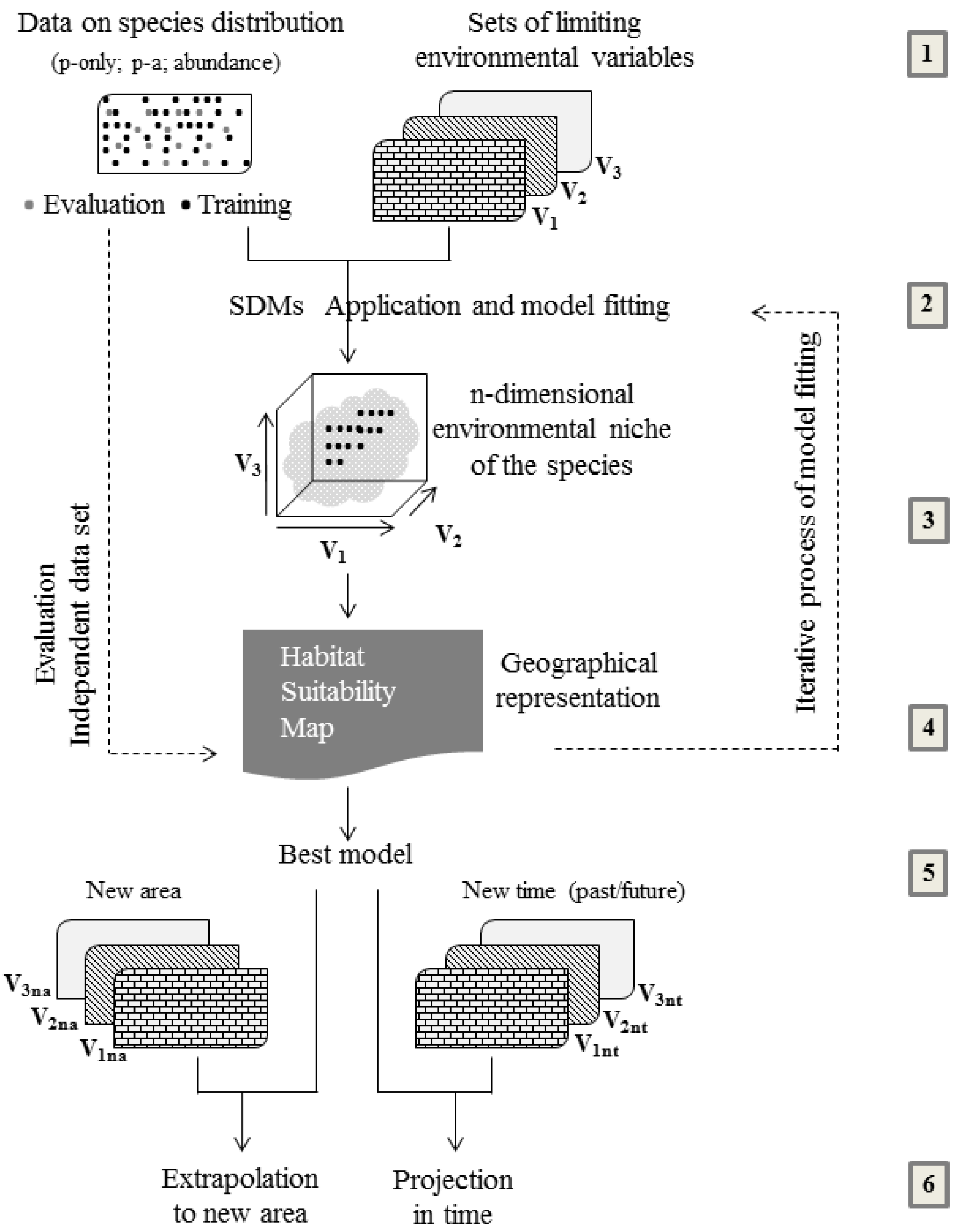


Figure 0.3 Flow diagram showing the main steps required for building and validating a SDM model when two independent dataset are available (one for model fitting, other for model testing). Step 6 corresponds to possible further application of the resulting models: (i) to predict distribution in a different area or region and (ii) to project to a different time period (e.g. under future climate change scenarios). Source: Modified from Valle et al.[92].

SDMs can be rapidly implemented for a large number of species, providing estimates of the direction and magnitude of species range shifts under changing climates. Several key ecological traits make planktonic species particularly well-suited for SDMs[93] : (i) their distribution reflects their environmental preferences, since plankton are short-lived, with population dynamics tightly connected to climate[94]; (ii) plankton are less commercially exploited than other marine species, and thus less prone to an anthropogenic bias in their natural occurrence patterns. In their simplest form, however, SDMs generally do not include ecological processes such as dispersal, species interactions, and intraspecific variability, which can be important in defining the distribution of a species[95-97]. Failure to explicitly include these factors can affect the predictive performance of SDMs[64,98,99].

0.3 Community structure and marine biodiversity

0.3.1 Dispersal and connectivity

Broadly, dispersal can be defined as any movement of individuals or propagules with potential consequences for gene flow across space[100]. Specifically, larval dispersal refers to the intergenerational spread of larvae away from a source to the destination or settlement site at the end of the larval stage. Most of marine organisms, whether pelagic, planktonic or benthic, are patchily distributed, consisting of local populations linked to a greater or lesser extent by dispersal[101]. When dispersal is combined with factors leading to survival of the dispersed organisms, the concept of population connectivity emerges i.e. the exchange of individuals among geographically separated subpopulations that comprise a meta-population[102]. A meta-population can be defined as local populations linked by dispersal, and similarly, a meta-community consist of local communities linked by dispersal of multiple species.

A schematic illustration of dispersal is a dispersal curve, a one dimensional representation of the number of settlers from a given source as a function of the distance from that source (Figure 0.4). The dispersal curve becomes a dispersal kernel with an associated probability density function, in n dimensions. Formally, the dispersal kernel is the probability of ending up at position x given a starting position y.

Through simply moving from one habitat patch to another, dispersal has pervasive ecological and evolutionary consequences for all living organisms[103,104], influencing gene flow and the potential for local adaptation[100,105,106], connectivity among local populations[107] and the dynamics of meta-populations[108,109], and the expansion or shifting of species' geographic ranges[110,111]. When dispersal is limited, processes to maintain species coexistence and regional diversity may be favored[112,113].

Contrary to the terrestrial domain, fluid characteristics in the ocean create the possibility for extremely long-distance dispersal[114]. At the same time, larval behaviors, life history traits, and persistent oceanographic features (biogeographic barriers) may limit dispersal, thus enhancing local retention of propagules[115-117] and regional biodiversity. Marine species often rely on a high propagule output, extended propagule persistence, propagule survival and extrinsic transport mechanisms (e.g. atmospheric and oceanic circulation) to achieve broad-scale dispersal, maintain population connectivity and colonize new territory[118-121].

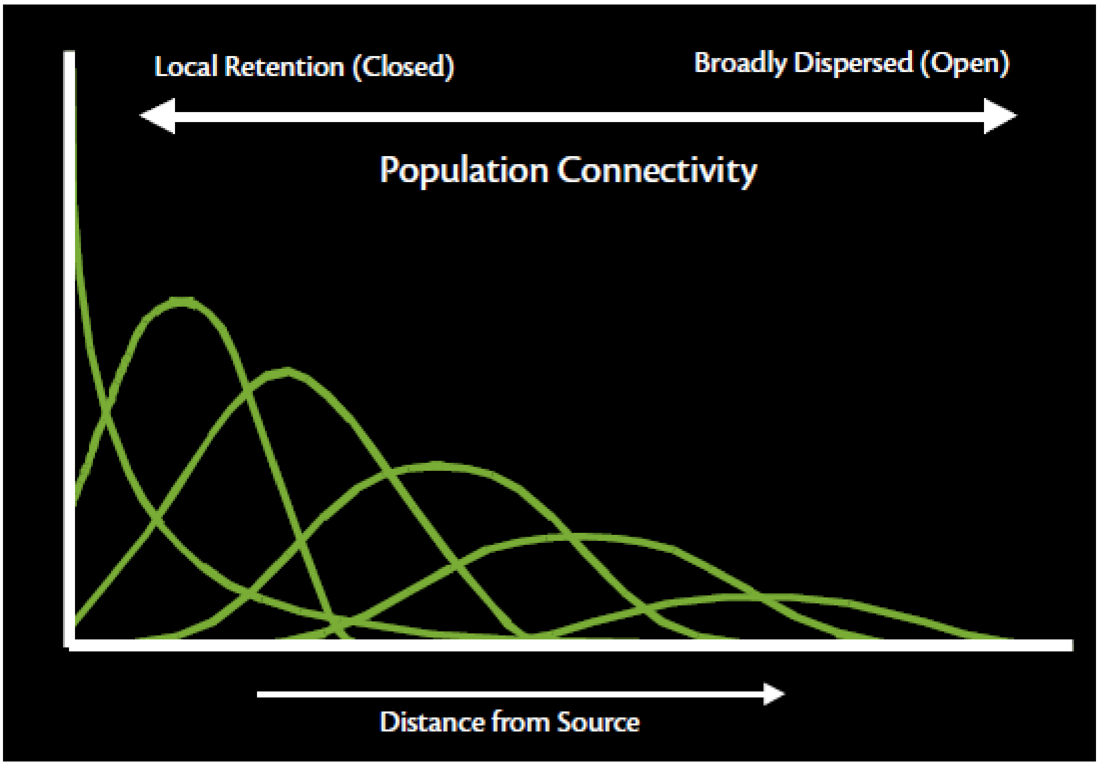


Figure 0.4 One dimensional, theoretical dispersal curve depicting dispersal from a source location ranging from strong retention to broadly dispersed. Source: Cowen et al.[102].

Knowledge of larval dispersal and connectivity can be acquired by (1) understanding the biological and hydrodynamic processes involved in the transport of larvae and (2) deriving larval origins and dispersal pathways using geochemical, genetic, or artificial markers. Larval dispersal refers to the intergenerational spread of larvae away from a source to the destination or settlement site at the end of the larval stage.

In marine systems, larval dispersal has traditionally been inferred from estimates of pelagic larval durations (PLD), from the modeled movements of passive particles by ocean currents, or from analyses of variation in allele frequencies of mitochondrial or nuclear genes[122]. Today, there are other techniques (see below) allowing estimating biological connectivity and dispersal of the organisms:

1. **Direct estimates by tracking**. *sensu* Slatkin[123]. Directly tracking movements of animals through the use of electronic tagging (acoustic and satellite telemetry), mainly targeting large pelagic animals. Ideally, dispersal is quantified by tracking

large numbers of individuals and observing their movements until settlement. It is often not possible to obtain direct measurements of movement of tiny propagules, such as seeds and larvae. Consequently, patterns of dispersal remain poorly understood for many marine planktonic species[107,124].

2. **Indirect measurements**. Due to the difficulty in empirically measuring dispersal of larvae in the open ocean, indirect methods are generally used to determine population connectivity:

    a. **Pelagic Larval Duration (PLD).** It is often considered as a proxy of the dispersal distance.

    b. **Genetic techniques**. The slope between genetic differentiation and the geographic distance (i.e. isolation-by-distance) for estimating dispersal distance with genetic markers (cf. section 3.2 Genetic Flow).

    c. **Beta-diversity studies and community theoretical models**. Whittaker[125] defined Beta-diversity as the variation in community composition along spatial gradients. According to the neutral theory of Biodiversity of Hubbell[126], when the migration rate between one local community to other is low (i.e. species are dispersal limited), species similarity is predicted to decline logarithmically with increasing geographical distance. The slope of this relation is a proxy of the meta-community connectivity (cf. sections 3.3 Community assembly and 3.4 Neutral theory of Biodiversity).

    d. **Numerical modelling** simulate the process of dispersal[127,128] and hence allow to quantitatively estimate the probability of population dispersal among sites[129-132]. These include (1) physical dispersal models that combine hydrodynamic models and agent-based modeling[133], and (2) bio-hydrodynamic models combining larvae traits (larval pelagic duration, buoyancy, mortality) and physical processes (currents, barriers due to environmental gradients)[134].

An important bulk of this PhD thesis (Chapter 3 and Chapter 4) analyzes the dispersal scales of a number of organisms, ranking from marine prokaryotes up to mesopelagic fishes, which have been inferred from genetic population techniques and community beta-diversity metrics.

0.3.2 Genetic flow

In population genetics, gene flow is the transfer of alleles or genes from one population to another within a meta-population. Migration into or out of a population may be responsible for a marked change in allele frequencies (the proportion of members carrying a particular variant of a gene). Immigration may also result in the addition of new genetic variants to the established gene pool of a particular species or population. There are a number of factors that affect the rate of gene flow between different populations. One of the most significant factors is dispersal, as greater mobility of an individual tends to give it greater migratory potential.

Marine populations with high dispersal will be less genetically structured compared to population with limited dispersal, where patterns of genetic structure may arise. Genetic structure in marine populations reflects the historical and contemporary interplay among a complex set of ecological, demographic, behavioral, genetic, oceanographic, climatic and tectonic processes[135-141]. The combined effects of these mechanisms, acting across a range of spatial and temporal scales, determine rates and pattems of dispersal of gametes, zygotes, larvae, and adults. It is these movements, along with the survival and successful reproduction of immigrants, that, in turn, control the scale and rate at which random (i.e. genetic drift) and natural selection processes build or erode structure within and among groups of individuals.

There are two basic **indirect** ways that population geneticists estimate gene flow: The first is based on **numerical modeling** (described before) and the second make use of **genetic markers** to identify degrees of differentiation between populations, from which inferences regarding the scale of dispersal and levels of exchange can be derived[142]. The most common metric for estimating gene flow, and hence, estimate dispersal distance of propagules with genetic markers are the:

a. **Wright's fixation index (F_{ST})**[143] which is a measure of genetic variation among a sample of geographically separated populations. In other words, The F_{ST} reflects the amount of genetic variance among subpopulations relative to the total variance of a meta-population.

b. **The IBD slope** is derived from 'isolation by distance' (IBD) analysis, which uses F_{ST} calculated pairwise between all sampled populations[143]. Under a 'stepping stone model' of dispersal, in which populations tend to exchange migrants (or propagules) with nearest neighbors along the coastline, the IBD theory suggests that pairwise genetic variation (for instance the Wright's fixations index F_{ST}) will increase with the geographic distance between the pair of populations (Wright[143]; Kimura[144]; reviewed in Selkoe and Toonen[145]). The IBD is a central concept of the neutral theory of molecular evolution developed by Kimura[144], which states that most of evolutionary changes at the molecular level is the result of randomly genetic drift acting on neutral alleles (not affecting fitness). IBD assumes neutral alleles (not affecting fitness) and populations at equilibrium between dispersal and genetic drift[146]. The slope of IBD is commonly used for estimating dispersal distance with genetic markers. To calculate the IBD slope, we can make a linear regression, and a plot, between the F_{ST} and the geographical distance.

0.3.3 Community assembly

Community assembly is defined as the association of populations of two or more different species occupying the same geographical area, the same meta-community, in a particular time. Understanding the processes that drive the assembly of a community has been a central theme of ecology ever since. It concerns basic questions such as how do we start from a regional species pool to assemble a structured community? How many species should be found at a given location? What is the relationship between community structure and the environment? Predicting how species will respond to global environmental change requires an understanding of the processes generating variation in patterns of diversity and distribution, which is the basis of macro-ecology. The decrease in community similarity with geographic distance is a universal biogeographic pattern observed in communities from all domains of life[147-149]. It is commonly described by the so-called "distance decay" which is the contribution of geographic distance to changes in community similarity (Nekola and White[147] see Figure 0.5). A number of studies have shown distance-decay patterns for specific taxa in different ecological systems, from terrestrial (e.g. rainforest trees[150,151]), to freshwater (e.g.

aquatic beetles[152]; fish and macroinvertebrates[153]), and marine communities (e.g. coral reefs[126]; marine bacteria and prokaryotes[154-156]; and plankton[157,158]). However, pinpointing the underlying causes of this "distance-decay" pattern continues to be an area of intense research[159-163], as such studies of β-diversity (variation in community composition) yield insights into the maintenance of biodiversity.

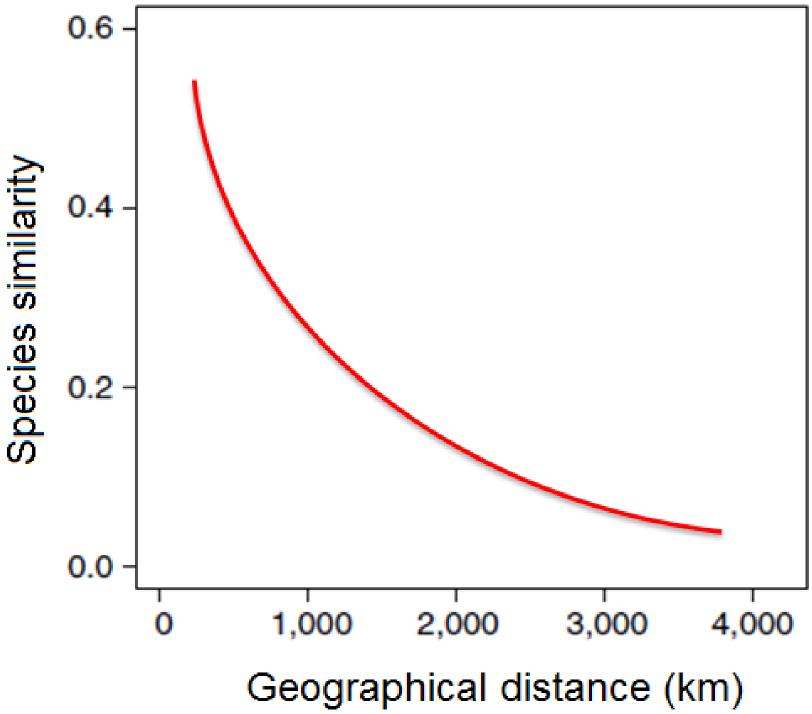


Figure 0.5 Distance-decay of species similarity[147].

In order to better understand how marine communities are spatially structured, we need to recall on the mechanism that generates variation in community composition along spatial gradients (i.e. β-diversity). Distance decay patterns in communities can be accounted for by at least three mechanisms: (1) local niche-based processes, with species differing in their ability to perform under different environmental conditions (cf. section 2.1). At the plankton, this idea follows the hypothesis of Baas-Becking[164] which states that under a 1 mm body size "*everything is everywhere but the environment selects*". (2) Community similarity can also decrease with distance even if the environment is completely homogeneous, due to organisms' limited dispersal, according to the neutral theory of Hubbell[126] (cf. section 3.4 below). Here, the similarity is not affected by environmental filtering, but rather by ecological drift, random dispersal and random speciation (Hubbell[126]). (3) The spatial configuration of the seascape can dictate the dispersal rate of organism among sites. In the open ocean there is no apparent dispersal barrier, but if any, community similarity should decrease more abruptly than in open and homogeneous settings[165]. However, it is a major challenge to elucidate whether marine planktonic communities are limited by dispersal or not, because the geographic distance is often correlated with specific environmental characteristics[126,166,167].

The difficulties to understand the processes generating patterns of diversity in plankton were originally described by Hutchinson[168] in its classical paper of the "*paradox of plankton*". The paradox of the plankton results from the clash between the observed diversity of plankton and the competitive exclusion principle (Gause's law[45]), which states that, when two species compete for the same resource, ultimately only one will persist and the other will be driven to extinction. Plankton life is diverse at all phylogenetic levels despite the limited range of resources for which they compete amongst themselves. Hutchison[168] proposed that the paradox could be resolved by factors such as vertical gradients of light or turbulence, symbiosis or commensalism, differential predation, or constantly changing environmental conditions. More generally, some researchers suggest that ecological and environmental factors continually interact such that the planktonic habitat never reaches an equilibrium for which a single species is favored[169,170].

During the past few years, there has been intensive debate on whether unicellular organisms exhibit biogeographic patterns different from those of macro-organisms[171]. The traditional view holds that, being small and extremely abundant, unicellular organisms are ubiquitous dispersers, flourishing wherever they find a suitable environment ('everything is everywhere, but the environment selects'). Thus, unlike most macro-organisms, they lack well-defined biogeographic patterns[172-174]. This generalization has now been challenged by a growing body of evidence showing that many microbial organisms have restricted distributions with well-structured spatial patterns of assemblage [148,175]. To provide evidence whether micro-organisms follow the same biogeographical rules as macro-organisms do, and to analyze which processes drive spatial distribution, dispersal scales and distance-decay patterns of community assembly have been analyzed for a number of planktonic and macro-benthic groups, at global scale within the 3rd and 4th Chapter of this PhD thesis.

0.3.4 Neutral theory of biodiversity

The neutral model of biodiversity developed by Hubbell[126] was inspired by MacArthur & Wilson's theory of island biogeography[176]. Hubbell proposed an individual-based, stochastic theory to explain patterns of species richness in ecological communities. In Hubbell's model, all individuals from all species are assumed to have the same prospects for reproduction and death (neutrality). This implies that biodiversity arises at random, as each species follows a random walk. In other words, the variability in relative abundances across species is solely due to demographic stochasticity or 'ecological drift'. It is a stochastic theory, based on mechanistic assumptions about the processes controlling the origin and interaction of biological populations at the individual level (i.e. speciation, birth, death and migration). This model further assumes a separation of spatial scales: demographic processes occur at the local scale of an ecological community, where species may go locally extinct through demographic drift. In the Hubbell model, local communities including J individuals are part of the larger meta-community and are connected to it by immigration at rate m of propagules from the regional pool. In this large regional pool, drift may also cause species to go extinct, and novel species arise through speciation, such that q new species are produced every generation. If $m = 1$, the local community is a random (Poisson) sample of the regional pool. In contrast, if m is close to zero, the local community is virtually isolated from the regional pool. Under this model, the local species abundance distribution is thus defined by only two model parameters, q and m. It is also a dispersal-assembled theory. This means that dispersal is assumed to have a leading role, in spatially structuring ecological communities. Because of the spatial effects of dispersal limitation, neutral theory predicts that the compositional similarity between communities will decrease as the distance between two points increases[151,177].

The Neutral theory has generated considerable controversy, because it claims that many mechanisms that have long been studied by ecologists (such as ecological niches) have little involvement in structuring communities[178]. However, there are a number of studies which reveal that biodiversity spatial patterns are mainly governed by neutral processes[177,178]. Either niche or neutral, the processes driving distribution are hard to distinguish in natural ecosystems, because as said before, a change in environmental conditions is often strongly correlated to a change in geographic distance[179,187,179]. Such processes often are not exclusive, but complementary. We can say that sometimes, ecological communities are more determined by niche-descriptors than dispersal-limited processes[151,152,180], and sometimes viceversa[154,158,181]. What is more, a recent publication shows that there can be is a transition in diverse ecological communities between a selection-dominated regime (the niche phase) and a drift-dominated regime[182].

0.4 Climate change threats

"No snowflake in an avalanche ever feels responsible" Voltaire

Today the scientific evidence is overwhelming: climate change is a reality and much of the ongoing change is a direct result of human activity[133]. In particular, burning fossil fuels, making cement and changing land use have driven atmospheric carbon dioxide concentrations (CO_2 [atm]) up from a pre-industrial value of about 280 part per million (ppm) to 400 ppm in 2016, according to what has been recently concluded in the Paris Agreement by the Intergovernmental Panel on Climate Change (IPCC)[183]. This is a whopping increase of 120 ppm in 250 years. By reorganizing natural systems[31,184], climate change is poised to be one of the greatest threats to biodiversity of this century[185,186], compromising the integrity, goods and services of living systems[187]. Therefore, climate change presents very serious, global risks that demand urgent responses[183,188,189]. Warming of the climate system has been detected in the atmosphere, the ocean, the cryosphere, and the hydrosphere[190]. Thus, questions concerning the extent and impacts of climate change are central to many ecological and biogeochemical studies, and addressing the consequences of climate change is now high on the list of priorities for funding agencies.

Observations show that ~84% of the total heating of the Earth system (oceans, atmosphere, continents, and cryosphere) over the last 40 years has gone into warming the oceans[191], altering the many natural system inhabiting on it[190,192]. These include a strong sea temperature warming (0.11°C $decade^{-1}$) in the upper 75 m between 1971 and 2010[183,193] (Figure 0.6), increasing wind velocity and storm frequency, changes in ocean circulation[194,195], vertical structure and nutrient loads[190], ocean acidification[183,196], as well as rising sea level by more than 15 cm in the last century due to thermal expansion[191,197,198] and presently by a mean of about 3.3 mm per year.

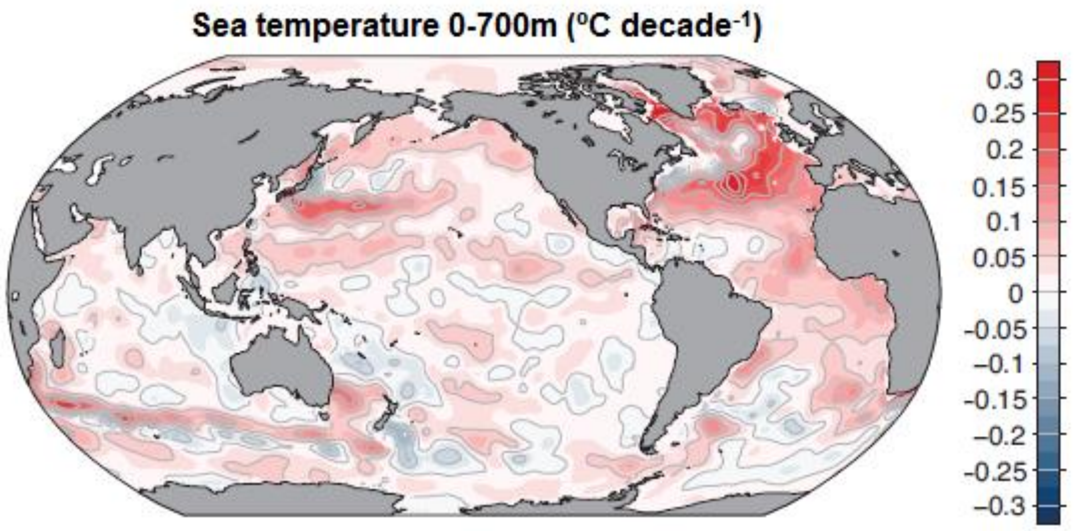


Figure 0.6 Depth averaged (0-700m) sea temperature trend for 1970-2010. Source: Levitus et al.[193].

0.4.1 Climate change impacts on marine organism and ecosystems

Sea temperature is one of the most important physical variables structuring marine ecosystems[13]. The evaluation of the vulnerability of marine organisms and ecosystems to temperature change needs to consider potential impact across all hierarchies of biological organization. These include gene expression, physiology, behavior of individuals, population dynamics, community and ecosystem structure, and trophic interactions. Meta-analyses applied across diverse species and ecosystems have provided strong evidence of global 'fingerprints' of recent climate change on natural systems[110,111,199,200]. Particularly, global climate change is expected to force species to respond in four different ways: (1) by adjusting their physiology; (2) by triggering adaptive evolution; (3) by altering time/space distribution, a process called species niche tracking; and (4) when none of these three responses are possible, extinction occurs. Within this context, dispersal is a central process; it determines the potential spread rate of a population and, as the process between populations, it influences the rate of adaptation to changing conditions and the potential for evolutionary rescue[201] (Figure 0.7). Hence, the vulnerability of marine communities to climate change will depend on the species capacity to adapt and disperse, and on the degree of connectivity of marine communities[157]. Whether populations and species will persist at the local and global scale, respectively, depends on their ability for endure future climate shifts[202].

0.4.1.1 Physiological adjustment

Global warming, by its effect on sea temperatures, will affect species physiology (e.g. growth and reproduction). When changed climatic conditions fall within the species' current tolerances ranges (i.e. the range of conditions upon which the population does not decline), no physiological or ecological modifications will be required for persistence. When environmental conditions fall outside of species' tolerance ranges, the physiological limits can be expanded via adaptation, through adjustment of traits that are phenotypically plastic and can change within an organism' lifetime, or through genetic changes requiring many generations[203]. For example, Urban et al.[204] showed that phenotypic plasticity plays and important role in the amphibians ability to adapt and cope with climate change.

0.4.1.2 Adaptive evolution

A change in functional or life story trait will be adaptive when the altered phenotype confers to the individual and advantage in the new environment; in other words, if the new phenotype increase individual fitness[205-207]. Adaptation wraps both phenotypic plasticity and genetically based evolutionary changes. Adaptation to a new environment via rapid evolution will be unlikely for those organisms that are isolate, dispersal-limited or and genetically depauperate. Whether adaptation can keep pace with environmental changes is still equivocal[208], and a growing number of studies show that rates of climate change can exceed adaptation capabilities[111,202,209] (but see Dam et al.[210]).

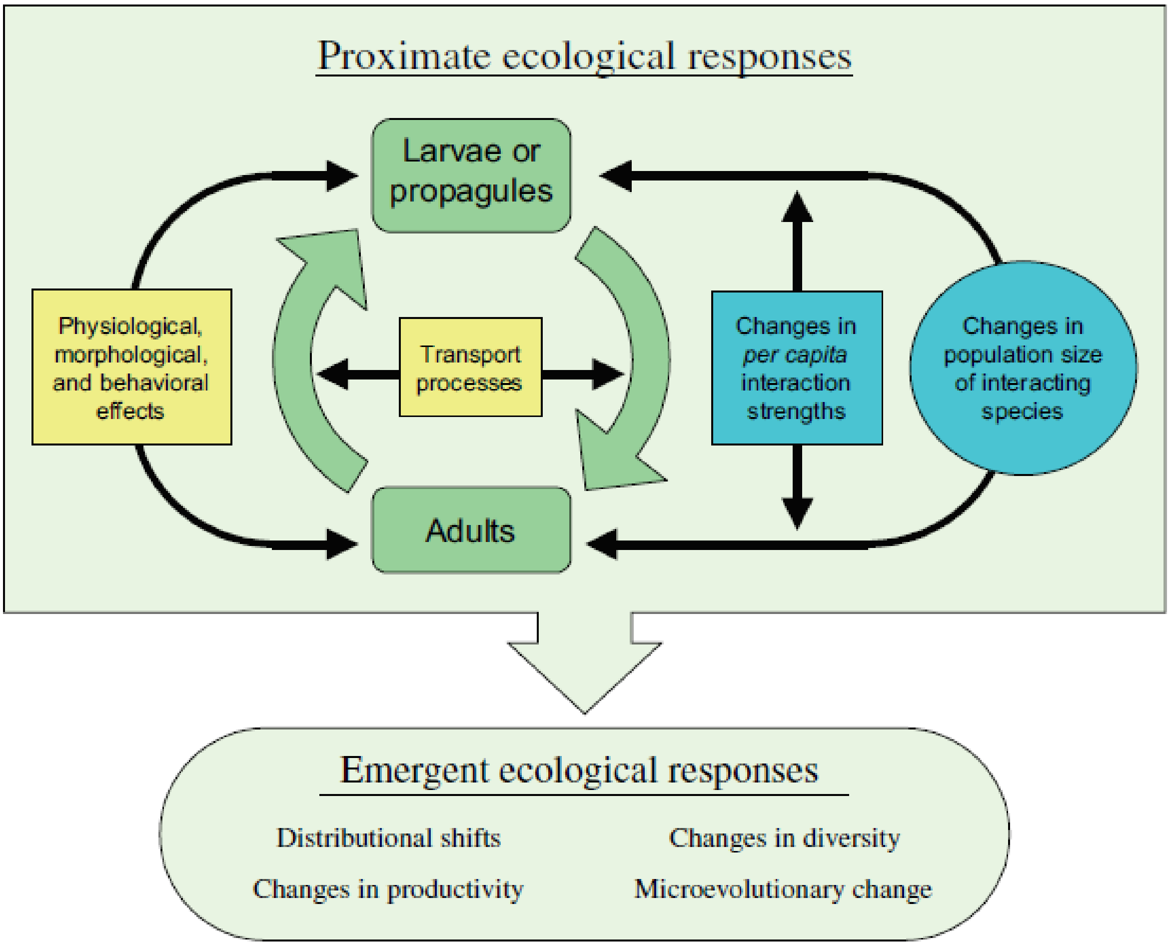


Figure 0.7 Potential ecological response to climate change. The life cycle of a generic marine species is show in green. Abiotic changes in the environment have direct impacts (yellow boxes) on dispersal and recruitment, and on individual performance at various stages in the life cycle. Additional effects are felt in the community level via changes in the population size and per capita effects of interacting species (in blue). The proximate ecological effects of climate change thus include shifts in the performance of individuals, the dynamics of populations, and the structures of the communities. Taken together, this proximal effects lead to emergent patterns such as changes in species distributions, biodiversity, and micro-evolutionary processes. Source: Harley et al.[211].

0.4.1.3 Niche-tracking

In the face of environmental change, species can move spatially to maintain existing physiological associations with particular climates that define each species' climatic niche. When environmental change occurs, species are expected to move geographically by tracking their climatic niches (niche-tracking) through time. To keep on their niche, the species ecological responses to warming oceans include earlier spring events and delayed autumn cycles (phenological shifts) at mid and high latitudes, and distribution shifts (bio-geographical shifts) (Figure 0.7).

0.4.1.3.1 Phenological shifts

There is now ample evidence that over the last decades, the phenology - the timing of seasonal activities such as migration, flowering or breeding[212,213] - of many plant and animal species has advanced and that these shifts are related to climate change[31,110,214,215]. When environmental conditions (e.g. temperature) change in a given region, the species first response to cope with new conditions will be to modify its life cycle in such a way that its critical developmental are "*tuned*" with seasonal environmental variability. If changes in timing are possible, the species will stay on the region. If not, it will decrease in abundance and might disappear locally, implicating a biogeographical shift. Spring phenology has been reported as advancing on average by 2.3 to 2.8 days/decade on land and by 4.3 days/decade at sea[111]. However, the strength of the phenological response to climate change for both marine and terrestrial species varies among taxonomic or functional groups[216]. For example, phytoplankton can respond rapidly to environmental changes with blooms occurring much faster (6.3±1.6 days/decade) compared to the flowering of trees and plants on land (1.1-3.3 days/decade)[215].

0.4.1.3.2 Biogeographical shifts

When processes of tolerance, acclimation, and adaptation are not enough to allow persistence *in situ*, redistribution is required for population or species persistence. Many marine species are predicted to undergo considerable range shifts in response to climate change as they attempt to track their preferred environmental envelopes. Broadly, species are predicted to move toward the poles and/or to greater depths with a warming climate[217,218]. However, the potential for such range shifts is heavily dependent upon the dispersal capacity of species, which is the key mechanism by which populations can persist through major environmental changes[120,219-221]. Due to its limited movement capacity, distributional shifts in plankton are related to extinction and colonization of the populations, while mobile species like fish are able to shift by themselves. Characteristic common among marine organism, such as high rate of propagule production and dispersal by ocean currents, has led to faster expansion of distributions than observed for plants and animals on land. For example, data from the CPR survey in the Northeast Atlantic Ocean indicate that zooplankton exhibit distribution range shifts in response to global warming that are among the fastest and largest of any marine or terrestrial group[13,222,223]. Meta-analysis studies reveal that average range shift for terrestrial communities to be of 6.1 km/decade[110] and from 1.4 to 72 km/decade for marine communities[58,111]. The rapid pace of climate change[224,225] means that range shifts are expected to be the dominant impact on ecosystem function and structure[226,227].

0.4.1.4 Extinction

Some of the most negative impacts of climate change are the loss of diversity – including genetic, species, and functional – that accompany extinctions. Sub-lethal and lethal effects of high temperature in populations at range edges occur when physiological thresholds are exceeded as environmental temperature increases, and are well-documented[228-230]. Species have a suite of mechanisms that allow them to cope with changes in climate, and the degree to which each of these is required for persistence depends on the magnitude of environmental alteration relative to the species' tolerance limits[219,231,232].

0.4.1.5 Changes in the structure of the community

Biological changes are often species dependent and can lead to community-level changes in time and space. These community re-assemblies are believed to be among the most dramatic consequences of climate change, as they can alter predator-prey relationships and thus ultimately modify entire food webs[31,233]. At the community level, climate influences species recruitment through changes in population dynamics and dispersal. At the ecosystem scale, trophic cascade intensifies the effect of climate change from phytoplankton and zooplankton to higher trophic levels, altering the strength of species interaction[32,234]. The combination of these effects results in emergent ecological responses, which include both phenological and biogeographical shifts[31,111,202,215,235]. In this context, the influence of climate-induced forcing on plankton has been particularly studied, this group being sensitive to subtle changes in temperature[88,91,209,236].

0.4.2 Climatic scenario for the XXI century

Of the various attempts to generate emissions projections for input into climate models, the IPCCs Special Report on Emission Scenarios[190] or SRES, is probably the most comprehensive and visible, and as a result has attracted considerable critical analysis. By 2100 most projections of human-induced climate change fall into ranges of about 1.3 to almost 4.5°C increase in annual global mean surface temperature compared to the period 1961-1990[183].

0.5 Hypothesis and objectives

This study aims to gain an understanding of the global biogeographical patterns of marine communities and its response to a changing climate. We identified some gaps of knowledges on how marine plankton populations are connected. We focused on plankton as case study because these organisms are not only a key component in the marine food-web but an excellent sentinel of climate change. This thesis pretends to report broad scale macro-ecological patterns of plankton communities in a multidisciplinary way, from genes to community level, from coastal areas to global ocean, from historical trends to future projections. For that, state of the art statistical tools have been applied in global datasets.

The PhD thesis is **structured** in two main parts and four chapters:

- **Part I**: Climate change and habitat modelling of plankton (Chapter 1 and 2)
- **Part II**: Connectivity and biogeographical patterns of plankton (Chapter 3 and 4).

Overall, we aimed to answer the following **questions**:

1. Can we characterize the ecological niche of zooplankton and test whether the zooplankton populations are tracking its thermal niche due to observed warming trends?

2. Will habitat models help to determine to which extent the future North Atlantic zooplankton biogeographical patterns will be affected by climate change by the end of the century?

3. Is marine plankton connectivity related to body size? Do macro- and micro-organism follow the same rules in terms of spatial patterns of community assembly?

4. Does dispersal shape similarly the population genetic and community composition of marine plankton and macro-benthic communities?

The underlying **hypothesis** posed to each questions are:

1. We expect zooplankton communities to keep pace with climate change by thermal-niche tracking. We also expect changes in the zooplankton community through time in response to climate.

2. Marine organisms typically respond to climate change by shifting their biogeographic ranges to keep their thermal regime[111]. We expect a response of zooplankton to climate change in terms of range shifts in distributional patterns, changes in the structure of the community, and an advance in the seasonal cycles by the end of the century.

3. We hypothesize that smaller the size micro-organism will have higher dispersal capacity compared to large bodied plankton. This is based on the fact that smaller micro-organism have higher population sizes hence are less prone to demographic stochasticity, which ultimately results in less ecological drift.

4. We hypothesize that planktonic species will have a higher dispersal distance than macro-benthic species at both the genetic and community levels. We base this prediction on constraints to movement in adult macroinvertebrates within the seabed, which are only partially compensated for by their larval stage. In comparison, pelagic plankton experience higher seascape connectivity.

In order to test the previous hypothesis four main **objectives** were stated within this PhD thesis:

1. Test whether the zooplankton community is responding (”what changes”) to the ongoing temperature change, as well as to detect the amplitude of the responses (”by how much”) and its timing and spatial scales.

2. Evaluate the impacts of climate change on plankton using habitat modelling techniques (GAMs), and its coupling to climatic models to determine the rate of migration and seasonal and community changes of these animals in the North Atlantic Ocean.

3. Assess the global connectivity patterns of pelagic communities in relation to geographical and ecological distances at different taxonomic groups (from microbial prokaryotes to small mesopelagic fish) based upon beta-diversity metrics.

4. Evaluate the vulnerability of marine biodiversity at global scale to climate change by analyzing the dispersion and connectivity patterns in populations of different marine ecosystems (plankton in open sea and benthic macroinvertebrates on the coast).

0.6 Thesis Structure

Beyond this **General Introduction** in the topic which aimed to give some insights on the concepts that will be discussed during the chapters, the main body of the thesis is structured in 4 chapters (**Chapter1-4**) followed by a **General discussion** and **Conclusions.**

- **Part I : Climate change and habitat modelling of plankton**

Chapter 1 Explores whether the significant sea warming trend that has already been observed in the North Atlantic and Mediterranean Sea during the last decade is having an effect on the ecological niche of the zooplankton communities.

Chapter 2 describes the potential impacts of future climate change on the structure, distributional patterns and phenology on zooplankton communities, by means of habitat modelling. The model and projections are supported by a temporal validation undertaken using the North Atlantic climate regime shift that occurred in the 1980s. Prior to the projections, the GAM model performance has been compared with other habitat model techniques (Maxent and Mahalanobis Distance Algortihm).

- **Part II: Connectivity and biogeographical patterns of plankton**

Chapter 3 reports we a global effort to identify characteristic connectivity scales and the factors driving them for pelagic organisms spanning from marine prokaryotes to mesopelagic fish. To that end, two unique datasets have been merged: (1) global estimates of timescales of ocean connectivity and (2) biological data collected globally along the Malaspina circumnavigation expedition. We check whether organismal body size is a key biological trait shaping the spatial patterns of community assembly.

Chapter 4 tests whether dispersal traits in marine species determine the connectivity degree among communities and among populations within species. To that end, we used meta-analysis data on the population genetic and community composition of plankton in the open ocean and macro-benthos in the coastal areas.

0.7 List of publications and oral communications

Part of the information in this Dr. Philos Thesis has been published (or in preparation) and presented in the following scientific articles and conferences

Publications

- **Villarino, E**., Chust G., Licandro P., Butenschön M., Ibaibarriaga L., Larrañaga A. & Irigoien X. (2015). "Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change". Marine Ecology Progress Series, 531, 121-142.
- **Villarino, E**., Watson, J.R., Jönsson, B., Gasol, J., Salazar, G., Acinas, S., Estrada, M., Massana, R., Logares, R., Giner, C., Pernice, M., Olivar, M.P., Citores, L., Corell, J., Ezpeleta, N., Acuña, J., Molina-Ramirez, A., González-Gordillo, J.I., Cozar, A., Marti, E., Cuesta, J., Agusti, S., Fraile-Nuez, E., Duarte, C., Irigoien, X., and Chust, G. "Large-scale ocean connectivity and planktonic body size". *Submitted to Nature Communications* (in review).
- **Villarino, E**., Irigoien, X., Villate, F., Iriarte, A., Uriarte, I., Zervoudaki, S., Carstensen, J., O`Brien, T and Chust, G. "Long-term trends of zooplankton and sea warming across the North Atlantic and Mediterranean Sea". *In prep.*
- Chust G., **Villarino E.,** Chenuil A., Irigoien X., Bizsel N., Bode A., Broms C., Claus S., Fernández de Puelles M.L., Fonda-Umani S., Hoarau G., Mazzocchi M.G., Mozetič P., Vandepitte L., Veríssimo H., Zervoudaki S. & Borja A. (2016). "Dispersal similarly shapes both population genetics and community patterns in the marine realm". Scientific Reports, 6, 28730.
- Chust, G., Vogt, M., Benedetti, F., Nakov, T., Villéger, S., Aubert, A., Vallina, S., Righetti, D., Not, F., Biard, T., Bittner, L., Benoiston, AS., Guidi, L., **Villarino, E**., Gaborit, C., Cornils, A., Buttay, L., Irisson, JO, Chiarello, M., Lima, AV, Blanco-Bercial, L., Basconi, L and Ayata, SD. "*Mare incognitum*: A glimpse into future plankton diversity and ecology". *Submitted to Frontiers in Marine Science.*

Collaborations in other publications related to the topic

- Lezama Ochoa N., Murua H., Chust G., Van Loon E., Ruiz J., Hall M., Chavance P., Delgado de Molina A. & **Villarino E.** (2016). "Present and future potential habitat distribution of *Carcharhinus falciformis* and *Canthidermis maculata* by-catch species in the tropical tuna purse-seine fishery under climate change". Frontiers in Marine Science, 3.
- Goldsmit, J., Howland, K., Archambault, P., Barber, D., Chust, G., Liu, G., Lukovich, J., McKindsey, C and **Villarino, E**. "Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic". Submitted to Axios review.

Oral communications

- **Villarino**, E., Chust, G., Ibaibarriaga, L., Licandro, P., Valle, M., Butenschön, M., Larrañaga, M., Irigoien, X. ICES ASC 2013, Reykjavik, September 23-27. "Modelling the future response of zooplankton species to climate change in the North Atlantic".
- **Villarino**, E., Chust, G., Ibaibarriaga, L., Licandro, P., Kreus, M., Butenschön, M., Larrañaga, M.,. Irigoien, X. ICES ASC 2014, La Coruña, September 15-19. "Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change"
- Chust, G., **Villarino**, E., Licandro, P., Ibaibarriaga, L., Butenschön, M., Irigoien, X. 2nd International Ocean Research Conference (IORC) "One Planet One Ocean", Barcelona, 17-21 November 2014. "Response of zooplankton to climate change from 1959 to 2100: observed trends and future projections".
- **Villarino**, E., Chenuil, A., Chust, G. Aquatic Science Meeting ASLO, Granada, February 2015. "Dispersal scales in marine plankton and benthic invertebrates: A meta-analysis approach".
- **Villarino, E**., Watson, J.R., Jönsson, B., Gasol, J., Salazar, G., Acinas, S., Estrada, M., Massana, R., Logares, R., Giner, C., Pernice, M., Olivar, M.P., Citores, L., Corell, J., Ezpeleta, N., Acuña, J., Molina-Ramirez, A., González-Gordillo, J.I., Cozar, A., Marti, E., Cuesta, J., Agusti, S., Fraile-Nuez, E., Duarte, C., Irigoien, X., and Chust, G. ICES ASC 2016, Riga Sept 19-23. "Large-scale ocean connectivity and planktonic body size"
- **Villarino**, E., Irigoien, X., Villate, F., Iriarte, A., Uriarte, I., Butenschön, M., Licandro, P., Zervoudaki, S., Carstensen, J., Chust, G. UHINAK 2016 Sept 27-28."Modelling the ecological niche of North Atlantic zooplankton communities in response to climate change"
- Goldsmit, J., Howland, K., Chust, G., **Villarino, E**., Liu, G., Lukovich, J., Barber, D., and Archambault, P. Aquatic invasive species in the Canadian Arctic: present and future high risk geographic locations and species. ASLO Aquatic Science Meeting, Granada, Spain. February 2015 .
- Goldsmit, J., Howland, K., Chust, G., **Villarino, E** and Archambault, P. Is the Canadian Arctic likely to be invaded by aquatic invasive species? A niche modelling study under various climate change scenarios. ICES Annual Science Conference, A Coruña, Spain. September 2014.

Part I: Climate change and habitat modelling of plankton

1. Chapter 1: “Long-term trends of zooplankton and sea warming across the North Atlantic and Mediterranean Sea”

Villarino, E., Irigoien, X., Villate, F., Iriarte, A., Uriarte, I., Zervoudaki, S., Carstensen, J., O`Brien, T and Chust, G. “*Long-term trends of zooplankton and sea warming across the North Atlantic and Mediterranean Sea*”. *In prep.*

The rapid warming detected in the North East Atlantic during the last decades has affected distributional patterns of marine communities. Here, we examine the correspondence between sea surface temperature warming and long-term trends of zooplankton abundance (1980-2012) at three locations in the North Atlantic (NE Bay of Biscay and the Kattegat Sea) and Mediterranean Sea (Gulf of Saronikos). We analysed the response of each species to climate to test the hypothesis of thermal niche tracking using time-series seasonal decomposition and habitat-modelling. Further, we explored zooplankton community changes through time based upon β-diversity metrics, and their relation to climatic conditions. Results at both levels reveal that the zooplankton composition is changing with time across the North Atlantic and Mediterranean Sea: (1) at species level, a major shift in species abundance has been observed, with 91% of the species showing significant changes in abundance. In 46% of the cases, the species abundance follows the expected trend by thermal niche, which is significantly higher (Kappa p-value 0.05), than what is expected by chance (41%). At community level, β-diversity changes were related to niche descriptors, mostly to changes in sea temperature, and environmental factors (21%). Our findings indicate a fundamental role of temperature in structuring zooplankton biodiversity, and reveal that changes in ocean temperature are rearranging coastal communities.

1.1 Introduction

The significant sea warming trend identified in the North Atlantic[237-240] and Mediterranean Sea[241] during the last decades has fostered the interest to test how warming is affecting temporal patterns of marine communities. In the last decades, a large number of studies have reported covariations between climate change and alterations in the abundance, spatial range and phenology of plankton[31,88,212,242,243]. These alterations include poleward movements in range shift distributions, shifts in the seasonal cycles and changes in abundance and community structure. In particular, shifts in plankton biogeography and community structure rank among the fastest and largest documented[111,222,244]. Species responses to climate change, hence, may lead to local extinction and invasions, resulting in changes in the temporal patterns of community assembly. The understanding of the climatic effects on marine populations is an essential step towards conserving and managing marine resources[245,246].

In this context, time series of environmental measurements and biological components are essential for detecting, measuring and understanding changes in marine communities. Monitoring of the zooplankton abundance, distribution and species composition is instrumental to detect ecological changes in oceanic and coastal environments. Zooplankton time-series provide useful tools to examine climate-ecosystem interactions: (1) population dynamics and physiological rates are directly influenced by water temperature[12,13], (2) zooplankters are ectotherms with short generation times, so they have the potential capacity to respond fast to environmental changes through phenotypic plasticity or evolutionary adaptation, and therefore, they are considered excellent sentinels of biotic responses to environmental change[15-17], (3) they are also a key link between primary producers and large predators. Additionally, major zooplankton population fluctuations are not missed by sampling at monthly intervals, zooplankton is an abundant, not commercially exploited group, and it can be easily quantified. Some zooplankton time series of ten years or more in length are now available for many geographically separated regions, carried out as part of different monitoring and research programs[247]. Today, however, within-regions time-series comparison studies are still scarce.

When environmental change occurs, species are expected to move geographically by tracking their climatic niches (niche-tracking) or adapting to local conditions phenotypically or evolutionarily. To keep on their niche, the species ecological responses to warming include earlier occurrence of seasonal events (phenological shifts), and biogeographical shifts. In this paper, we have carried out a two-fold analysis: (1) First, at species level, we have checked whether the population is responding ("what changes") to the ongoing temperature change, and if this response is consistent with species thermal niche tracking[248,249]. We have also analysed the amplitude of the responses ("by how much") and its timing and spatial temporal scales ("when and where rates of changes are strongest"). (2) Second, at community level, we have explored if assemblage composition varies through time, due to sea warming. We expect zooplankton similarity to decay with time, owing to the occurrence of new colonizing species coming from the south and other local species moving to the north, to keep their niches. To answer these questions, we analysed long-term trends of zooplankton and temperature at three locations across the North East Atlantic (SE Bay of Biscay and the Kattegat Sea) and the Mediterranean Sea.

1.2 Methods

1.2.1 Study sites

Study sites are located in three coastal zones: the Kattegat, between the Baltic and the North Sea, the mouth of the estuary of Urdaibai in the southern Bay Of Biscay, and the Gulf of Saronikos, in the eastern Mediterranean Sea (Figure 1.1). We merged the Alborg Bay, Ven and Gniben stations species abundance and abiotic parameters into one "big" Kattegat station, due to their proximity and low number of species on each location (Figure 1.1).

The Kattegat is a transition zone between the Baltic Sea and the North Sea, with a substantially higher salinity range (and variability) than in the sea areas it connects. Mean temperature ranges from 0.9°C in February to 17.3°C in September[250,251]. Temperatures are influenced by several processes, including incoming solar heat flux and the mixing of warmer saline water from North Sea and outflow of colder brackish Baltic Sea water. The flow in the Kattegat is mostly governed by wind speed and direction, and hence quite variable. The mean depth is ~20 m with a maximum depth above 90 m at the northern boundary, and half the area is shallower than 25 m [252]. Sampling is conducted according to the HELCOM COMBINE manual for zooplankton [253]. Zooplankton is sampled using a WP-2 net with 180 µm mesh towed from 25 m to the surface, with variable (monthly or seasonal) sampling frequency and periodic gaps. We have analysed monthly-seasonal data from 1980 to 2012 (Table 1.1, Figure 1.1).

The estuary of Urdaibai (43°22′N, 2°43′W) is a temperate estuary located on the Basque coast, in the inner Bay of Biscay. It is a relatively short (12.5 km) and shallow (mean depth = 3 m) meso-macrotidal system, with a maximum and minimum width of 1.2 km and <20 m in the outer and inner areas. Sea surface temperature ranges from 11ºC to 23ºC [254] with a rate of increase of 0.019 $°C \cdot year^{-1}$ over the last 50 years [237,238,255]. Most of the estuary exhibits marine dominance, with high salinity waters in the lower half and a stronger axial gradient of salinity towards the head, where it receives most of the freshwater inputs from its main tributary, i.e. the Oka River[20]. The zooplankton time-series at Urdaibai estuary is a monitoring program initiated in 1997[20]. Surveys are carried out monthly at neap tides in different salinity sites of the estuary. We have analysed monthly data from 1999 to 2013 in the marine zone (35 salinity). Vertical profiles of salinity, dissolved oxygen saturation, and samples for chlorophyll-a determination and zooplankton analysis are taken at mid-depth below the halocline. Niskin bottles are used for water samples and zooplanktons are sampled by horizontal hauls with 200 µm plankton nets. More details on the plankton sampling monitoring program can be seen in Uriarte et al.[256]. These data is supplemented by hydro-meteorological data obtained from the Council of Bizkaia, The European Centre for Medium-Range Weather Forecasts (ECMWF) http://www.ecmwf.int/en/research/climate-reanalysis/era-interim, and the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center[256] (http://www.cpc.ncep.noaa.gov/).

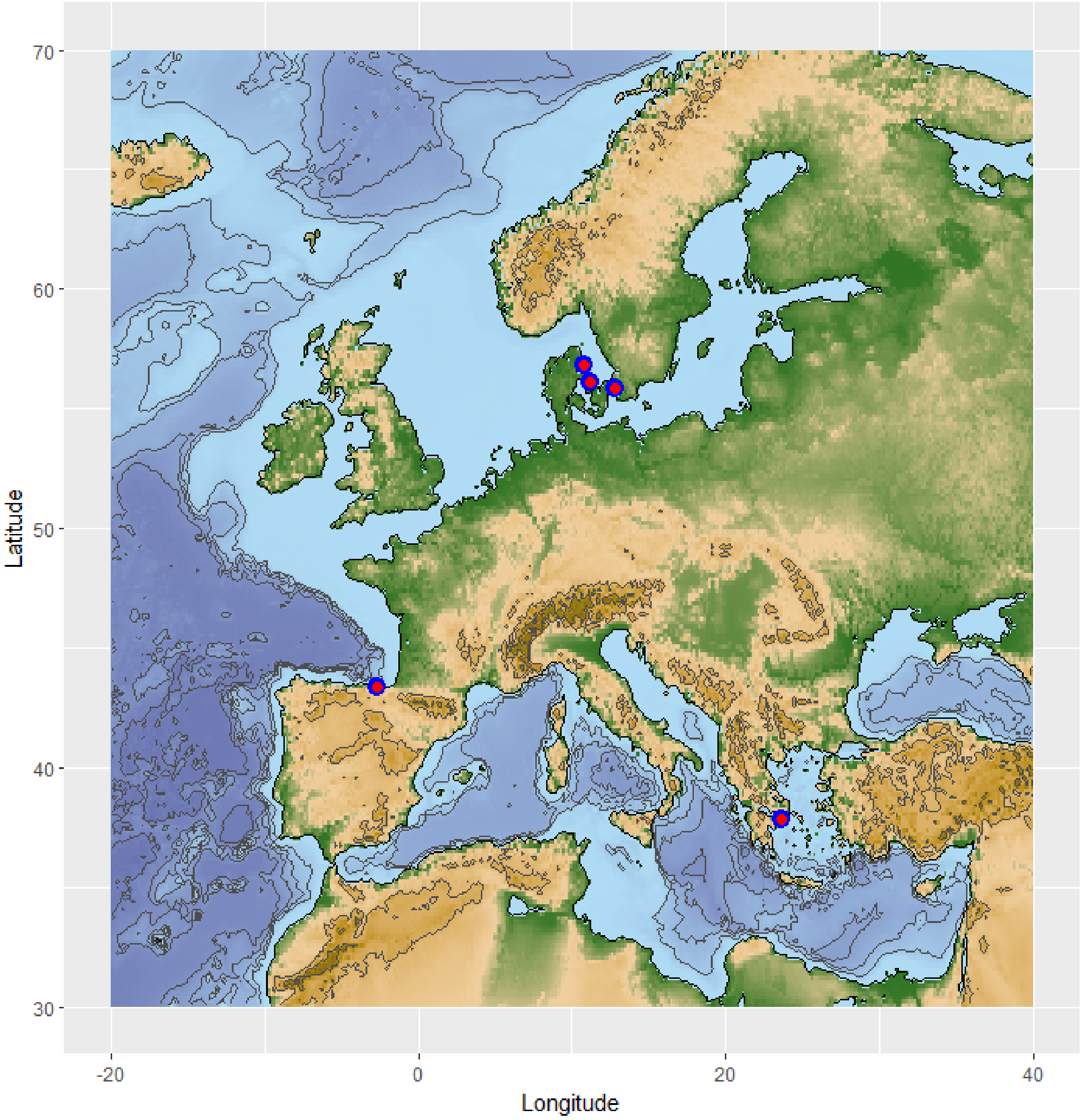


Figure 1.1 Map showing the location of the Kattegat, Urdaibai and Saronikos time series.

The Gulf of Saronikos is a semi-enclosed embayment on the western coastline of the Aegean Sea. Saronikos Station 11 (Saronikos S11) is located in the Saronikos Gulf at the 37° 52.36' N 23° 38.30'with a bottom depth of 78 m. Mean monthly sea surface temperatures (SST) vary from 8°C in the north during winter, up to 26°C in the south during summer. The overall spatial SST and SSS (Sea Surface Salinity) distribution pattern is controlled by distribution of the (colder) Black Sea Waters; advection of the (warmer) Levantine Waters, from the southeastern part of the Aegean; upwelling and downwelling; and, to a lesser extent, but locally important, freshwater riverine inflows[257]. Saronikos S11 is located 7 km from the Athens domestic sewage outfall. Zooplankton at Saronikos sampling station is sampled with a WP2 net (56 cm diameter, 200 µm mesh) from a depth of 75 m to the surface. Monitoring of zooplankton and abiotic factors began in 1987, with variable (monthly or seasonal) sampling frequency and periodic gaps. We have analysed the 1987-2009 period (Table 1.1,Figure 1.1).

1.2.2 Sea temperature time-series

In order to provide a common long-term dataset of water temperatures, data from the NCEP Global Ocean Data Assimilation System (GODAS) was employed at each site for the 1980-2015 period. GODAS provides monthly water temperature data on a 0.333º x 1º latitude-longitude grid, and at multi-water layers (http://www.esrl.noaa.gov/psd/). Additionally, for the Urdaibai station, we used SST data obtained by The Oceanographic Society of Gipuzkoa in the Aquarium of San Sebastian (43º19' N, 2º 00' W), which is located within the southeastern marginal part of the Bay of Biscay. This time-series records daily SST since 2nd July 1946, on a (nearly) daily basis[238]. We have used monthly means of SST for the 1980-2015 period, in this study.

1.2.3 Species by species analysis

First we have analysed the observed abundance of copepod species and the potential temperature at each station. Second, we have compared the observed and expected abundance of copepod species in relation to (1) its thermal optimum, and (2) the species geographical gravity center.

1.2.3.1 Observed zooplankton and temperature trends

Two different time series have been analysed: zooplankton abundance and the potential sea temperature. We have used monthly means for each variable. A root mean square transformation has been applied on the copepod abundance dataset to better observe the trends. Decomposition procedures have been used to disaggregate the trend from the seasonal factors and irregular components for each time-series using moving averages with the *stats* package in R, and filling the missing values using a seasonal Kalman filter with the *zoo*[258] package in R. Subsequently, we have analysed the trend of each variable at the time series (Figure 1.2) by fitting a linear model to estimate the slope and significance of the slope of the trends. To evaluate the statistical significance of the trends, we have used bootstrap cross-validation techniques, derived from non-parametric confidence intervals, which are implemented in the *boot*[258] package of R. We have categorized the observed trends into three classes: increase or decrease (p-value < 0.05; significant bootstrap 95% confidence intervals) and constant (p-value > 0.05; non-significant bootstrap 95% confidence interval). An example of *Oithona similis* abundance trends in shown in (Figure 1.2), for each site.

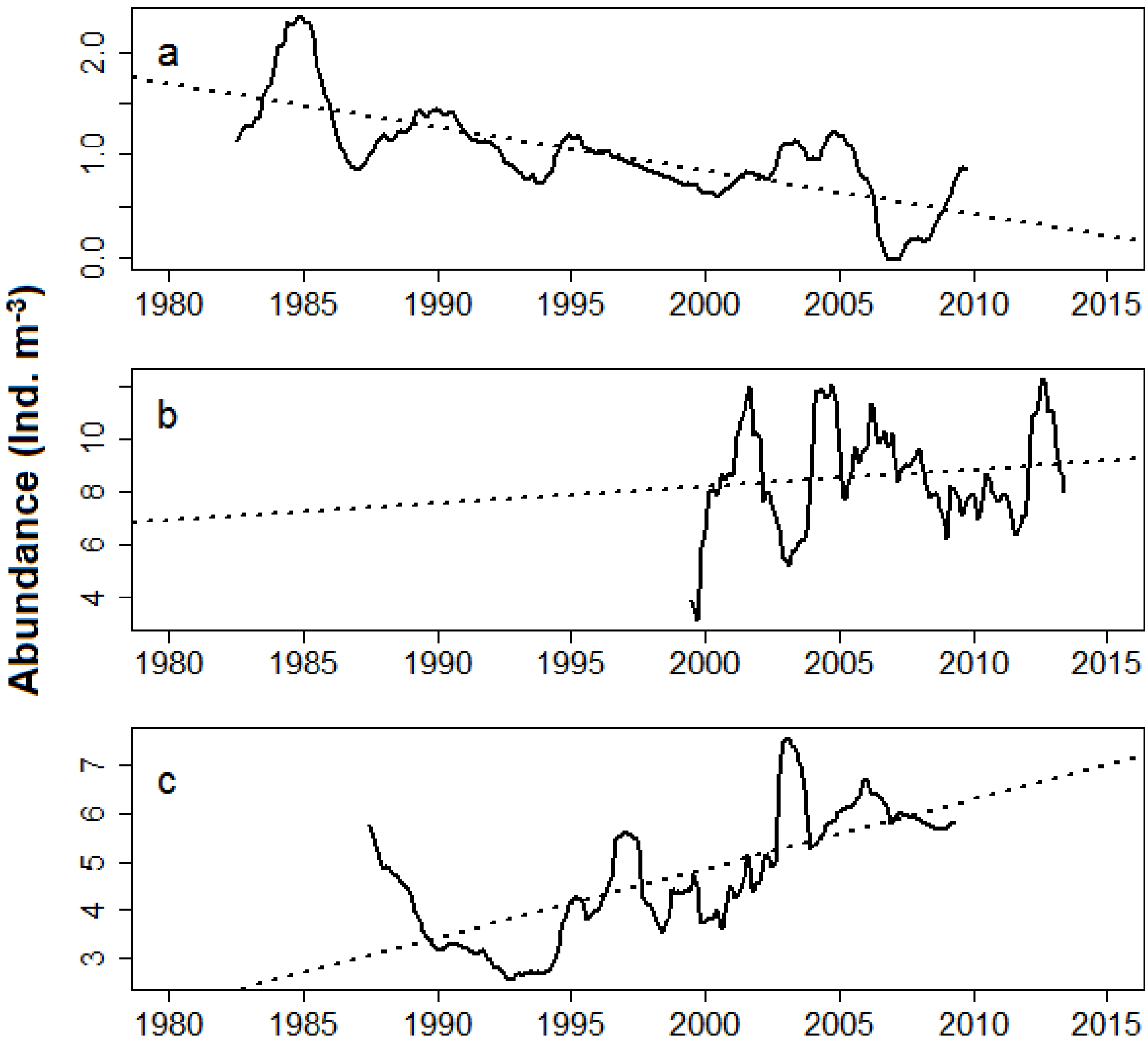


Figure 1.2 An example of *Oithona similis* abundance trends for each station: a) Kattegat, b) Urdaibai, c) Saronikos.

1.2.3.2 Expected zooplankton abundance trends

We have used two descriptors to calculate the expected species abundance trends: (1) each species global thermal optimum, and (2) the species geographical center of gravity, where occurrences are the highest. We have defined the species thermal optimum as the temperature corresponding to the geographical center of gravity of each species. To do so, we have used annual mean SST data for the 1982-1999 period obtained from Aquamaps (http://www.aquamaps.org). For the gravity center calculation we have used species occurrence data obtained from the OBIS global database (Ocean Biogeographic Information System http://www.iobis.org). The centre of gravity has been defined as the mean geographic location of a population [259].

We expect that if the species thermal optimum range is above the potential temperature of the site where that species occurs, the abundance of that particular species to increase with time, due to sea warming. When the species thermal optimum range “falls” within the site’s average potential temperature, the species abundance is not expected to change (Figure 1.3). Similarly, we expect that if the geographical gravity center of the species is below the site`s latitude where the species is observed, the species abundance to increase with time, due to the sea temperature warming trend. On the other hand, if the species geographical gravity center range ”falls” within the site´s latitude, we expect the species abundance trend to keep the same with time.

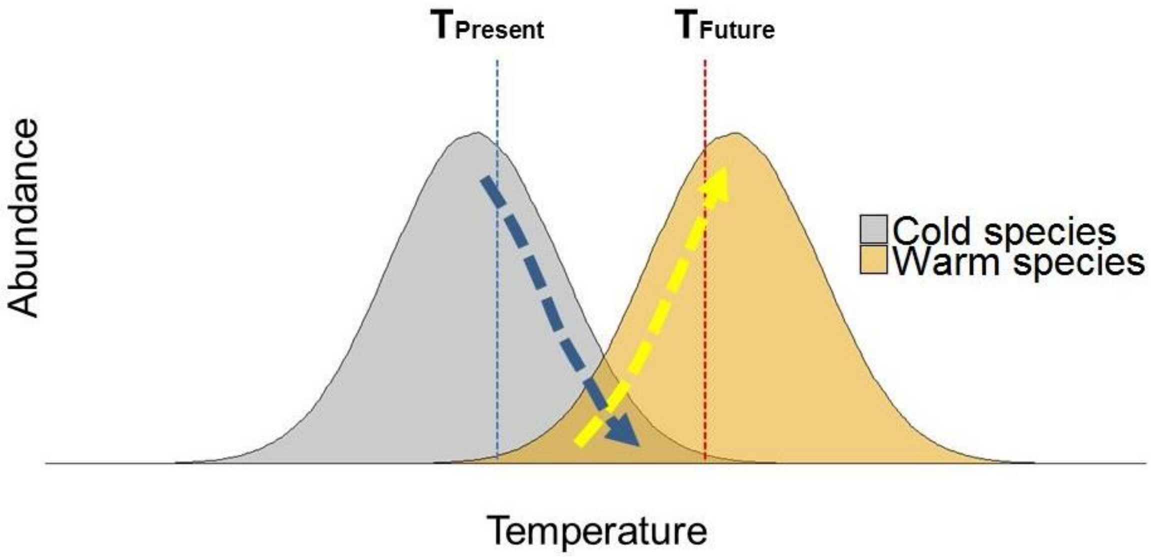


Figure 1.3 A schematic representation showing an example of the abundance response curve of a cold water and warm water species. The vertical lines depict for the SST at the present (blue) and future (red).

1.2.3.3 Statistical test

The correspondence between zooplankton abundance and sea surface temperature trends may be due to random processes, because the species are changing its abundance according to their thermal niche requirements or other environmental changes. To test if the zooplankton population are tracking its thermal niche, we have compared the observed and expected abundance cases using a Kappa test [260]. The Kappa value is calculated from the observed and expected frequencies on the diagonal of a square contingency table. The null-hypothesis is that the extent of agreement between the observed and expected zooplankton abundance trends is the same as random expectation; in that case the Kappa statistic is close to zero. The alternative hypothesis is that the extent of agreement between observed and expected zooplankton is not random. The Kappa value can range from –1 to +1, indicating very good agreement values close to 1, and poor agreement values close to 0 or <0. The Kappa statistic has been used to test the agreement between the observed vs expected zooplanktons abundance trends due to thermal niche, and due to geographical gravity center. If changes in zooplankton abundance are due to "chance", we expect a 1/3 of agreements between observed and expected values because we have 3 categories (decrease, increase and same). The test has been undertaken at each individual station, and for all stations together.

Table 1.1 Evaluation of the statistical significance of the potential temperature trends for the 1980-2015 period using data of (a) GODAS monthly means and (b) SST time series data (monthly means) of the Aquarium of San Sebastian, Spain. The slope of the linear models between the sea surface temperature and time are shown, as well as and non-parametric bootstrap cross-validation confidence intervals and spearman correlations.

(a)

Site	lm slope	p-value lm	°C increase year^{-1}	Boot.corr min	Boot.corr max	Spearman p-value	trend	Temp. range
Kattegat	9.30E-04	0.000433	0.011	0.0564	0.2697	< 0.0001	increase	8.56-8.96
Urdaibai	1.70E-03	< 0.0001	0.020	0.5009	0.6172	< 0.0001	increase	15.91-16.64
Saronikos	1.96E-03	<0.0001	0.023	0.4815	0.6112	< 0.0001	increase	17.01-17.86

(b)

Site	lm slope	p-value lm	°C increase year^{-1}	Boot.corr min	Boot.corr max	Spearman p-value	trend	Temp. range
Aquarium	1.65E-03	<0.0001	0.019	0.3740	0.4994	< 0.0001	increase	8.56-8.96

1.2.4 Community analysis

1.2.4.1 Distance and similarity matrices

At the community level we have analysed how the zooplankton community varies (species temporal turnover) with time at each station, and we have tested if these changes are due to climatic conditions, by controlling for temporal autocorrelation. For that purpose, we have investigated time-decay patterns analysing seasonal and inter-annual variation on species assemblages. To do so, we have calculated three similarity or distance matrices from species composition, environmental factors and time at seasonal and inter-annual basis.

For the biotic similarity matrix, we have calculated pairwise species similarities for each station using the Bray-Curtis dissimilarity (BC) index[261] with species abundance data to infer the variation of the species assemblages (β-diversity matrix):

$$BC = 1 - \frac{2c}{a+b} \qquad (1)$$

where c is the sum of the minimum abundances of the various species, this minimum being defined as the abundance at the site where the species is the rarest; and a and b are the total number of specimens observed at each site, respectively.

The environmental matrix has been computed using the Euclidean distance among the variables (Table 1.5). Variables have been scaled to give equal weight in distance calculations. The environmental variables used have previously shown to be important variables determining zooplankton distribution[88]. The best subset of variables shaping the zooplankton community assembly has been selected using the BIOENV approach [262]. The BIOENV function finds the best subset of environmental variables, so that the Euclidean distances have the maximum (rank) correlation with community dissimilarities.

The time matrix has been calculated using the Euclidean distance between each time step in order to describe the temporal autocorrelation[261]. In this case, each time step belongs to a consecutive month.

1.2.5 Correlations of species turnover with time and environmental predictors

Mantel correlations[263] between species composition dissimilarity and environmental distance have been carried out for causal modelling and to infer the temporal patterns of zooplankton community structure. Similarly, we have analysed the influence of SST as a unique environmental driver accounting for community variation. Since relation between community dissimilarity and environment may also result from temporal autocorrelation[261], partial Mantel tests and Canonical Correspondence Analysis (CCA) have been used for partialling out the time, using the *vegan* [263] package in R.

We regressed assemblage similarity and temporal distance and obtained the slope of the linear regression as an indicator for the rate of temporal turnover. The slope was measured as a decrease in assemblage similarity per year. Steeper (i.e. more negative) slopes indicate faster temporal turnover, whereas a slope = 0 indicates no turnover with time. For each station, Bray-Curtis similarities have been plotted against each time lag from 1 to n (depending on the length of each time series). That way, we have represented the similarity composition against the temporal autocorrelation looking the similarity at each consecutive pairs of times. We have undertaken the analysis at seasonal and inter-annual basis taking into account each month or year lag, and explored time-decay patterns.

1.3 Results

1.3.1 Temperature trends

Sea temperatures obtained from the GODAS dataset revealed a significant increase in the 1980-2015 period at the three sites (p-value < 0.001) (Figure 1.4). The sea warming rate of increase was faster in Saronikos (0.023 °C $year^{-1}$) and Urdaibai (0.020 °C $year^{-1}$), compared to the Kattegat Sea (0.011 °C $year^{-1}$) (Table 1.1a). Very similar warming trends were found for the SST values in NE Bay of Biscay measured at the Aquarium of San Sebastian (0.019 °C $year^{-1}$) (Table 1.1a and b).

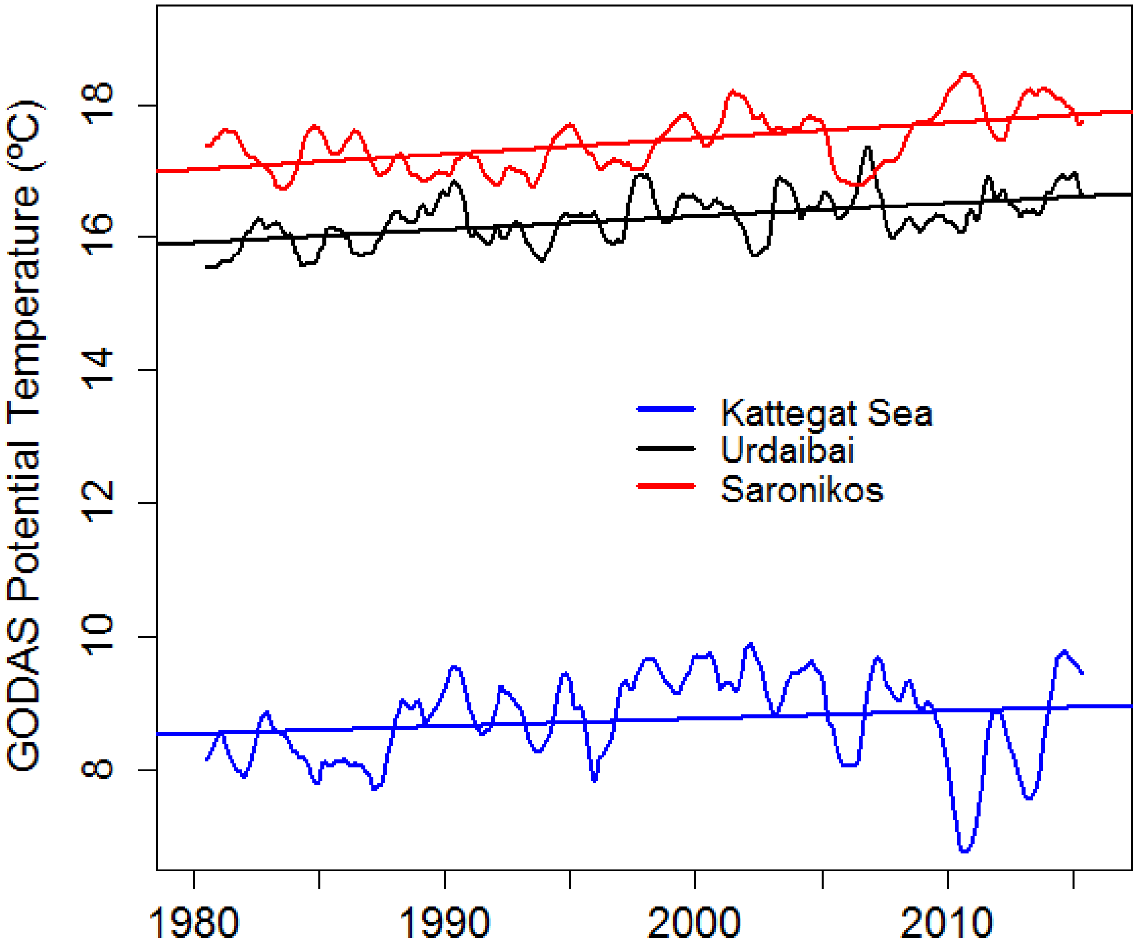


Figure 1.4 GODAS potential temperature trends for the period 1980-2015 at each station.

1.3.2 Species by species analysis

Saronikos showed the most biodiverse community out of the three considered here with 57 species, followed by Urdaibai (34 species) and the Kattegat stations (22 species) (Table 1.2). When all stations are considered, strong temporal variations in species abundance were observed, with significant changes in abundance: in the majority of cases (61) the species showed a significant trend (increase or decrease) whereas in 2 cases we did not observe any significant trend. Overall, there is a significant correspondence between the observed and expected trends due to thermal niche, and due to the geographical center of gravity, according to the Kappa test (p-value = 0.04), with 46% of agreements (Table 1.3a and b), which is higher of what is expected by chance (41%). At each individual station, the Kattegat zooplankton community is responding to a warming trend as expected by thermal niche and gravity (Kappa p-value = 0.01) with 50.90% of agreements, but the zooplankton communities of Urdaibai and Saronikos are not responding as expected by predictors.

Table 1.2 Time series stations and the median potential temperature of each of them according to GODAS.

Site	Long.	Lat.	Depth (m)	Number of species	Period	Potential temp.
Kattegat	11.56	56.28	36	22	1980-2012	8.54
Urdaibai	12.75	43.36	4.5	34	1999-2013	15.2
Saronikos	11.16	37.87	77	57	1987-2009	17.3

1.3.3 Community analysis

Figure 1.5 shows the temporal development of the copepod community similarity at each time-lag, for each site. At all the sites, the similarity decreased significantly with time at both, month and year basis (Table 1.4a). However, the time-decay slopes are higher in the year-to-year analysis. Here, similarity also decayed with time. In terms of the seasonal patterns, a marked seasonal signal is observed at the Urdaibai site (Figure 1.5 b), followed by the Kattegat, with some irregular seasonal cycles, and the Saronikos, where no regular pattern is observed (Figure 1.5 b and c).

Table 1.3 Cohen's Kappa statistic to measure the degree of agreement between (A) the observed zooplankton abundance frequencies vs the expected zooplanktons abundance frequencies due to thermal niche, and (B) the observed zooplankton abundance frequencies vs the expected zooplanktons abundance frequencies due to gravity center. Kappa p-value < 0.05 means that there is a statistical significance relationship between observed and expect frequencies.

a)

			decrease	increase	same	(%) agreements by predictor	Kappa p-value	Number of species	(%) agreements by chance
Agreements observed vs expected due to thermal niche	**All sites**	decrease	16	22	10	45.98	0.04	137	40.85
		increase	15	45	16				
		same	4	7	2				
	Kattegat	decrease	10	3	7	50.90	0.01	55	36.79
		increase	7	17	7				
		same	0	3	1				
	Urdaibai	decrease	5	5	0	38.46	0.45	26	37.42
		increase	2	5	4				
		same	2	3	0				
	Saronikos	decrease	4	13	1	53.57	0.33	56	50.76
		increase	7	25	2				
		same	1	2	1				

b)

			decrease	increase	same	(%) of agreements by predictor	Kappa p-value	Number of species	(%) agreements by chance
Agreements observed vs expected due to gravity center	**All sites**	decrease	16	22	10	45.98	0.04	137	40.85
		increase	15	45	16				
		same	4	7	2				
	Kattegat	decrease	6	7	7	50.90	0.01	55	41.28
		increase	6	21	4				
		same	0	3	1				
	Urdaibai	decrease	5	5	0	38.46	0.45	26	37.42
		increase	2	5	4				
		same	2	3	0				
	Saronikos	decrease	5	10	3	44.64	0.34	56	42.09
		increase	7	19	8				
		same	2	1	1				

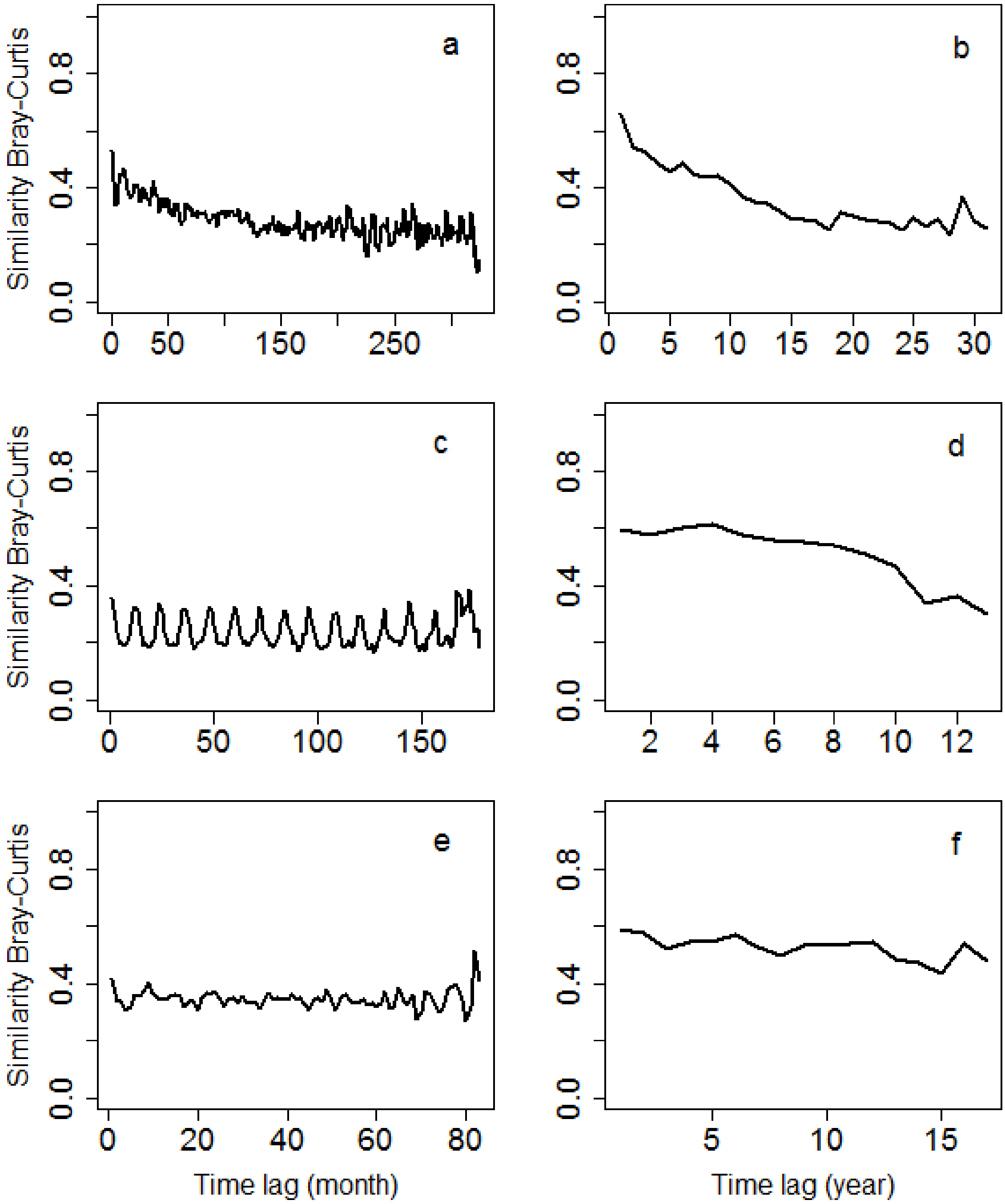


Figure 1.5 Relationship between community similarity and each time lag for month and year: Kattegat (a-b), Urdaibai (c-d) and Saronikos (e-f).

Figure 1.6 shows the relationship between the Bray-Curtis zooplankton community similarity and the environmental distance at each station. Similarity decays more abruptly with environmental distance, with slopes an order of magnitude higher in most cases, at both month and year analysis, compared to the time-decay slopes (Table 1.4a). In addition, slopes are similar if we take into account SST as the unique environmental driver limiting zooplankton temporal distributional patterns (Table 1.4a).

Table 1.4 (a) Slope of the parametric linear models between Bray-Curtis plankton similarity and time, environmental distance, and temperature. (b) Mantel correlations between Bray-Curtis plankton similarity and time, environmental distance, and temperature. Mantel partial correlations after controlling for the effects of time, environmental and temperature descriptors, in significant cases. The statistical significance of comparisons was assessed using Mantel and partial Mantel tests based on Pearson's product moment correlation using 9999 permutations (* = < 0.05 ; ** = <0.01).

(a)

Period	Site	Sim.vs time (lm slope)	Sim. vs env. (lm slope)	Sim. vs temp. (lm slope)
Month	Kattegat	-0.0003**	-0.0430**	-0.0458**
	Urdaibai	-0.0001**	-0.0204**	-0.0263**
	Saronikos	-0.0002**	-0.0722**	-0.0722**
Year	Kattegat	-0.0113**	-0.0175**	-0.0596**
	Urdaibai	-0.0194**	-0.0799**	-0.1053**
	Saronikos	-0.0051*	-0.0397**	-0.0460**

(b)

Period	Site	Mantel sim. vs time	Mantel sim. vs env	Mantel sim. vs temp.	P.mantel sim vs time (out env.)	P.mantel sim vs env(out time)	P.mantel sim vs time (out temp.)	P.mantel sim vs temp. (out time)
Month	Kattegat	0.1117**	0.2246**	0.1788**	0.0752**	0.2095**	0.1118**	0.1787**
	Urdaibai	0.0248	0.1202**	0.1189**	0.03098	0.1234**	0.0279	0.1196**
	Saronikos	0.0331	0.3828**	0.3828**	0.05045	0.383**	0.0504	0.3830**
Year	Kattegat	0.3205**	0.3600**	0.2385	0.1876*	0.2606*	-	0.2030
	Urdaibai	0.3238**	0.6086**	0.5518	0.2095	0.5694*	-	0.5310
	Saronikos	0.1843*	0.3337*	0.3099*	0.1378	0.3022*	0.1503	0.2933*

At monthly basis, β-diversity is not significantly correlated with time in Urdaibai (r = 0.0248; p-value > 0.05) and in Saronikos (r = 0.0331; p-value > 0.05), contrary to the year analysis, where correlations are significant in all the sites (Kattegat, r = 0.3205 and p-value < 0.01; Urdaibai, r = 0.3238 and p-value < 0.01; Saronikos, r = 0.1843 and p-value < 0.05) (Table 4b). However, the Mantel correlations between β-diversity and the environmental distance are significant in all stations at both year and month periods, and much higher compared to the correlations between β-diversity and time (Table 1.4b). The partial Mantel correlation between β-diversity and environmental distance, controlling for the time, remain significant for each station (Table 1.4b). This also reveals low covariation between environmental distance and the time. Results from the CCA for the inter-annual time-lag analysis (Figure 1.7) showed that in the Kattegat, time and environmental predictors accounted for approximately equal portions of variation (18-26%) with few overlap between both (4%). In turn, the relative contribution of environmental factors is much higher in Urdaibai and Saronikos, compared to temporal autocorrelation (Figure 1.6). The best subset of environmental drivers has been selected using BIOENV (Table 1.5). At all sites and both periods, SST is selected by the BIOENV models, indicating a key role shaping the zooplankton temporal changes. Hence, the niche descriptors (and in particular, SST) were significantly explaining the copepod community variation at the 3 sites, after partialling out for temporal autocorrelation. However, a large part of the β-diversity variance remained unexplained according to residuals at all three sites (Kattegat = 52%, Urdaibai = 72% and Saronikos = 68%).

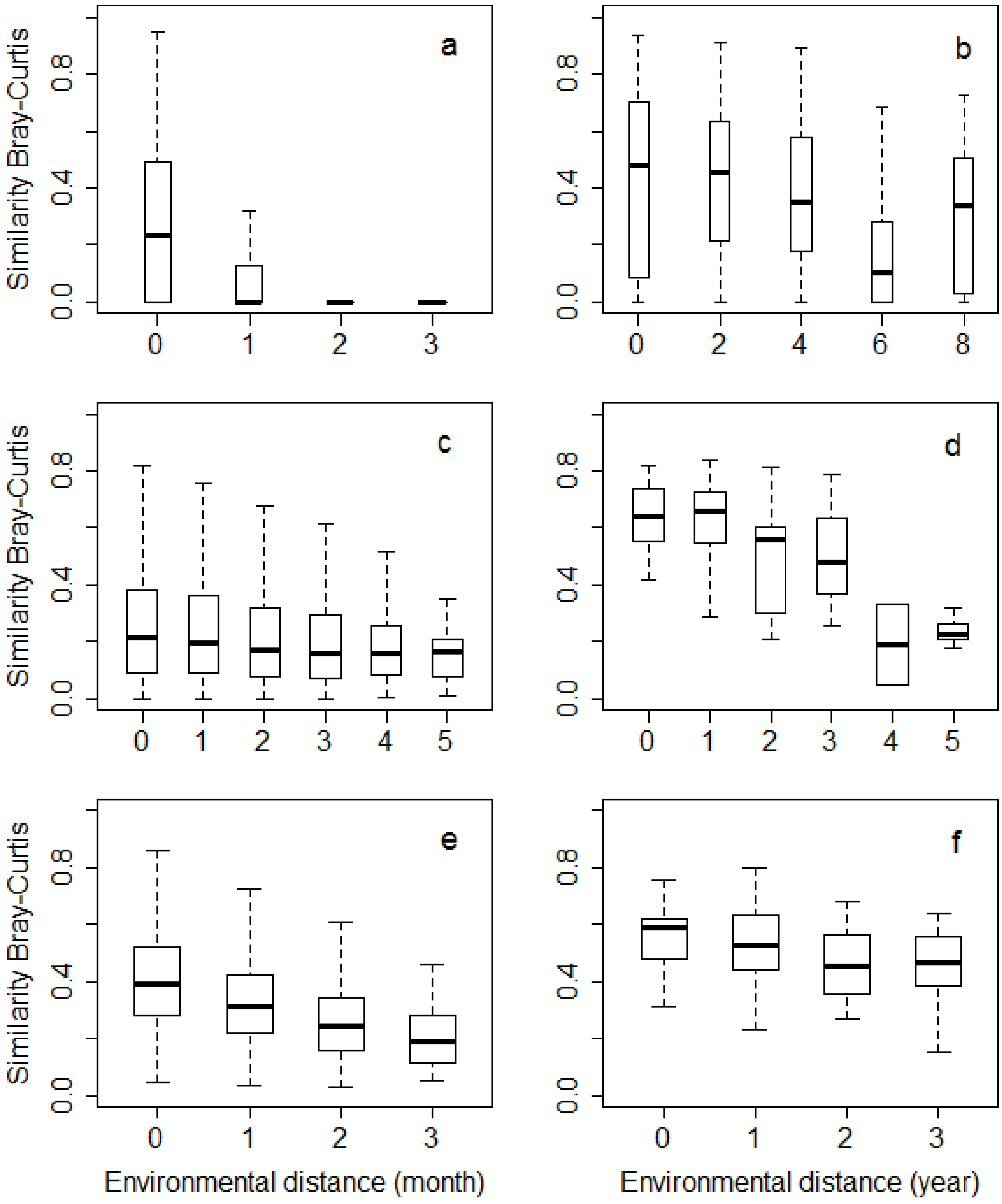


Figure 1.6 Relationship between community similarity and environmental distance for month and year: Kattegat (a-b), Urdaibai (c-d) and Saronikos (e-f).

1.4 Discussion

We have characterized the ecological niche of zooplankton and analysed the zooplankton abundance variation with time in relation to climate at three different time series across the North Atlantic and Mediterranean Seas. The analysis of the GODAS potential temperature time series evidenced a SST significant increase in the three regions for the 1980-2015 period. The GODAS SST warming trends found in this study in the Urdaibai and Saronikos, with a velocity of warming of 0.20ºC decade^{-1} are similar to the range of warming found in previous works in the Bay of Biscay [238,240,241] and slightly lower than the rates of warming found in the Mediterranean Sea [241,264-266]. The GODAS SST warming rate found here for the Baltic Sea (0.11ºC decade^{-1}) is lower than the faster warming velocities reported for the same area and similar periods [251,267].

When a species responds to climate change, individuals tend to select climatic conditions experienced prior to the shift, in agreement with their ecological-niche. Long-term links between the zooplanktons abundance *vs.* SST found here revealed that the plankton community is changing with time. By change, we mean that the relative abundance composition of the species has linearly changed. Significant correlations between SST and long-term zooplankton abundance fluctuations have been well described in the North Atlantic [247,268-274] and Mediterranean Sea[275]. In this study, the species temporal dynamics seems to be governed by niche-tracking processes, according to the significant correspondence found between the observed and the expected zooplankton abundance due to thermal niche. Some planktonic species exhibit local adaptation[210,276,277] or consist of several ecotypes with different environmental preferences, and phenotypic plasticity, dispersal, and evolutionary changes that can help mitigating climate change impacts through adaptation to changing conditions[104]. However, in our study we observe a community similarity decay with time that does not correspond to the expectations of an adaptation process. A lack of species thermal adaptation has been also reported in Hinder et al.[209], for two key calanoid species (*Calanus finmarchicus* and *C. helgolandicus*) in the North Atlantic Ocean using Continuous Plankton Recorder data. Similarly, Helaouet & Beaugrand[268] found strong support of niche-conservatism in *C. finmarchicus* at multidecadal scale using the same dataset along the North Atlantic Ocean. Hence, it seems that climatic changes results in zooplankton community shifts and the species move their distributions following their thermal niche. It is also possible that the speed of change overcomes the capacity of adaptation of the different species.

Table 1.5 Environmental variables and best BIOENV model selection for each of the different plankton groups.

Period	Site	Environmental variables	BIOENV. variable selection
Month	Kattegat	Sal, SST, Chl-a, O_2, Secchi Depth, Station Depth, TP, TN, DIN, DIP, DSI	SST + O_2 + TN + DIN + DIP
	Urdaibai	Sal., SST, Chl-a, Precipitation, Flow, DOS $Temp_{air}$, EA, AMO, NAO	SST + $Temp_{air}$
	Saronikos	Sal, SST, DO, Chl-a	SST
Year	Kattegat	Sal, SST, Chl-a, O_2, Secchi Depth, Station Depth, TP, TN, DIN, DIP, DSI	SST + O_2
	Urdaibai	Sal., SST, Chl-a, Precipitation, Flow,DOS $Temp_{air}$, EA, AMO, NAO	SST + $Temp_{air}$
	Saronikos	Sal, SST, DO, Chl-a	SST + DO

Abbreviations:

- TN: Total Nitrogen (μM)
- TP: Total Phosphorus (μM)
- DIN: Dissolved Inorganic Nitrogen
- DIP: Dissolved Inorganic Phosphorus
- DSI: Dissolved Inorganic Silica
- EA: East Atlantic index
- AMO: Atlantic Multidecadal Oscillation index
- NAO: North Atlantic Oscillation index
- O_2: Oxygen (mg/L)
- Station Depth : is the water depth at the station (m)
- SST : Sea Surface Temperature (°C)
- Flow : Water flow (m^3/s)
- Secchi Depth: Secchi Depth (m)
- Precipitation: (mm^3)
- DO = Dissolved Oxygen (mg/L)
- DOS = Dissolved Oxygen Saturation (%)

One of the most important factors affecting the rate of species temporal turnover is latitude. High latitudes are usually characterized by strong seasonality, which may lead to faster temporal turnover toward poles[278]. Here, a small turnover latitudinal gradient[157] is also observed among the time-series, being the “northern” sites’ (Urdaibai and Kattegat) temporal turnover (time-decay slope) an order of magnitude higher compared to Saronikos, in the year-to-year analysis.

Changes in assemblage similarity in time are not necessarily linear. This is especially true for intra-annual data sets where similarities may include a seasonal signal. For example, zooplankton assemblages in spring and autumn may share more species within each other than assemblages in spring and summer, due to environmental distance. In these cases, similarity decay in time may show a nonlinear pattern, as we have seen in the monthly analysis. At year-to year analysis, all sites showed negative linear patterns, as expected, mirroring a rearrangements of the communities with time[222]. However, Hsieh et al.[279] reported a lack of correlation between fish populations and environmental signals in the coastal and coastal-oceanic assemblages of the Pacific Ocean for the 1951-2002 period, indicating that these species might show nonlinear biological responses to external forcing rather than a simple linear tracking of environmental variables.

Temporal regression analyses revealed SST as the most important environmental predictor highly related to temporal β-diversity across sites. Our findings indicate a fundamental role of temperature in structuring cross-taxon zooplankton β-diversity, and reveal that changes in ocean temperature, in conjunction with other environmental changes, may ultimately rearrange the global distribution of life in the ocean. Understanding characteristic variation in coastal zooplankton community composition through time can inform us about processes driving community assembly and the ability of species to respond to perturbations. We have analysed the extent to which the temporal distribution of coastal zooplankton is controlled by local environmental selection, controlling for temporal autocorrelation. Our results strongly support the hypothesis that environmental selection rather than time-derived stochastic processes dominates the zooplankton temporal community structure. In fact, the portion of the variance that has been explained by the stochastic replacement of individuals from the community with time has been smaller compared to environmental variables. However, most of the variance remains unexplained, suggesting there are other explaining factors not controlled or that a part of the variability is purely random. Niche descriptors dominating temporal patterns of plankton community assembly has been also well reported in the North Atlantic[180] and globally[158]. In our study, the fact that the niche descriptors are more important than the temporal autocorrelation, and more specifically that the SST is the most important variable limiting the ecological niche of the zooplankton communities, is in line with the species by species analysis we undertook, where we found relevant links between the variability of zooplankton abundance and the variability of temperature trends. Hence, we can conclude that the zooplankton community is changing at the three stations, with different but significant velocities of change, and these changes are attributed to the climate.

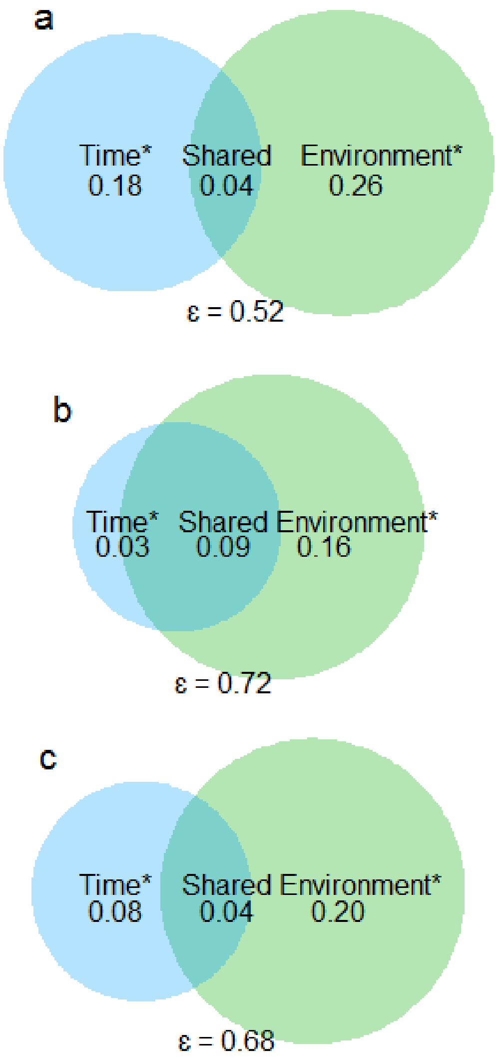


Figure 1.7 Variation partitioning (Venn diagrams) of unique contribution of time (interannual analysis) and environmental components to zooplankton β diversity distribution, for the Kattegat (a), Urdaibai (b) and Saronikos (c). Overlapping fractions represent the shared variation between the environmental and time components. The residual variation unexplained by the multivariate model is also shown. The p-values (* = < 0.05) showing the significance of each fraction of variation were estimated with 1999 permutations under the full model.

2. Chapter 2: “Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change”

Villarino, E., Chust G., Licandro P., Butenschön M., Ibaibarriaga L., Larrañaga A. & Irigoien X. (2015). “*Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change*”. Marine Ecology Progress Series, 531, 121-142.

Advances in habitat and climate modelling allow us to reduce uncertainties of climate change impacts on species distribution. We evaluated the impacts of future climate change on community structure, diversity, distribution and phenology of 14 copepod species in the North Atlantic. We developed and validated habitat models for key zooplankton species using continuous plankton recorder (CPR) survey data collected at mid-latitudes of the North Atlantic. Generalized additive models (GAMs) were applied to relate the occurrence of species to environmental variables. Models were projected to future (2080–2099) environmental conditions using coupled hydroclimatic-biogeochemical models under the Intergovernmental Panel on Climate Change (IPCC) A1B climate scenario, and compared to present (2001–2020) conditions. Our projections indicated that the copepod community is expected to respond substantially to climate change: a mean poleward latitudinal shift of 8.7 km per decade for the overall community with an important species range variation (□15 to 18 km per decade); the species seasonal peak is expected to occur 12–13 days earlier for *Calanus finmarchicus* and *C. hyperboreus*; and important changes in community structure are also expected (high species turnover of 43–79% south of the Oceanic Polar Front). The impacts of the change expected by the end of the century under IPCC global warming scenarios on copepods highlight poleward shifts, earlier seasonal peak and changes in biodiversity spatial patterns that might lead to alterations of the future North Atlantic pelagic ecosystem. Our model and projections are supported by a temporal validation undertaken using the North Atlantic climate regime shift that occurred in the 1980s: the habitat model built in the cold period (1970–1986) has been validated in the warm period (1987–2004).

2.1 Introduction

Plankton communities can quickly respond to climatic variability (e.g. Beaugrand et al.[222]). Impacts of global warming affect the whole pelagic ecosystem from plankton to higher trophic levels[32,90,280]. Such impacts can result in poleward movements in species distribution[91,202,281-283], shifts in phenology[31,284] or changes in abundance and community structure[234,285,286]. Species responses to climate change may lead to local extinction and invasions, resulting in changes in the pattern of marine species richness and trophic mismatches[58]. Therefore, assessing how these biogeographic processes will change in the future is a key prerequisite to anticipate consequences of climate change on marine ecosystems.

Sea temperature is one of the most important physical variables structuring marine ecosystems. There is overwhelming evidence that the composition, abundance and phenology of plankton communities are closely linked to water temperature[13]. Throughout the North Atlantic Ocean, a general increase in temperature has been observed in the past century[287] and future ocean temperatures have been forecasted to increase according to coupled atmosphere–ocean general circulation models (AOGCMs). In particular, the North Atlantic has warmed faster than all other ocean basins, and climate change scenarios project sea surface temperature isotherms to shift up to 600 km northwards by the end of the 21st century[288].

Habitat suitability (species distribution) models[72,289] have been widely used to project how species ranges might change in the future. These models aim to define the species ecological niches by relating the occurrence of species to environmental variables (e.g. temperature, depth and phytoplankton) in the same area. They rely on the environmental niche concept of Hutchinson[40], in which a multi-dimensional hypervolume is defined by the combination of multiple environmental conditions that requires a species population to survive and reproduce. Habitat suitability models have been widely used to project how species ranges might change in the future. Then, using projections from the Intergovernmental Panel on Climate Change (IPCC), we can investigate how environmental changes will affect future species distributions[65].

In the past decade, several studies using species distribution models and continuous plankton recorder (CPR) data with future climate change scenarios have been published. For example, Helaouët & Beaugrand[63] forecasted a poleward movement of *Calanus finmarchicus* of 1° latitude by the end of the 21st century; Beaugrand et al.[290] analysed the reasons behind the climate-driven ecosystem future shifts of cod, zooplankton and phytoplankton; Reygondeau & Beaugrand[291] and Beaugrand et al.[81] used the Non-Parametric Probabilistic Ecological Niche Model (NPPENM) to project *C. finmarchicus* distribution through the next century; while Beaugrand et al.[292] investigated how climate-induced changes in temperatures will alter marine zooplankton both locally and globally. Most of these studies have used the NPPENM, which is based on the Mahalanobis distance (MD) algorithm[293]. A recent work by Chust et al.[91] shows that generalized additive models (GAMs) perform well in detecting latitudinal shifts of species and identifying the causes.

So far most of the bioclimatological research is concentrated on a single species[236,268,291,292,294,295] and there are very few works at community level[235,271,283,296,297]. Yet, some of the publications analysed the historic plankton biogeographical shifts in the North Atlantic Ocean (e.g. Reygondeau & Beaugrand[291]). However, little is known about the future spatial distribution of copepod biodiversity, seasonal changes and latitudinal shift in the North Atlantic Ocean, despite their importance in marine food webs.

Here, we analyzed a zooplankton community to detect future biogeographic changes in species distribution and phenology, and to identify spatial and temporal patterns of diversity. This will allow us to project the community shifts and their consequences in the North Atlantic Basin. In particular, our aim was to develop and validate habitat models in key zooplankton species using CPR survey data collected at mid-latitudes of the North Atlantic (35 to 65° N, Figure 2.1) to be reliably extrapolated to future climate scenarios. To do that, we built a model using the data from a cold period (1970–1986) and evaluated its performance under a warm regime (1987–2004). Subsequently, the model was used to project species distributions, community composition and phenological changes by the end of the century under climate change scenarios.

2.2 Methods

2.2.1 Environmental data

A set of 7 environmental variables was used to build the N-dimensional ecological niches of copepod species and to predict their probability of occurrence over the North Atlantic Ocean: sea surface temperature (SST), sea surface salinity (SSS), bathymetry, oxygen, pH, sea surface phytoplankton biomass (Pc) and mixed layer depth (MLD). SST and SSS (salinity especially in coastal environments) are essential factors because of their recognized influence on spatial distribution of *Calanus spp.*[63,268,291,298]. Bathymetry was selected because it has been suggested that it influences the distribution of some copepod species in regions such as the southern North Sea[291]. Phytoplankton is an important food source for *Calanus spp.* that dominates zooplankton biomass in the North Atlantic[299-301]. MLD is an important parameter for phytoplankton production and controls the spatial distribution of many plankton species[302]. Oceanic pH influences calcifying organisms such as coccolithophorids, foraminifers, corals and pteropods[303,304].

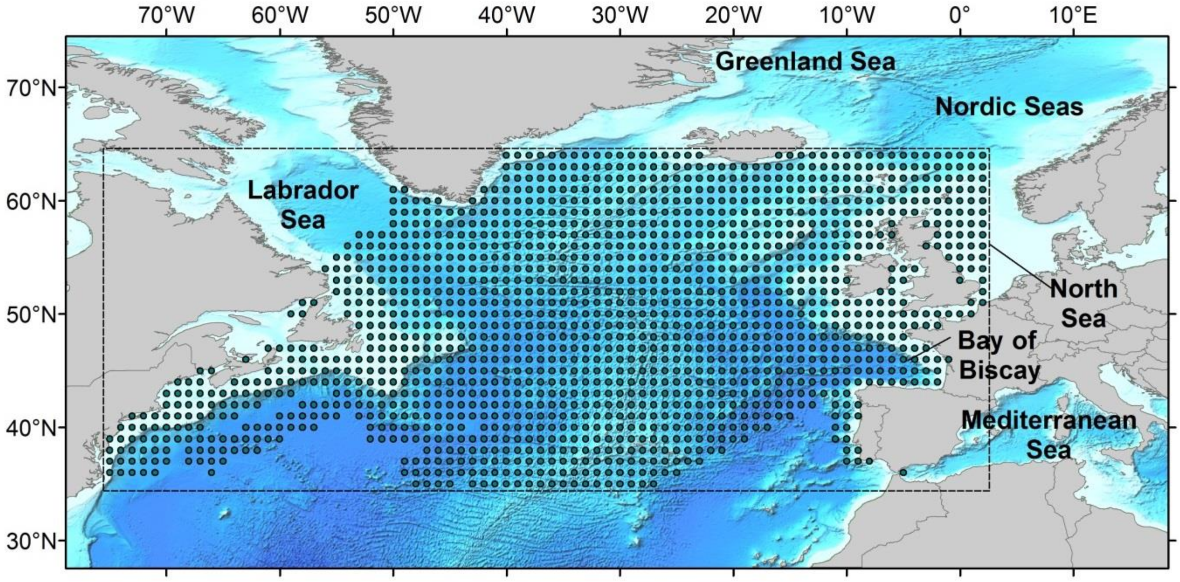


Figure 2.1 The North Atlantic Basin. The domain of the studied area is 35 to 65° N and 75° W to 2° E. Source of bathymetry: ETOPO1, NOAA, Amante and Eakins[305]. Dots represent continuous plankton recorder (CPR) sampling points of *Calanus finmarchicus*, *C. helgolandicus*, *C. glacialis* and *C. hyperboreus* in the 1970–2004 period.

SST, SSS, Pc, oxygen and pH data were extracted from a 1960–2004 hindcast of an implementation of the NEMO-ERSEM model forced with atmospheric reanalysis data from the Drakkar Forcing Set 4 (DFS4) composite of NCEP and European Centre for Medium-

Range Weather Forecasts (ECMWF) fields. MLD data were obtained from the Center for Marine and Atmospheric Sciences (ZMAW, Hamburg) and used as a proxy of water column stability. MLDs were obtained from vertical profiles of temperature and salinity[306], using the classical density criterion of 0.125[307]. Bathymetry was extracted from ETOPO1 global model (NOAA)[305]. Data were organized in 1° longitude and 1° latitude grid resolution available for every month of the period 1970–2004.

2.2.2 Biological data

Data on the abundance (mean density ind. m^{-3}) of 4 species (*Calanus finmarchicus, C. glacialis, C. helgolandicus* and *C. hyperboreus*) were obtained from the CPR database. The CPR survey is an upper-layer plankton monitoring programme that has regularly collected samples, at monthly intervals, in the North Atlantic and adjacent seas since 1946 (Warner & Hays[30]).

These calanoids are key species in subarctic (*C. finmarchicus*) and temperate shelf-edge (*C. helgolandicus*) regions of the North Atlantic Ocean[294,308]. *C. helgolandicus* is considered to be a pseudo-oceanic species, i.e. a species that can be found in oceanic and neritic waters, but it is mostly abundant above the shelf edge[235]. *C. glacialis* and *C. hyperboreus* are Arctic species, while *C. finmarchicus* is a subarctic species that overlaps in size range with *C. helgolandicus*. *C. hyperboreus* is the largest among them.

In order to have a better representation of the copepod community at North Atlantic Basin scale, data on another 10 copepod species (ind. m^{-3}) (*Candacia armata, Centropages typicus, Centropages hamatus, Metridia lucens, Paraeuchaeta norvegica, Paraeuchaeta hebes, Pleuromamma borealis, Pleuromamma robusta, Pseudocalanus elongatus and Temora longicornis*) were downloaded from the National Marine Fisheries Service NMFS-COPEPOD global plankton database www.st.nmfs.noaa.gov/copepod/data/sahfosatl/index.html between 1995 and 1999. It is also based on CPR survey and it represents one-third of the CPR records collected in the same region. Those species were selected as they were the most abundant copepod taxa identified at species level (with more than 100 occurrences in the data set). The selected 14 species represent 49.3% of the total occurrences sampled in the community, hence, well representing the overall community in terms of abundance. All CPR data used in the present study were gridded within 35 to 65° N and -75° W to 2° E at 1 by 1° spatial resolution using the inverse-distance interpolation method, and analysed monthly.

2.2.3 Habitat modeling

We generated models based upon the prominent climate drivers for the most abundant 14 copepod species in the study area. First, model selection and validation was evaluated for 4 species (*Calanus finmarchicus, C. glacialis, C. helgolandicus and C. hyperboreus*) using the entire time series from 1970 to 2004. In particular, we compared GAMs with other habitat model algorithms (MD and MaxEnt), and validated the model using randomly independent data sets and comparing cold (1970–1986) with warm (1987–2004) climate regimes. That way we assessed the capacity of the model to be extrapolated to future climate. Second, we built habitat models on the other set of copepod species (10 species) in the same way as we did for the main 4 *Calanus spp*. using data from the 1995–1999 period. Thus, we built habitat models of 14 species to (1) evaluate the impacts of future climate change on community structure in the 2080–2099 period compared to present conditions (2001–2020), (2) quantify the poleward shift of species distribution, and (3) analyse phenological changes of the species in the North Atlantic Ocean at community level, with model outputs corresponding to the IPCC Special Report on Emissions Scenarios A1B global warming scenario[190].

Species distribution models assume that observations represent a species at equilibrium with its environment. Here, GAMs[76,309] were used to model occurrences for each of the 4 *Calanus spp*. as a function of environmental factors (SST, SSS, MLD, pH and bathymetry) and potential food resource (Pc). The strength of GAMs is due to their capacity to deal with highly non-linear relationships between the response and the set of explanatory variables, allowing asymmetrical unimodal distributions, since interaction between species and extreme environmental gradients may cause skewed responses[62]. GAMs also enable us to model the seasonal response of the species. A GAM using the binomial error distribution and *logit* function of the *mgcv*[309] package in R was used to relate copepod presence-absence data and the explanatory environmental variables, following Chust et al.[91]. The CPR data set used here includes 112161 samples across the spatial domain and irregularly distributed at yearly and monthly intervals.

Prior to model building, we tested for collinearity between explanatory variables by calculating variance inflation factors (VIF) with the *AED*[310] package in R. We excluded any variable that had a VIF > 3, and then recalculated VIF for the remaining variables. We iterated this process until all variables had a VIF < 3. The variable most often thrown out was oxygen, which highly correlated with temperature, thus we excluded it from the subsequent analysis.

We built and compared different GAMs for each species to find the optimal set of explanatory variables. Variable importance was assessed first by removing variables that were not statistically significant and second, by adding and removing terms and noting the change in deviance or gain (>1%) in a forward stepwise procedure. For environmental variables, the degree of smoothness of model terms was restricted from 3 to 5 in order to assume a unimodal, ecologically meaningful niche model *sensu* Hutchinson[40], but allowing asymmetry. After characterizing the ecological niche of each species, the environmental space was projected into geographical space and the probability of occurrence of *Calanus spp*. was calculated. To prevent overfitting, we first restricted the degrees of smoothness to ecologically interpretable responses according to niche theory; second we analysed the response of species occurrence to each environmental predictor; and third we used cross-validation methods to evaluate the reliability of the models (see section below).

2.2.4 GAM vs. MD and MaxEnt

GAM has been also compared with other 2 habitat models (MaxEnt and MD algorithm) in order to assess its performance. Both MaxEnt and MD algorithm are ecological niche models using presence-only species records, although they can use absences to model validation. They are implemented in the dismo[311] R package, which is specially designed to model species distributions that do not migrate or shift during seasonal cycle, since it uses static environmental layers. Contrary to MD algorithm and MaxEnt habitat model techniques, GAM presents the advantage to model the seasonal response of the species resulting in a more 'dynamic' habitat modelling technique. Hence, only for the purpose of comparing performances of GAM with MaxEnt and MD algorithms, we reduced the data set into a unique spatial layer by accumulating occurrences of all years and months. The MD algorithm technique for a given point expresses the distance between this point and the species optimum in the ecological space[77,312-314]. MaxEnt uses the principle of maximum entropy to estimate a set of functions that relate environmental variables and habitat suitability in order to approximate the niche and potential geographic distribution of the species[80]. MaxEnt model minimizes the relative entropy between 2 probability densities (presence data and the landscape data) defined in a covariate space[289,315]. Although MaxEnt has been widely used in terrestrial species (e.g. Graham & Hijmans[316], Monterroso et al.[317], Young et al.[318], Yates et al.[319]), applications in pelagic species are still scarce.

2.2.5 Model validation

The 3 models used were validated using independent data sets for model building and model validation[86]. We validated the models in 2 ways: (1) k-fold random resampling, and (2) temporal cross-validation. In the first procedure, the data is first partitioned into k equally sized segments or folds. Subsequently, k iterations of training and validation are performed so that within each iteration a different fold of the data is held-out for validation while the remaining k - 1 folds are used for model fitting[320]. We used k = 5, hence, 80% of the CPR observations were used for model building, and the other 20% (i.e. independent) for model validation in an iterative procedure that was repeated 5 times. Hold-out validation avoids the overlap between training data and test data, yielding a more accurate estimate for the generalization performance of the algorithm. The comparison between the accuracy (the proportion of true results) of the model (all observations) and that of cross-validated results also permits the detection of model overfitting, which reduce the usefulness of such models for extrapolation.

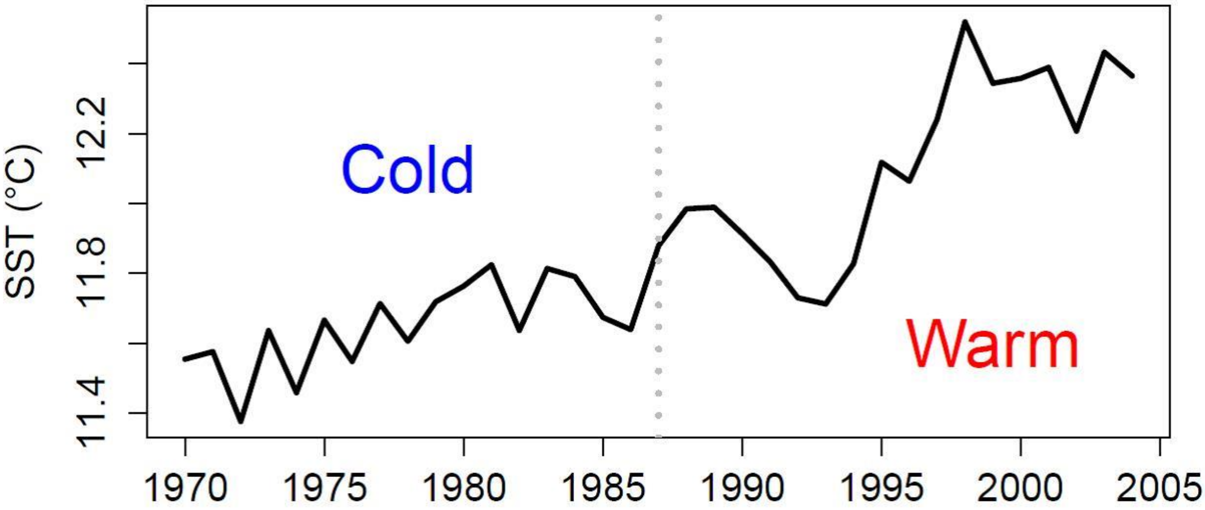


Figure 2.2 Mean SST time series. Cold (1970–1896) and warm (1987–2004) periods are indicated.

Second, the North Atlantic regime shift in the 1980s[321-323] was taken into account to perform a temporal cross-validation of the models (i.e. the second procedure of model validation). A wide range of studies have investigated the North Atlantic and North Sea climate decadal fluctuations that affect phytoplankton[269,321,324], zooplankton[222,274,322] and fish populations[321,325]. To this end, we performed a Wilcoxon rank sum test[326] between a cold period from 1970 to 1986 (mean SST: 11.64 ± SE 0.12°C) and a warm period from 1987 to 2004 (mean SST: 12.10 ± SE 0.26°C) and defined in our time series 2 different climatic regimes (p-value < 0.0001) (Figure 2.2). Subsequently, we built the models and compared the 4 *Calanus spp.* between cold (1970–1986) and warm (1987–2004) periods. We tested the habitat model predictive capacity validating the cold period into the warm period and vice versa, using the area under the receiver operating characteristic curve (AUC)[327,328] and confusion matrix accuracy assessment indices[329] (see section below). This approach enabled us not only to explore the model behaviour for different climates but also to see to what degree of reliability we can project the model to future warmer climate conditions. The temporal cross-validation was undertaken only to the 4 *Calanus spp.*, since the NMFS-COPEPOD time series (1995–1999) including the other set of 10 copepod species is too short.

2.2.6 Model evaluation

We assessed the predictive performance of the overall model and the held-out folds using the AUC, a measure of the ability of the predictions to discriminate presence from absence, and accuracy indices derived from confusion matrix. To this end, the species presence modelled probability was converted to either presence or absence using probability thresholds following 2 criteria: sensitivity (true predicted presences) = specificity (true predicted absences), and maximization of sensitivity plus specificity, as reported in Jiménez-Valverde & Lobo[85]. Thus, the cases above this threshold are assigned to presences, and below to absences. Given the threshold value, a confusion matrix was calculated yielding outputs of correctly identified records of presence and absence to have an overall accuracy estimate of model performance. Overall accuracy ranges from 0 to 100% and AUC values from 0.5 (random sorting) to 1 (perfect discrimination). Accuracy is a good indicator of model performance since it is the proportion of true results, either true positive or true negative, in a population.

2.2.7 Climatic scenario for the 21st century

In order to assess the copepod response to climate change, selected habitat models were projected to future conditions and thresholds were applied to the resulting probability maps. We used modeled environmental predictors (SST, SSS and Pc) from the DKRZ-CERA database (http://cera-www.dkrz.de) at IPCC A1B scenario for the 2001–2099 period. More in detail, we used the Hamburg Ocean Carbon Cycle (HAMOCC) model for the phytoplankton, and the Max Planck Institute’s Ocean General Circulation Model (MPIOM)[330] for the physical set up. HAMOCC, embedded into MPIOM, simulates the oceanic cycles of carbon and other biogeochemical elements[331]. Technical details of the ocean model MPIOM can be found in Marsland et al.[332].

2.2.8 Assessing impacts of climate change on copepods

The impacts of climate change on copepods were assessed by estimating latitudinal shifts of each species, phenological changes and spatial patterns of biodiversity indices.

The latitudinal shift (km) of the species was calculated by comparing the geographic centre of gravity of its suitable area for present (2001–2020) and future scenarios (2080–2099). The centre of gravity is defined as the mean geographic location of a population[333]. Gravity centres of habitat models showing well-separated east to west population patches (*C. armata, C. hamatus* and *P. hebes*) were calculated separately and then averaged. We assumed unlimited copepod dispersal to estimate the extent of gain or loss of suitable space from present to future modeled conditions.

We computed the changes in the seasonal cycle or phenology of *Calanus spp.* by analysing the difference in terms of days on the annual maxima of the copepods' probabilities of occurrence in both present and future conditions. The timing of the peak was determined as the date when the modelled species occurrences reached the annual maximum. Monthly mean species occurrences were used to build a GAM fitted function (with a Gaussian link and cyclic cubic regression spline) to predict the seasonal peaks, and to quantify the phenological shifts in days.

We carried out a seasonal quantitative analysis only on *C. hyperboreus* and *C. finmarchicus* since their predicted phenological patterns matched relatively well with observed ones. We did not perform any phenology analysis in the NMFS-COPEPOD set of species either, due to time series shortness.

Changes in local biodiversity were assessed in terms of species turnover, colonization and extinction. In particular, we mapped 4 biodiversity components of change: (1) stability, i.e. the number of species that were present or absent at both present and future scenarios at each pixel; (2) extinction, i.e. the number of species that were present at present and were absent in the future; (3) colonization, i.e. the number of species that were absent at present and present in the future; and (4) turnover, i.e. the number of species that suffer either colonization or extinction.

Species assemblages were categorized following Beaugrand et al.[283] in 2 main groups: (1) the 'cold-water species assemblage', including the cold-temperate mixed water (*Pleuromamma robusta*), subarctic (*Calanus finmarchicus*) and Arctic (*Calanus hyperboreus* and *Calanus glacialis*) species assemblages, and (2) the 'warm-water species assemblage', including the warm-temperate oceanic and pseudo-oceanic (*Pleuromamma borealis, Paraeuchaeta norvegica, Metridia lucens* and *Paraeuchaeta hebes*), the temperate pseudo-oceanic (*Centropages typicus, Candacia armata* and *Calanus helgolandicus*) and continental shelf (*Pseudocalanus elongatus, Temora longicornis* and *Centropages typicus*). This simplified way of proceeding enabled us to understand which set of species was more affected by environmental change.

2.3 Results

2.3.1 Future environmental changes

MPIOM SST model projections forecasted an average (±SD) increase of 1.54 ± 0.35°C (Wilcoxon rank sum test, $p < 0.0001$) from 2001-2020 to 2080-2099 in the North Atlantic study area (Figure 2.3) Our spatial examination of changes in SST reveals regional differences. For instance, SST increased by 4 to 6°C in areas of the Gulf Stream extension and the Newfoundland continental shelf, south of the Oceanic Polar Front (i.e. 60–45° W and 43–48° N). On the other hand, in some areas of the subarctic region south of the Labrador Current in the North Atlantic Gyre (i.e. 40–30° W and 55–60° N), SST is expected to decrease between 1 and 0°C.

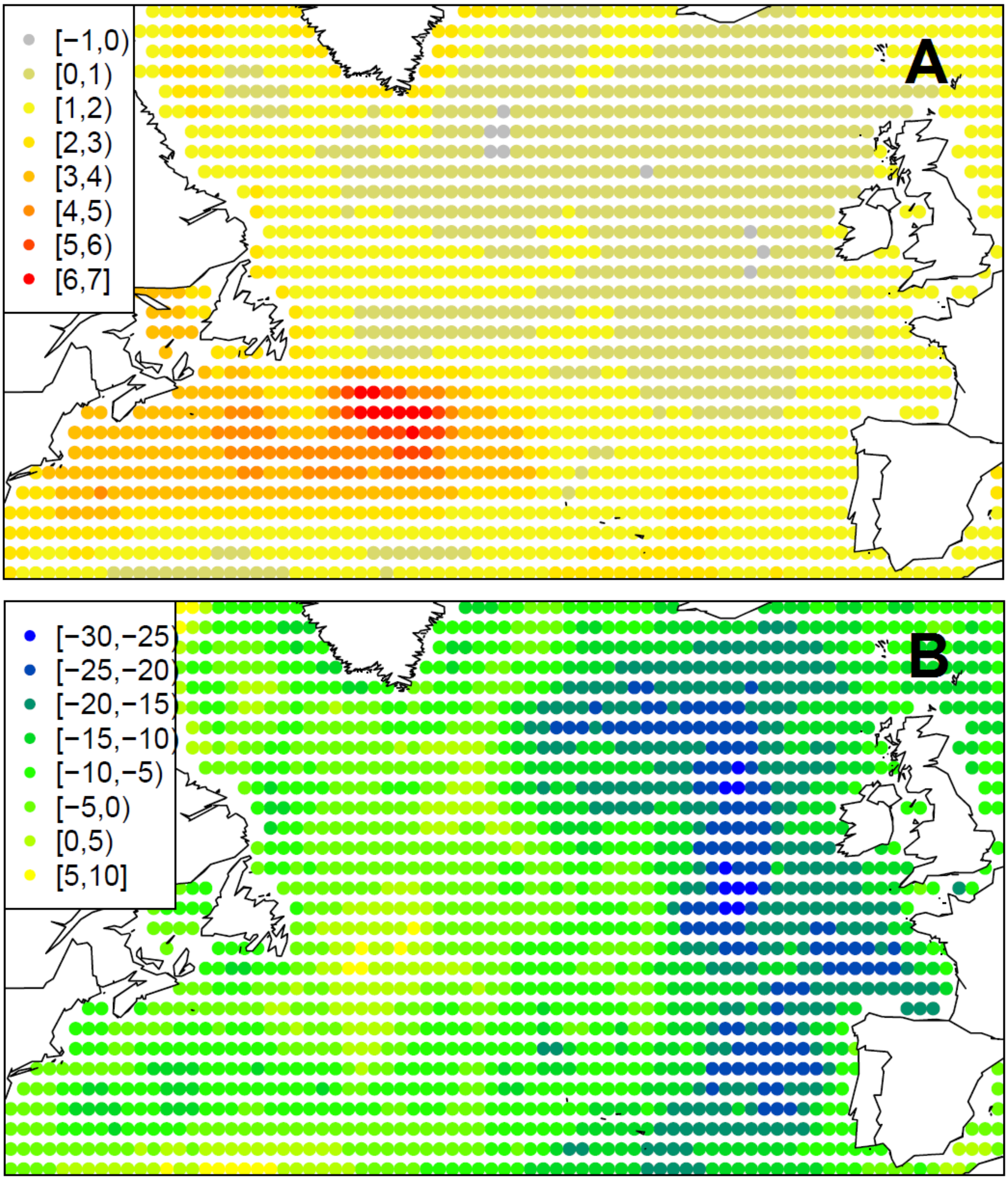


Figure 2.3 Difference models of (A) sea surface temperature (°C) and (B) surface phytoplankton biomass (mg m−3) for present (2001–2020) and future (2080–2099) periods.

The HAMOCC biogeochemical model projects a general Pc decrease by the end of century in the North Atlantic. Results showed a clear east to west asymmetry on Pc changes, with strong negative differences (-30 to -20 mg C m^{-3}) along the east of the Oceanic Polar Front, from the subarctic region south of Iceland down to the Bay of Biscay and the Southern European shelf edge (i.e. 25–5° W and 38–60° N). In turn, a slight increase in Pc (0–10 mg C m^{-3}) is projected along the Flemish Cup area and extending thought the Oceanic Polar Front (i.e. 50–40° W and 43–50° N) (Figure 2.3).

2.3.2 GAM habitat models

We evaluated the response of the *Calanus spp*. to each explanatory variable individually using GAMs (Table 2.1). SST was the most important environmental driver in the *Calanus ssp*. environmental space, followed by SSS, depth and Pc. Oceanic pH and MLD explained less deviance of species occurrence, although pH was considered in the model selection as it accounted for more than 1% of deviance for all models.

Table 2.1 Generalized additive model. Explained deviance (%) of *Calanus spp*. occurrence in the North Atlantic Basin according to each environmental factor. SST: sea surface temperature, SSS: sea surface salinity, Pc: surface phytoplankton biomass, Chl a: chlorophyll a, MLD: mixed layer depth.

	SST	SSS	O_2	pH	Pc	Chl *a*	MLD	Depth
C. finmarchicus	14.2	15.1	18.9	4.4	6.2	6.1	0.6	5.5
C. helgolandicus	11.3	5.4	3.4	1.8	0.4	0.3	2.8	14.1
C. glacialis	29.6	25.5	25.9	1.9	4.2	3.2	0.7	0.1
C. hyperboreus	21.5	13.0	30.8	6.6	16.5	12.0	0.3	4.8

Habitat suitability models were constructed for the 4 *Calanus spp*. (Figure 2.4). All the subsequent environmental variables, i.e. SST, SSS, depth, pH and Pc, were included in all models except for *C. glacialis* (without pH and Pc) and for *C. helgolandicus* (without Pc).

The random cross-validation of models is shown in Table 2.2. The habitat models in the 4 *Calanus spp*. showed a slight drop in the accuracy measure if we compare all observations (74–85%) vs. the k-fold cross-validation (69–85%); this is owing to a slight signal of model overfitting. Here, *C. helgolandicus* showed low overall deviance explained (25.4%) in the habitat suitability models, whilst the other species deviance explained was higher: *C. finmarchic*us (46.9%), *C. glacialis* (34.1%) and *C. hyperboreus* (42.3%).

The temporal cross-validation enabled us to assess the model reliability to be extrapolated to different climates. Results have shown that model accuracy is relatively good (75–84%) for the models built in the cold period and extrapolated and validated in the warm period (Table 2.3). Therefore, species models can be used to be projected in future climate simulations with relative confidence.

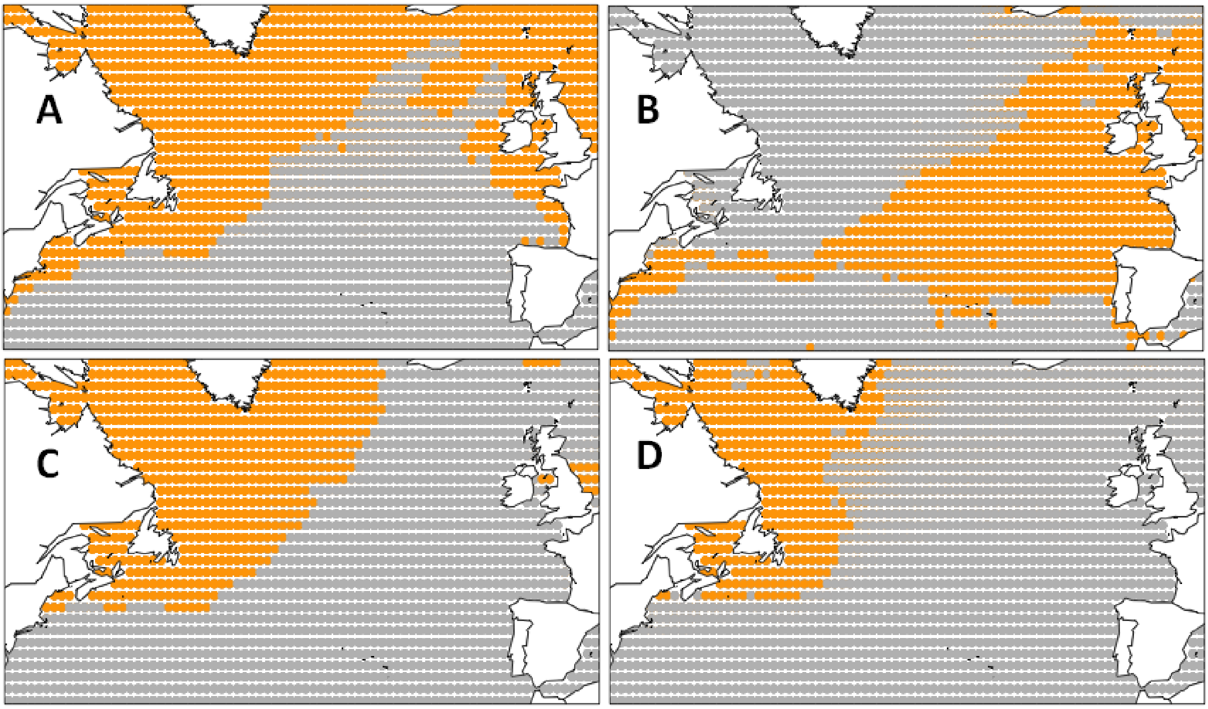


Figure 2.4 Occurrence models of *Calanus spp.* in the 1970–2004 period. Orange: presence; grey: absence. (A) *C. finmarchicus*, (B*) C. helgolandicus*, (C) *C. glacialis* and (D) *C. hyperboreus*.

GAM habitat models for the non-*Calanus spp.* set of copepods (Table 2.4) showed a slightly lower accuracy (64–74%) than for the 4 *Calanus spp.* Moderate deviance explained was found in *Centropages typicus* (25.4%), *Centropages hamatus* (28.7%), *Paraeuchaeta norvegica* (27.5%), *Paraeuchaeta hebes* (35.4%) and *Temora longicornis* (24.9%). For the remaining set of species the deviance explained was lower (17.5–7.7%), as were the accuracy values. The difference in the accuracy values of the model using all the observations (76–63%) and those cross-validated (53–57%) indicated a slight overfitting in these latter models (Table 2.4).

2.3.3 Model comparison: GAM vs. MD and MaxEnt

MaxEnt ranked first in terms of model accuracy or performance, followed by GAM and MD, with similar values for *C. glacialis* and *C. helgolandicus* but higher values for GAM in *C. hyperboreus* and *C. finmarchicus* (Figure 2.5).

However, we have shown that GAM, which is a presence-absence-based model, predicts correctly the potential distribution of *C. glacialis* along the Labrador Sea, Newfoundland shelf and the Davis Strait, where it is abundant according to Head et al.[334] and Pomerleau et al.[335], whilst both MaxEnt and MD predicted absence.

Table 2.2 Evaluation of generalized additive models (yearly accumulated) with k-fold cross-validation. Variables entered: sea surface temperature (SST), sea surface salinity (SSS), bathymetry, surface phytoplankton biomass (Pc) and pH. Thresholds for conversion of probability of species presence to either presence or absence in model validation: 0.08 (*Calanus hyperboreus*), 0.11 (*C. glacialis*), 0.48 (*C. helgolandicus*) and 0.63 (*C. finmarchicus*). Values in the AUC column refer to model with all observations/mean k-fold cross-validation. Values in the accuracy column refer to model with all observations/mean k-fold cross-validation (%). edf: estimated degrees of freedom. All $p < 0.001$.

Species	Variables selected	edf	Overall deviance explained (%)	AUC	Accuracy
C. hyperboreus	SST	1.99			
	SSS	1.00			
	Depth	2.17			
	pH	1.96			
	Pc				
			42.3	0.845/0.698	85.34/69.84
C. glacialis	SST	1.95			
	SSS	2.88			
	Depth	1.00			
			34.1	0.816/0.642	81.90/71.25
C. helgolandicus	SST	1.99			
	SSS	2.99			
	Depth	2.85			
	pH	1.97			
			25.4	0.749/0.754	74.94/75.40
C. finmarchicus	SST	1.97			
	SSS	2.74			
	Depth	2.88			
	pH	1.83			
	Pc				
			46.9	0.852/0.851	85.19/85.13

2.3.4 Latitudinal shift under climate change scenarios

Despite the different thermal window of each of the 14 species analysed, all centres of gravity have been located in the central temperate part (45–55° N) of the North Atlantic Ocean, both at present and future periods (Figure 2.6 and Figure 2.7). Distribution centroids of most of our studied species were projected to shift poleward under climate change (Table 2.5). All copepod assemblages showed a northward shift of 0.1–13.5 km per decade for the shelf-sea association species (*Paraeuchaeta hebes, Paraeuchaeta norvegica* and *Temora longicornis*), of 3.7–11.3 km per decade in the Arctic and subarctic association (*Calanus hyperboreus, Calanus glacialis* and *Calanus finmarchicus*) and of 1.9–17.8 km for temperate or warm-water species association (*Metridia lucens, Pleuromamma robusta, Pleuromamma borealis, Calanus helgolandicus, Centropages typicus* and *Candacia armata*). A southward migration in centre of gravity of *ca.* 11–15.4 km per decade was found in other shelf-sea and temperate association species (*Pseudocalanus elongatus* and *Centropages hamatus*). On average, a poleward community shift of 8.7 km per decade was predicted, with an important species range variation (-15 to 18 km per decade). Poleward shifts of the warm-temperate copepod assemblage were more important than the range contraction of the subarctic and Arctic species assemblage. These shift rates were generally associated with a reduction located at the southern edge of the species spatial distribution. Such changes could be linked to regional SST warming.

At species level, projections revealed a poleward shift with a slight contraction of the southern limit of habitat suitability distribution of the *C. finmarchicus, C. glacialis* and *C. hyperboreus*, and a shelfward constriction of *C. helgolandicus*, disappearing from oceanic warm waters south of the Oceanic Polar Front (Figure 2.7).

The average northward retreat is more clearly seen in *C. finmarchicus, C. glacialis* and *C. hyperboreu*s, with local projected shifts of up to 25–70 km per decade in the southern limits of their distribution. We observed that the probabilities of *C. finmarchicus* occupying large areas of the Labrador Sea and Buffin Bay will increase considerably by the end of the century, as well as in the northern North Atlantic Gyre and the Irminger Current. The *C. hyperboreus* and *C. glacialis* map showed a similar pattern: their distribution will be mainly reduced northwestward, from Labrador to Newfoundland and the Greenland Sea. The ecological niche of *C. finmarchicus* and *C. glacialis* will suffer an important habitat reduction in the warm-temperate waters of the central North Atlantic around the Gulf Stream and the North Atlantic Drift provinces, with potential local extinctions. A mean poleward migration of *C.*

glacialis of 11.3 km per decade is estimated, much more acute than in *C. finmarchicus* (3.7 km per decade). Its habitat suitability will probably respond to future warmer SST shifting northward to the Irminger Current, Faroe-Shetland Channel and Norwegian Trench (Figure 2.6 and Figure 2.7). A noticeable habitat gain in *C. glacialis* is predicted in the northern subarctic region, south of Iceland and the northern European shelf edge; this has contributed to a higher poleward shift of the centroid. Future projections of *C. hyperboreus* habitat suitability have also indicated a reduction in the southwestern edge of its spatial distribution where the species might face extinction. It will have a straightforward climatic response with a poleward mean latitudinal shift of ca. 8 km per decade. The species might disappear also from the southward flow of the East Greenland Current. Our models also predicted that *C. helgolandicus* might disappear from the warm-temperate subtropical areas of the North Atlantic and some areas of the Bay of Biscay and southern European shelf edge, and that it will colonize the North Atlantic Drift province and the east of the Oceanic Polar Front, with a relatively high net northward movement of *ca.* 18 km per decade (Figure 2.6 and Figure 2.7).

Ecological niche models of warm-temperate pseudo-oceanic (*Candacia armata* and *Centropages typicus*) and continental shelf assemblages (*Pseudocalanus elongatus*) also project a habitat gain in the temperate North Atlantic and along the Gulf Stream and North Atlantic Current. The warm-temperate *Pleuromamma borealis* and the cold mixed water *Pleuromamma robusta* also will gain habitat in the Oceanic Polar Front and subarctic region of the North Atlantic. The temperate *Paraeuchaeta norvegica* might face local extinction along the southern limits of its distribution. The overall suitable habitat is therefore expected to increase in these temperate-warm and shelf species assemblages. The habitat suitability of other sets of studied species did not show any latitudinal shift, but rather an east to west asymmetry: *Centropages hamatus* might colonize the Bay of Biscay and the southern European shelf edges, and Paraeuchaeta hebes would become extinct from the North Sea and the southern European shelf edge. The model explained deviance for *M. lucens* is too low (7.7%) to draw conclusions on its habitat suitability change.

The warm-temperate and continental shelf sets of species assemblages have shown the highest local northward shifts. Southern temperate regions are becoming warmer and are expected to provide suitable habitat for the warm-temperate and temperate pseudo-oceanic species assemblages. Thus, overall, warm species assemblages will respond faster to climatic change and cold species assemblages will retract their core distribution northward at a slower pace.

2.3.5 Phenology changes under climate change scenarios

Our projections showed an earlier timing of predicted occurrences of the annual maxima of 12 d in both copepod species (*C. finmarchicus* annual maxima at present was 15 April and in future was 3 April; *C. hyperboreus* at present was 27 April and in future was 15 April) (Figure 2.8).

Table 2.3 Evaluation of generalized additive models (yearly accumulated) with temporal cross-validation. Models built in cold period validated in warm period. Variables entered: sea surface temperature (SST), sea surface salinity (SSS), bathymetry, surface phytoplankton biomass (Pc) and pH. Values in the AUC column refer to model with all observations/mean *k*-fold cross-validation. Values in the accuracy column refer to model with all observations/mean *k*-fold cross-validation (%). edf: estimated degrees of freedom.

Species	Variables selected	edf	p	Overall explained deviance (%)	AUC	Accuracy
Calanus hyperboreus	SST	1.99	<2e-16			
	SSS	1.00				
	Depth	2.90				
	pH	1.98				
	Pc					
				48.1	0.845/0.807	85.34/80.80
C. glacialis	SST	1.73	<2e-16			
	SSS	2.84				
	Depth	1	0.0143			
				30.7	0.816/0.691	81.90/74.33
C. helgolandicus	SST	1.99	<2e-16			
	SSS	2.99				
	Depth	2.95				
	pH	1.98				
				27.3	0.749/0.745	74.94/74.83
C. finmarchicus	SST	1.95	<2e-16			
	SSS	2.87				
	Depth	2.80				
	pH	2				
	Pc					
				45.2	0.852/0.857	85.19/85.73

Table 2.4 Generalized additive models for the period 1995–1999. All observation-based models vs. *k*-fold cross-validated models. Threshold for conversion of probability of species presence to either presence or absence in model validation: 0.09 (*Candacia armata*), 0.24 (*Centropages typicus*), 0.07 (*Centropages hamatus*), 0.35 (*Metridia lucens*), 0.14 (*Paraeuchaeta norvegica*), 0.1 (*Paraeuchaeta hebes*), 0.1 (*Pleuromamma borealis*), 0.08 (*Pleuromamma robusta*), 0.2 (*Pseudocalanus elongatus*) and 0.26 (*Temora longicornis*). Values in the AUC column refer to model with all observations/mean *k*-fold cross-validation. Values in the accuracy column refer to model with all observations/mean *k*-fold cross-validation (%). edf: estimated degrees of freedom.

Species	Variables selected	edf	p	Overall explained deviance (%)	AUC	Accuracy
Candacia armata	SST	1.80	6.49E-08			
	SSS	1	0.000589			
	Depth	1.79	4.60E-10			
				15.4	0.738/0.558	75.1/55.9
Centropages typicus	SST	1.002	<2e-16			
	SSS	1	0.000587			
	Depth	2.413	<2e-16			
	pH	1.965	2.12E-08			
				25.4	0.761/0.730	76.2/73.0
Centropages hamatus	SST	1.95	1.67E-05			
	SSS	1.96	2.46E-05			
	Depth	2.62	7.84E-06			
	pH	1.88	9.46E-06			
				28.7	0.846/0.747	80.3/74.7
Metridia lucens	SST	1.98	6.74E-11			
	SSS	2.70	1.87E-07			
	Depth	2.92	2.06E-06			
	pH	1.89	1.17E-05			
				7.65	0.637/0.574	63.3/57.4
Paraeuchaeta norvegica	SST	1.99	6.44E-07			
	SSS	2.71	5.68E-16			
	Depth	2.95	<2e-16			
	pH	1.86	2.67E-07			
				27.5	0.783/0.644	78.2/64.4
Paraeuchaeta hebes	SST	1.96	1.12E-08			
	SSS	2.88	0.0896			
	Depth	2.75	1.80E-15			
	pH	1.44	6.87E-11			
				35.4	0.854/0.700	84.5/70.0
	SST	1.95	7.37E-08			
	Depth	2.59	1.22E-10			
	pH	1.89	6.82E-06			
				23.3	0.770/0.672	78.3/67.3
Pleuromamma borealis	SST	1.91	1.68E-05			
	Depth	2.29	9.25E-12			
	pH	1.81	0.0231			
				15.7	0.767/0.530	76.7/53.0
Pleuromamma robusta	SST	1.93	1.20E-04			
	Depth	2.74	9.54E-09			
	pH	1	0.0028			
				11.4	0.713/0.530	71.3/52.9
Pseudocalanus elongatus	SST	1.35	2.78E-02			
	SSS	2.88	3.93E-05			
	Depth	2.49	<2e-16			
	pH	1.79	1.01E-08			
	Pc					
				17.5	0.723/0.631	71.8/63.1
Temora longicornis	SST	1.00	8.93E-04			
	SSS	1.26	6.83E-15			
	Depth	2.61	<2e-16			
	pH	1.40	1.52E-06			
				24.9	0.779/0.730	78.1/73.1

2.3.6 Species turnover under climate change scenarios

Results have shown a high species turnover area (4–11 species) south of the Oceanic Polar Front (42.8–78.5%) compared with the overall North Atlantic (ca. 10%), covering vast areas of the centre of the North Atlantic Drift and extending up to the northern boundary of the influence of the Mediterranean water (Figure 2.9) Another moderate turnover rate (2–4 species, 21.4%) was found in coastal zones of southern Bay of Biscay and in the continental shelf current. High intensity of species invasion (3 to 5 new species) was projected to be concentrated along through the Oceanic Polar Front (Figure 2.9C). Local extinctions were projected to be most common (3–6 species lost) in temperate waters of the North Atlantic, south of the Oceanic Polar Front and by the northern boundary of the influence of Mediterranean water (Figure 2.8B). Areas of high turnover overlap with areas of both highest SST and Pc changes between present and future periods (Figure 2.3), and also correspond relatively well with the southern edge of the cold-temperate, subarctic and Arctic species assemblage (*C. hyperboreus, C. glacialis* and *C. finmar*chicus), and the northern biogeographic boundaries of the warm-temperate species assemblage (*C. armata* and *C. typicus*) (Figure 2.7).

2.4 Discussion

2.4.1 Habitat suitability models

Habitat suitability modelling enabled us to identify 3 key environmental variables (SST, SSS and depth) that determine the present distribution of *Calanus spp*. SST is, in general, the environmental driver explaining most of the variance of species occurrence in the 4 *Calanus spp*. (especially in *C. glacialis*) habitat models. Previous niche-model-related works[91,292] showed similar results. It is interesting to pinpoint that models also included Pc and pH. Pc seems to be a controlling factor in the probability of occurrence and distribution of *C. hyperboreus* and *C. finmarchicus,* but not of *C. glacialis* and *C. helgolandicus*. These variables have not been used frequently in zooplankton habitat modelling to date, since they explain low variance of *Calanus spp*. occurrence, as has been shown in previous attempts (e.g. Reygondeau & Beaugrand[291]). This is probably because Pc represents only a part of the food available and because food is not a limiting factor above the mixed layer depth.

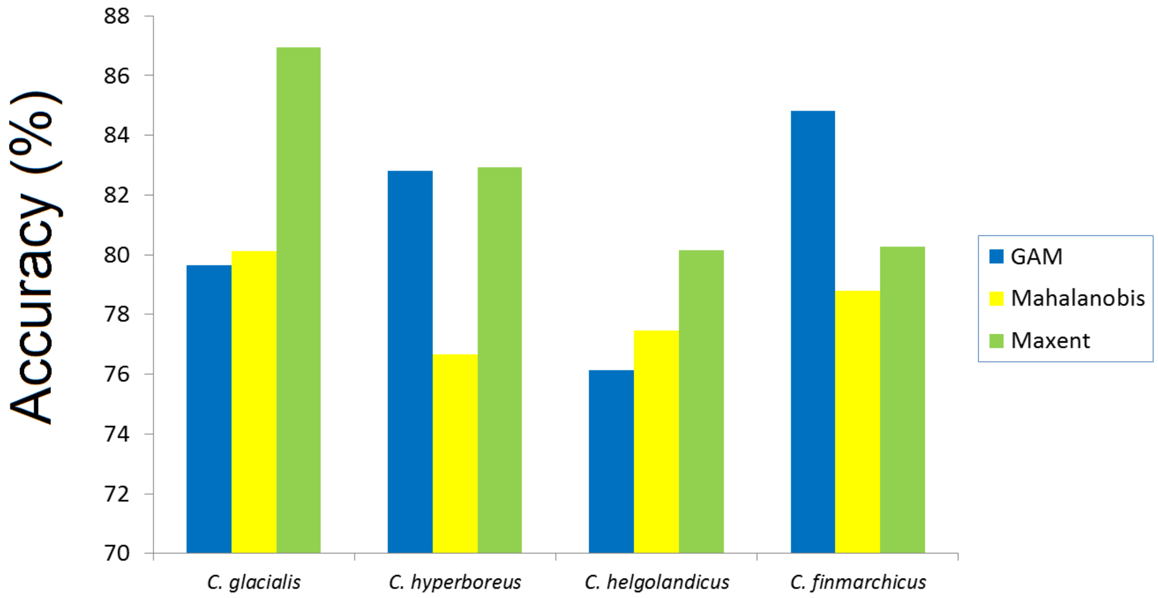


Figure 2.5 Accuracy of each different model according to *Calanus spp*. GAM: generalized additive model.

The MD and MaxEnt species distribution models failed in predicting the spatial distribution of *C. glacialis* along the Labrador Sea, Newfoundland shelf and the Davis Strait, probably because the CPR routes do not regularly cover the northern Labrador Sea area and these types of models are based only on the presence points while not accounting for absence points. Instead, GAM has proved to be a useful and accurate model to quantify the ecological niche of *Calanus spp*. in the North Atlantic. This conclusion is based on (1) the accuracy values of random (69–85%) and temporal (74–85%) validation, (2) its flexibility to incorporate seasonal variability, and (3) its performance comparing both accuracy values and spatial distribution maps with MaxEnt and MD algorithms. The relatively good accuracy of temporal cross-validation enabled us to use confidently the GAM-based habitat models generated for *Calanus spp*. in the future climate simulation.

It should be noted that there are some local differences (especially south of the Oceanic Polar Front) between the GAM habitat models built with the NEMO-ERSEM model and the MPIOM-HAMOCC for the present time in the 4 *Calanus spp*. The latter habitat suitability models are biased, having their gravity centres located farther south. However, since we are using the same model (MPIOM-HAMOCC) to make the projections at future and present conditions, then differences in environmental covariates will stay relative and vary accordingly in time.

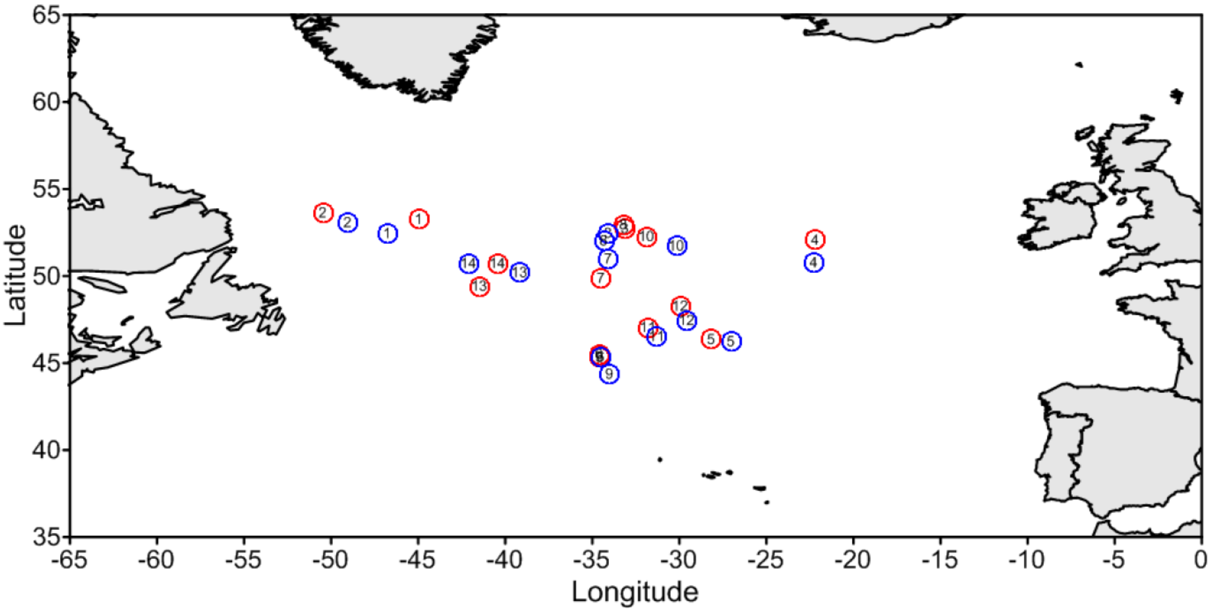


Figure 2.6 Latitudinal shift of species in the North Atlantic by taking into account the gravity centre of each. Position of the gravity centre at present (2001–2020)(blue circles); position of the gravity centre for the future (2080–2099)(red circles); 1: *Calanus glacialis*; 2: *Calanus hyperboreus;* 3: *Calanus finmarchicus;* 4: *Calanus helgolandicus;* 5: *Candacia armata;* 6: *Centropages typicus;* 7: *Centropages hamatus;* 8: *Paraeuchaeta norvegica;* 9: *Paraeuchaeta hebes;* 10: *Metridia lucens;* 11: *Pleuromamma borealis;* 12: *Pleuromamma robusta;* 13: *Pseudocalanus elongatus;* 14: *Temora longicornis.*

One of the limitations of the niche modelling approach is that in principle it does not include the effects of dispersal that can play a significant role in the distribution of plankton[157,181]. However, it has to be taken into account that when we use field distribution data to build the model we partially include such effects, albeit in an indirect way. Some of the areas where we find a species, and therefore model as suitable niche, may actually be suitable due to transport, not because of the environmental conditions. Therefore, the model is likely to let zooplankton distribute in a wider area than its optimal niche.

2.4.2 Latitudinal shift

This study showed that the Hutchinson's ecological niche of *C. finmarchicus* and that of *C. helgolandicus* will keep well separated in the future. This species niche separation was well described for the historic CPR data set (1942–2002) in Helaouët & Beaugrand[295]. The modelled spatial distribution of *C. finmarchicus* showed that this species mainly occurred in areas above the Oceanic Polar Front[336]. It has a broader tolerance interval than its congener *C. helgolandicus*[295], though it is able to support larger environmental variations. In fact, it co-occurs with the arctic *C. glacialis* and *C. hyperboreus* [337](Hirche 1991) at the northern edge of its distribution, i.e. north of Iceland, while in the northeastern North Atlantic, the North Sea and in the southern part of the Norwegian Sea, it co-occurs with *C. helgolandicus*[338]. Results also showed that the biogeographical range of *C. glacialis* and *C. hyperboreus* will be rather similar. The present biogeographic features of *C. finmarchicus, C. hyperboreus* and *C. glacialis* have been relatively well resolved by our habitat models. *C. helgolandicus*, instead, is more adapted to the temperate waters of the Atlantic Westerly Winds Biome[339] although our projections have shown that it will mainly present along shelf edges in the Mediterranean, the Northeast Atlantic, the North Sea and south of Iceland. The ecological niche of this species will respond fast to climate change, from local extinction in the warming waters of the temperate west North Atlantic to colonization in waters of the Newfoundland continental shelf. Therefore, *C. helgolandicus* can be considered a climate-sensitive species.

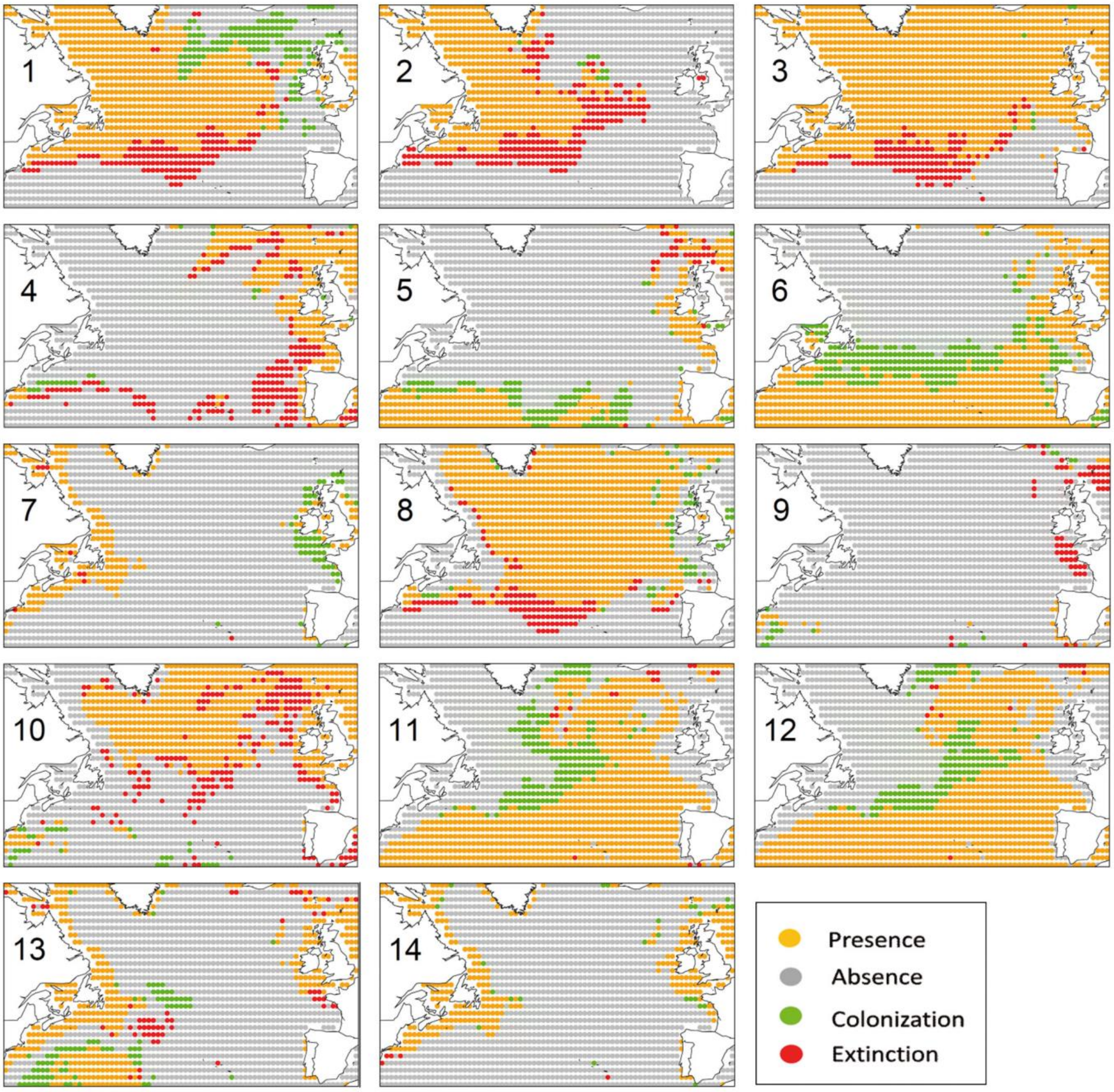


Figure 2.7 Habitat suitability models for each of the species at present (2001–2020) and in future conditions (2080–2099). Green: colonization area, species was absent in present and present in future; red: extinction area, species was present at present and absent in future; orange: present in both periods; grey: absent in both periods; 1: *Calanus glacialis*; 2: *Calanus hyperboreus*; 3: *Calanus finmarchicus*; 4: *Calanus helgolandicus*; 5: *Candacia armata*; 6: *Centropages typicus*; 7: *Centropages hamatus*; 8: *Paraeuchaeta norvegica*; 9: *Paraeuchaeta hebes*; 10: *Metridia lucens*; 11: *Pleuromamma borealis*; 12: *Pleuromamma robusta*; 13: *Pseudocalanus elongatus*; 14: *Temora longicornis*.

Our GAM models projected a plankton community poleward latitudinal shift of 8.7 km per decade on average, within the range of 1.4–28 km per decade estimated by Cheung et al. [58] for marine fishes and invertebrates, but substantially less than the 190 km per decade estimation of Sorte et al.[232] for 129 marine species. At species level, the rate of northward movement projected in *C. finmarchicus* (3.7 km per decade) is considerably lower than the change in distribution suggested by Helaouët & Beaugrand[63] for nearly the same area, period and climate change scenario (1º latitude and *ca.* 111 km per decade). The main differences between those studies and ours are the taxa assemblage analysed, the statistic considered (distribution limits vs. geographic centres) and the model algorithm used.

In this study, the use of GAMs to predict the habitat suitability of the species has been limited to a geographical subset in the North Atlantic; hence, the biogeographic range of the species is not fully represented. This limitation results in an underestimation of the poleward mean latitudinal shift of the species. Not all the species are projected to shift northward: *Centropages hamatus* (15.4 km per decade) and *Pseudocalanus elongatus* (11 km per decade) will shift southward by the end of century. This could be because the southern colonized area of these 2 species is larger compared to the north area, yielding a net southward migration. SST is not the main driving effect in the distribution of these 2 continental shelf species assemblages (6.6% out of the total 28.7% explained deviance in *C. hamatus* and 1.0% out of 17.6% in *P. elongatus*) and other environmental variables, such as Pc, appear to be more important. We think that although covering the whole biogeographic range of the species is preferable, the estimation of gravity centre considered here is relatively reliable to capture population shifts.

Table 2.5 Latitudinal and longitudinal shift of the species in the North Atlantic by taking into account the gravity centre of each. The shift is calculated as the distance (km) between the gravity centre of each species at present (2001–2020) and in the future (2080–2099).

Species	Latitudinal shift (km per decade)	Longitudinal shift (km per decade)
Calanus finmarchicus	3.7	8.1
Calanus glacialis	11.3	15.1
Calanus helgolandicus	17.8	0.8
Calanus hyperboreus	7.8	-11.9
Candacia armata subpopulations[a]	1.9	-10.8
Centropages hamatus subpopulations[a]	-15.4	-3.7
Centropages typicus	2.2	-0.8
Metridia lucens	7.3	-14.7
Paraeuchaeta hebes subpopulations[a]	13.5	-5.6
Paraeuchaeta norvegica	12.8	9.6
Pleuromamma borealis	7.2	-4.7
Pleuromamma robusta	11.2	-3.4
Pseudocalanus elongatus	-11.0	-20.6
Temora longicornis	0.1	14.6

2.4.3 Phenology changes

Our models predicted an advance in the annual peaks of 12–13 days between present time and the end of the 21st century for *C. finmarchicus* and *C. hyperboreus*, which is in line with previous studies highlighting the advance in spring seasonal peaks for zooplankton time series; Edwards & Richardson[31] reported a 10 d advance in annual maxima in North Sea copepods from 1958 to 2002, while Greve et al.[340] estimated an annual peak occurring 37 days earlier in Helgoland Road cladocerans from 1975 to 1999.

Zooplankton timing variability is often linked with temperature and/or Pc during the preceding weeks or month[341]. For taxa that have their maximum occurrences or abundances and activity in spring-summer like *C. finmarchicus* and *C. hyperboreus*, the usual pattern is 'earlier when warmer'[31,342]. Our projected seasonal peak of the 2 species is also occurring earlier, responding to a climate warming trend by the end of the century; these changes may propagate higher up in the food web.

Results of the phenology model showed that after the SST seasonal peak by mid-April, zooplankton maxima will occur: *C. finmarchicus* and *C. hyperboreus* showed a positive relationship with a 'sudden' increase in SST by the beginning of April. On the other hand, modelled phytoplankton blooms will only advance a week from the present to 2100 (data not shown), which presumably shows a higher dependency on day length and light intensity rather than temperature[343]. Results also showed that phytoplankton blooms will occur 1 or 2 weeks later than *C. finmarchicus* and *C. hyperboreus* annual peaks, underlining the higher dependence of these copepods on temperature rather than food availability. Melle et al.[344] also reported positive relationships between maximum abundances of *C. finmarchicus* and maximum temperatures in the North Atlantic, with no clear relationship with Pc maximum.

The aforementioned phenology studies as well as our modelled phenology approach are spatially limited because they take into account only a subset of the entire geographic range of the species. If the overall distribution area had been analysed, we would not expect to obtain substantial shifts in phenology, since the species would shift poleward in the future to a similar thermal window where it could succeed. On the contrary, local studies of zooplankton phenology (e.g. Mackas et al.[345]) in a subarctic Pacific station (Bornhold et al.[346], in the Strait of Georgia), reported higher shifts (30–60 days), since local environmental changes are subjected to more variability and the climatic response of the species will be more pronounced. Our spatial scale is in-between local and entire biogeographic range studies, which might explain the intermediate mean shifts values found.

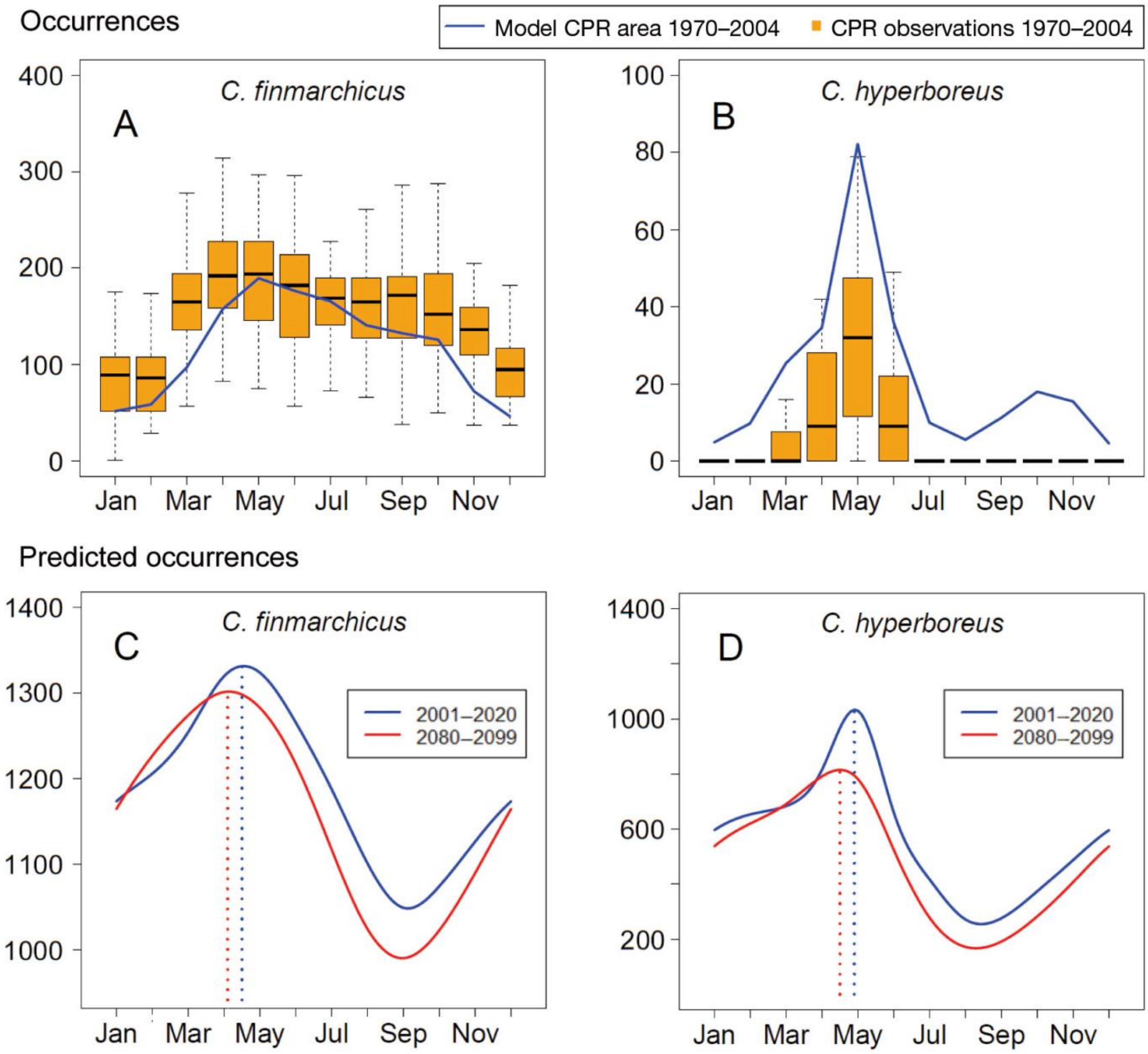


Figure 2.8 (A) *Calanus finmarchicus* and (B) *C. hyperboreus* continuous plankton recorder (CPR) number of observations vs. the habitat model predictions for the CPR sampling area in 1970 to 2004. Predicted occurrence phenology of (C) *C. finmarchicus* and (D) *C. hyperboreus* at present (2001–2020) and future (2080–2099) in the whole study area. Vertical dotted lines represent the seasonal peak of each species at each period.

2.4.4 Species turnover

Habitat models projected that the boundaries of species biogeographic domains are prone to suffer higher extinction or colonization rates. These areas with high turnover of species coincide with a large predicted SST increase by the end of century, where warm species assemblages could benefit to settle their populations there, while the southern limits of the cold subarctic and Arctic species assemblages will retract.

These projections, which follow basic constraints on the eco-physiology of animals[347], support the theory that marine communities at the extreme ends of their ecological niche are especially sensitive to local extinction due to climate change. The retreat of the southern biogeographical limits of species leads to a general range constriction, and the poleward expansion of the species in the subpolar regions is limited by the availability of suitable habitats. The Oceanic Polar Front[336] has acted as a sharp boundary for shelf edges and warm-temperate species associations limiting dispersal northward. These predicted species turnover patterns will trigger changes in the community structure of copepods, which are key species at the base of the marine food webs, and these changes may propagate through higher trophic levels[234,286], having an ecosystem-wide effect on the North Atlantic marine provinces.

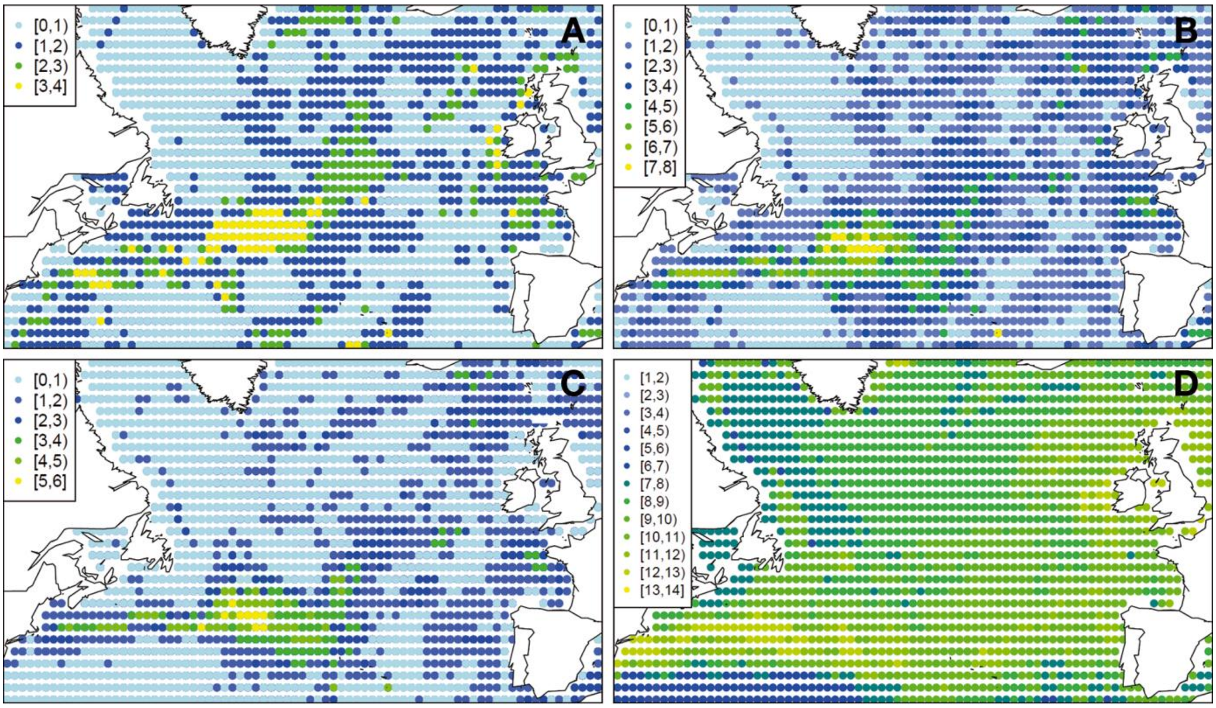


Figure 2.9 (A) Turnover model: number of species that will either colonize or go extinct at each pixel by 2080–2099. (B) Extinction model: number of species that will disappear at each pixel by 2080–2099. (C) Colonization model: number of new species that will occur at each pixel by 2080–2099. (D) Species richness model at present (2001–2020).

2.4.5 Model uncertainties and implications

Our study projects the spatial distribution of a representative subset of the North Atlantic copepod community. We have gained new insights on where the species are potentially able to expand or extinct locally. GAM-based distributions of *Calanus spp*. in the 1970–2004 period are in agreement with the observed spatial distribution from CPR surveys[236], conventional sampling data sets[291,348], CPR data reconstruction studies[91] and with other distribution studies inferred from models[209,308,349,350]. Therefore, the general agreement of our models with occurrence records and other modelled distribution studies supports the view that climatic (mainly SST), and also SSS, depth and biological (phytoplankton) factors are enough to provide a first approximation of niche shifts under climate warming[99,351].

In their simplest form, habitat suitability models are limited, since they ignore the adaptive potential of species. Indeed, there is some evidence that species may adapt to changing conditions with a rapid genetic response to natural selection instead of a direct reaction of the species following their ecological niche[210,352]. This has been documented for small and spatially isolated zooplankton such as *Calanus helgolandicus*[353], or chaetognats[354] in the Northeast Atlantic, Mediterranean and Black Sea, but not in the North Atlantic for *C.*

finmarchicus[355]. On the other hand, niche conservatism has been observed on palaeoclimatic scales[356]. In this sense, we assumed that on the time scale of this study, zooplankton have a limited evolutionary response capability to climate change[63,291,357]. Therefore, our projections assume no thermal adaptation of the species (*sensu* population fitness) to a changing environment. This assumption is supported by a recent study revealing that *C. finmarchicus* and *C. helgolandicus* show a lack of thermal adaptation to rising temperatures[209]. Species that fail to acclimatize physiologically or evolve genetically to increasing temperature will either move northward following their habitats[110,202,212,358,359] or become extinct[360].

Successful shifting species may have characteristics similar to those postulated for successful introduced species, such as high dispersal rates, climatic tolerances and competitive abilities[361]. However, we have considered the Hutchinson fundamental niche concept with unlimited dispersal of species that does not consider species competition processes.

There are uncertainties related to our projections: first, to the climate model itself; second, to the habitat model; and third, to the coupling of both. Moreover, our models do not incorporate other ecological processes such as dispersal limitation (in a direct way) and population dynamics. Future research efforts should focus on including these 2 mechanisms in the habitat modelling frame, in the same way as has already been done for fishes and invertebrates (e.g. Cheung et al.[58]). The application of the combined analytical methods beyond those traditionally used by ecologists will shed new light on the understanding of climate impacts on plankton communities.

We have addressed a community of copepods with different ecological requirements, though the use of statistical models (GAMs) is a more suitable approach than that of mechanistic models. GAMs offer the possibility to investigate the effect of climate change on multiple species without requiring sophisticated and time-consuming mechanistic models that depend on detailed knowledge of vital rates and life traits for each species (e.g. in *C. finmarchicus* or *C. helgolandicus* in Maps et al.[362]; see also Melle et al.[344]).

In summary, projections of 14 main copepod species in the North Atlantic by the end of the century under climate change scenarios indicate: (1) a prevailing poleward shift of most of the studied species, with poleward community shift of 8.7 km per decade on average, with an important species range variation from - 15 to 18 km per decade; (2) an area characterized by high species turnover of local colonization and extinction located south of the Oceanic Polar Front where SST is projected to increase by the end of the century; and (3) an earlier seasonal peak of copepods in response to the ocean warming trend. All these changes may propagate higher up in the food web. The precision of projection changes is subjected to limitations of the data set, mainly for those species with low occurrences and with short time period.

Part II: Connectivity and biogeographical patterns of plankton

3. Chapter 3: "Large-scale ocean connectivity and planktonic body size"

Villarino, E., Watson, J.R., Jönsson, B., Gasol, J., Salazar, G., Acinas, S., Estrada, M., Massana, R., Logares, R., Giner, C., Pernice, M., Olivar, M.P., Citores, L., Corell, J., Ezpeleta, N., Acuña, J., Molina-Ramirez, A., González-Gordillo, J.I., Cozar, A., Marti, E., Cuesta, J., Agusti, S., Fraile-Nuez, E., Duarte, C., Irigoien, X., and Chust, G. "*Large-scale ocean connectivity and planktonic body size*". *Submitted to Nature Communications* (in review).

Global patterns of planktonic species diversity are in large part determined by the dispersal of propagules with ocean currents[132,363]. However, the role that body-size plays in determining spatial patterns of diversity remains unclear[166]. Here, we quantified the dispersal scale and community structure – β-diversity – for a number of planktonic and micro-nektonic organisms spanning a range of body-sizes, from prokaryotes to small mesopelagic fishes. Global patterns of β-diversity for these communities were then compared to the timescales of surface ocean connectivity, derived from a global circulation model[363]. Our results reveal that β-diversity is negatively correlated with the timescales of ocean connectivity, more so than with differences in environmental factors. We also found that large-bodied plankton and micro-nekton communities in near-surface epipelagic waters have significantly shorter dispersal scales and larger spatial species-turnover rates when compared to small-bodied plankton. These results confirm that the dispersal scale of planktonic and micro-nektonic organisms is determined by body-size, ultimately setting global patterns of diversity.

3.1 Introduction

The oceans can be considered the largest continuous environment on Earth, and over long timescales, all marine ecosystems are connected to each other by ocean currents[132]. However, oceanic connectivity is not uniform as there exist barriers to dispersal in the form of land masses, frontal systems, gyres, and other oceanographic features[302,364]. Further, dispersal along ocean currents and the realized effect of these "physical barriers" varies across taxa. In particular, learning from terrestrial examples[365-368], differences in expected body-size amongst taxa is hypothesized to play a major role in determining both the distributional patterns and scale of dispersal for planktonic species[166,172,173,369]. As a consequence, in order to understand how marine biodiversity is maintained locally and structured spatially[112,126], it is necessary to investigate the relationship between planktonic dispersal and body-size[369,370].

Spatial patterns in the diversity of marine communities, namely β-diversity, are known to be strongly influenced by seascape features, for example differences in temperature as well as geographic distance[363]. Further, the scale-dependence of β-diversity can be described by as a "*distance-decay*" rate[147], which is set by three major mechanisms in both oceanic and terrestrial domains[112,371]: (1) local niche-based processes, which is epitomized by the hypothesis that, below 1-mm body size, "*everything is everywhere, but the environment selects*"[164,172]; (2) the effects of dispersal limitation[372], as hypothesized by the neutral theory of biodiversity of Hubbell[126], which leads to declines in community similarity with geographic distance even if the environment is completely homogeneous; and (3) the spatial configuration of the seascape, which can also dictate the rate at which organism disperse among sites[165,363]. However, it is a major challenge to elucidate weather or not marine planktonic communities are limited by dispersal, because the geographic distance is often correlated with specific environmental characteristics[126,166,167]. Distance-decay patterns have been observed for specific taxa in different ecological systems, from terrestrial (e.g. rainforest trees[150,151]), to freshwater (e.g. aquatic beetles[152]; fish and macroinvertebrates[153]), and marine communities (e.g. coral reefs[126]; marine bacteria and prokaryotes[154-156]; and plankton[157,158,373]). However, no robust pattern has been found for how distance-decay relationships vary *across taxa* or across physiological traits such as body-size, for any of these systems. Dispersal limitation has been hypothesized to increase with body size in planktonic communities[172,370,374]. That is, smaller organisms have in general larger population sizes[375], hence should yield lower local extinction rates[376] and therefore, reduced demographic stochasticity and ecological drift[126]. As a consequence, smaller organisms are more likely to disperse further, with oceanic currents for example[173], leading to shallower distance-decay slopes when compared to those of larger organisms[154,166,172,377].

Here, we quantify distance-decay slopes for a number of planktonic and micro-nekton organisms ranging greatly in body-size, from prokaryotes to small mesopelagic fishes, and test the hypothesized size-dependence of oceanic dispersal and resulting spatial patterns of regional connectivity. We also compared the distance-decay relationship for pelagic organisms with that of buoyant micro-plastics[378], providing a neutral, passively dispersed "test community", with no life traits. In order to estimate dispersal scales for each group, firstly, we test the importance of surface ocean connectivity in explaining spatial patterns of community structure (β-diversity), while controlling for the relative contribution of environmental filtering[261]. These analyses are based on unique samples of pelagic communities collected across the subtropical and tropical ocean during the Malaspina 2010 Circumnavigation Expedition[25] (Figure 3.1).

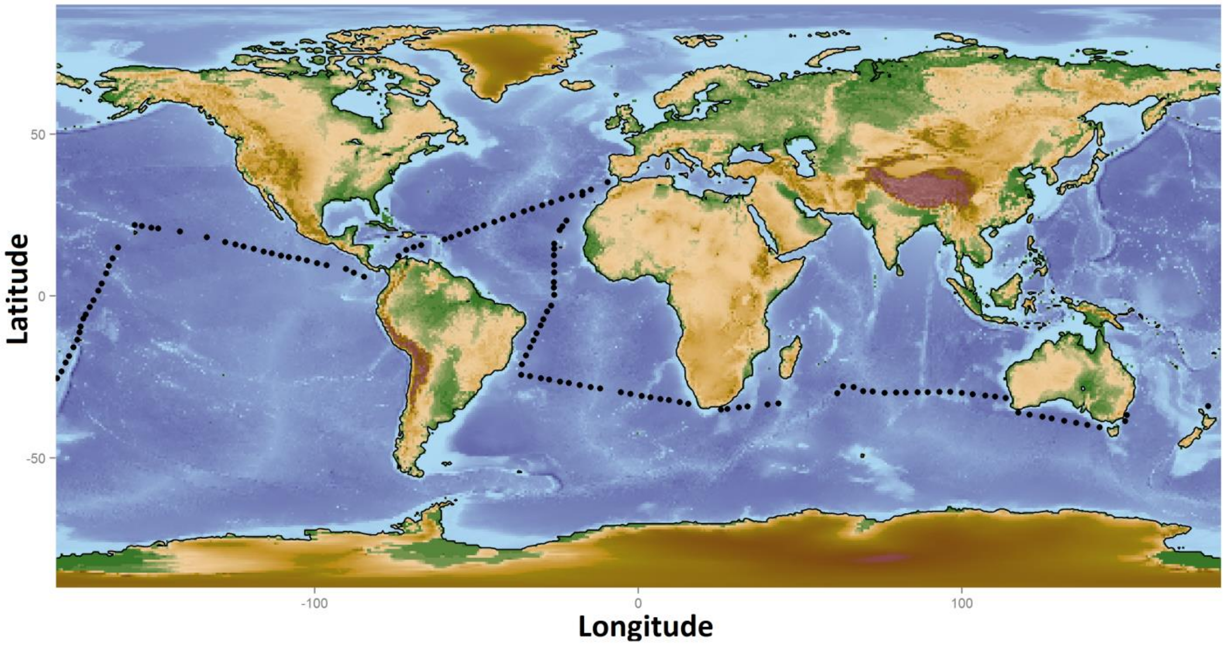


Figure 3.1 Sampling stations of the Malaspina 2010 Circumnavigation Expedition.

3.2 Methods

3.2.1 Biological data

The Malaspina Expedition sailed the subtropical and tropical Atlantic, Indian and Pacific Ocean on board R/V Hesperides, with a balanced distribution of sampling effort to characterize pelagic communities across the open ocean in the northern and southern hemisphere[25] (Figure 3.1). The samples include pelagic communities encompassing six orders of magnitude in body length, including prokaryotes and non-photosynthetic microbial eukaryotes (~0.0002-0.02 mm), phytoplankton (~0.002-0.5 mm), meso-zooplankton (~0.3-5 mm), macro-zooplankton (~0.1 -15 mm), gelatinous zooplankton (>5 mm), and myctophid fishes (20-110 mm) (Table 3.1). We focus on the neuston, epipelagic and mesopelagic communities. (1) Neuston communities include halobates insects, marine micro-plastics and larval stages of macro-crustaceans. (2) Epipelagic communities include meso-zooplankton, diatoms, cocolithophores and dinoflagellates, surface prokaryotes and other microbial eukaryotes. Abundances of diatoms, coccolithophores and dinoflagellates were vertically integrated (0-160 m), as well as the abundances of meso-zooplankton (0-200m). (3) Mesopelagic communities include myctophid fishes (Table 3.1).

Marine prokaryotes and microbial eukaryotes have been sampled by filtering 20 L of seawater collected from 3 m depth to retain the 0.3-20 µm size. Water samples for nano- and micro- autotrophic plankton (for simplicity, hereafter “phytoplankton”) determination were taken using a 30 L Niskin bottle from surface waters (3 m), and using a Rosette sampler system fitted with 24, 10 L Niskin bottles and a SeaBird CTD sensor for the depth receiving 20% of the light (PAR) incident just below the surface, and the depth of the chlorophyll maximum. 100 mL aliquots of these samples were settled in composite samples and examined under an inverted microscope, classifying phytoplankton cells into coccolithophores, diatoms and dinoflagellates[379]. Gelatinous zooplankton, macro-zooplankton, myctophid fish and micro-plastics were sampled using a neuston sampler (80 cm wide, 30 cm high) fitted with a 200 µm mesh size, towed at 2-3 knots during 10-15 minutes at a distance of 5 m from the starboard side of the hull[380]. Deeper meso-zooplankton communities (0–200 m) were sampled with a multi-net (300-5000 µm mesh size) (Table 3.1).

Table 3.1 Main- and All Groups, with the number of species and OTU and its habitat. E = Epipelagic. N = Neustonic. M = Mesopelagic. * = number of colors of the micro-plastics.

Main Groups surface	**Number of species / OTU**	**Number of stations**	**Habitat**
Prokaryotes	1218	120	E
Microbial eukaryotes	6409	120	E
Coco. 0-160m	46	133	E
Dino. 0-160m	237	133	E
Diatom 0-160m.	172	133	E
Meso-zooplankton	4282	36	E
Gelatinous zooplankton	11	89	N
Macro-zooplankton	45	92	N
Myctophids	12	95	M
All Groups surface			
MES - Small H. flagellates	1013	112	E
MES – Green Algae	450	112	E
MES - Fungi	58	112	E
MES - Parasites	20465	112	E
MES - Cercozoa	83	112	E
MES – Large flagellates	374	112	E
MES - Dino	8390	112	E
MES - Diatom	84	112	E
Plastics	16*	109	N

Traditional taxonomy was used to identify species of phytoplankton[379], gelatinous zooplankton[380], and juvenile and adult stages of myctophids[381]. Partial sequences of 16S rDNA and Cox1 genes were used to identify macro-zooplankton specimens, including larval stages[382]. Meso-zooplankton was identified using the 18S rRNA gene sequences[383]. High-throughput sequencing of the 18SRNA gene was used to classify the small microbial eukaryotes[384], and 16 sRNA for prokaryotes (unpublished sequences) following a similar protocol used for the deep waters samples[154]. Analysis of macro-organisms was conducted at the species level and that of meso-zooplankton and heterotrophic prokaryotes and eukaryotes was conducted at the OTU (Operational Taxonomic Units) level.

The resulting dataset includes nine main groups with a high sample spatial resolution and species occurrence (Table 3.1): prokaryotes (120 stations and 1218 OTUs), microbial eukaryotes (120 stations and 6409 OTUs), coccolithophores (133 stations and 46 species), dinoflagellates (133 stations and 237 species), diatoms (133 stations and 172 species), meso-zooplankton (36 stations and 4282 OTUs), gelatinous zooplankton (89 stations and 11 species), macro-zooplankton (92 stations and 45 species) and myctophids (95 stations and 12 species). Additionally, in order to infer the relationships between size and plankton connectivity we split the surface microbial eukaryotes group into 8 subgroups labelled as MES (from Microbial Eukaryotes Surface) - small heterotrophic flagellates (1013 OTUs), MES - green algae (450 OTUs), MES – fungi (58 OTUs), MES – parasites (20465 OTUs), MES – cercozoa (83 OTUs), MES – dinoflagellates (8390 OTUs) and MES – diatoms (84 OTUs) (Table 3.1).

3.2.2 Distance and similarity matrices

In Figure 3.2 we show a general flow diagram with the steps we carried out to figure out the dispersal patterns of planktonic communities. The analysis involves the calculation of three similarity or distance matrices, including biotic similarity, environmental distance, and oceanic currents, underpinning biogeographic analyses[261].

(1) For the biotic similarity matrix, we have calculated pairwise species similarities for each group using the Jaccard dissimilarity (d_j) index[385] with species presence absence data to infer the variation of the species groups' assemblages (β-diversity matrix):

$$d_j = \frac{b+c}{a+b+c} \qquad (1)$$

where a is the number of species shared between the two sites, and b and c are the total number of species that occur in site 1 and 2, respectively.

(2) The environmental matrix. Distance matrices for environmental variables are based on the Euclidean distance between surface pair-sites (Table 3.2). Variables have been converted into Z scores [(x-mean)/standard deviation] to give equal weight to each variable in distance calculations. The environmental variables used (see Table 3.2), previously shown to be the main variables potentially determining organismal distribution[88,180,381,386]. The best subset of environmental drivers shaping the plankton community assembly has been selected using the BIOENV approach. The BIOENV function finds the best subset of environmental variables,

so that the Euclidean distances of scaled environmental variables have the maximum (rank) correlation with community dissimilarities[262].

Table 3.2 Environmental variables and best BIOENV model selection for each of the different plankton groups.

Group	Environmental Variables	BIOENV variable selection
Prokaryotes	T,S,O2,Conduct, Fluo, PARi, SPARi, Turb, Beam-att-1m, O2volt, ZMax	O2, Turb, Beam-att-1m, Zmax
Microbial eukaryotes		Turb, Zmax
Coco. 0-160m	T,S,O2,Chla,Conduct,O2volt,FL,PARi,SPARi,Turb,Beam-att-1m	SPARi
Dino. 0-160m		SPARi
Diatom 0-160m.		O2volt
Meso-zooplankton	Not available	Not available
Gelatinous zooplankton	SST (remotely sensed),Temp_SADO, Sal_SADO, Chla,W, Z	Z
Macro-zooplankton	T,S,O2,Chla,Conduct,O2volt,FL,PARi,SPARi,Turb,Beam-att-1m	Turb,S
Myctophids	T,S, O2,T400, T200,S400,S200,O_{2min},SF, F_{max},	T400

1) Beam-att-1m = Beam attenuation coefficient at 1m depth
2) Chla = Chlorophyll-*a* concentration
3) Conduct = Conductivity
4) F_{max} = Maximum Fluorescence
5) O_2 = Oxygen (ml l^{-1})
6) O_2volt = Oxygen volt.
7) O_{2min} = Oxygen minimum concentration
8) PAR_i = Photosynthetic Active Radiation irradiance
9) S=Salinity
10) S200 = Salinity at 200 m
11) S400 = Salinity at 400 m
12) SF = Surface Fluorescence
13) $SPAR_i$ = Surface Photosynthetic Active Radiation irradiance
14) S-SADO = Salinity in situ
15) SST = Sea Surface Temperature
16) T = Temperature
17) T200 = Temperature at 200 m
18) T400 = Temperature at 400 m
19) T-SADO = Temperature in situ
20) Turb = Turbidity
21) W=Wind
22) Z = Depth of station

(3) Surface ocean transit time matrix. To calculate the particle transit times between any two points in the ocean, a Lagrangian particle simulation based on velocity fields from a Regional Oceanic Modeling System (ROMS) has been used, quantifying their separation along ocean currents[18]. Dispersal is likely to be influenced not only by geographical distance but also by the oceanic currents that could draw a very different path[387]. Hence, timescales of global surface connectivity taking into account oceanic currents (current-based transit times) have been calculated for every pair of sampling sites, for each groups, using the approach developed by Watson et al.[363] (Figure 3.2).

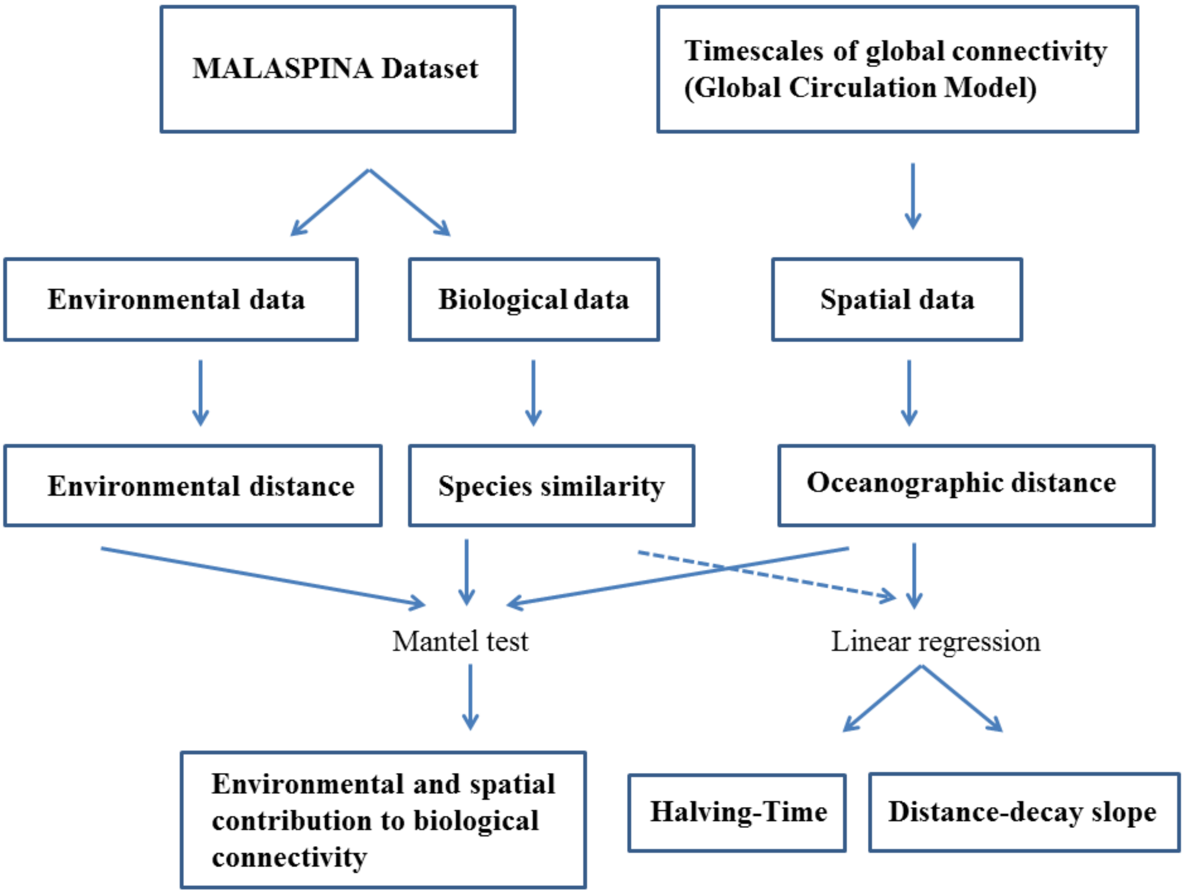


Figure 3.2 Main diagram of the methodology used to estimate the connectivity, in terms of dispersal scales and species spatial turnover of the organism.

3.2.3 Halving-Distance and distance-decay slope

To estimate rates of community dispersal and species spatial turnover we have used two connectivity descriptors: (1) the halving-distance metric, which is a distance-decay based proxy of the dispersal scale of the organisms and (2) the distance-decay slope[147,388], which is a proxy of species turnover rate (Figure 3.2). The halving-distance reveals the distance at which community similarity halves, and provides relevant information regarding the spatial scale of community variation[388]. We applied this metric to the surface ocean transit times, instead of geographic distance, therefore estimating halving-times (t_H), rather than having distances, after removing the environmental contribution. The difference between using the halving-distance or the distance-decay slope arises from the intercept of the relationship between species similarity and distance (Figure 3.3). The higher the species occurrences along the stations, the higher its similarity over distance, and consequently the intercept will be higher too. Since the halving-distance depends on the intercept, this will vary accordingly (Figure 3.3). Both descriptors, the halving-time and distance-decay slope, are key to unravel patterns of plankton community assembly embedded in distance-decay relationships[363].

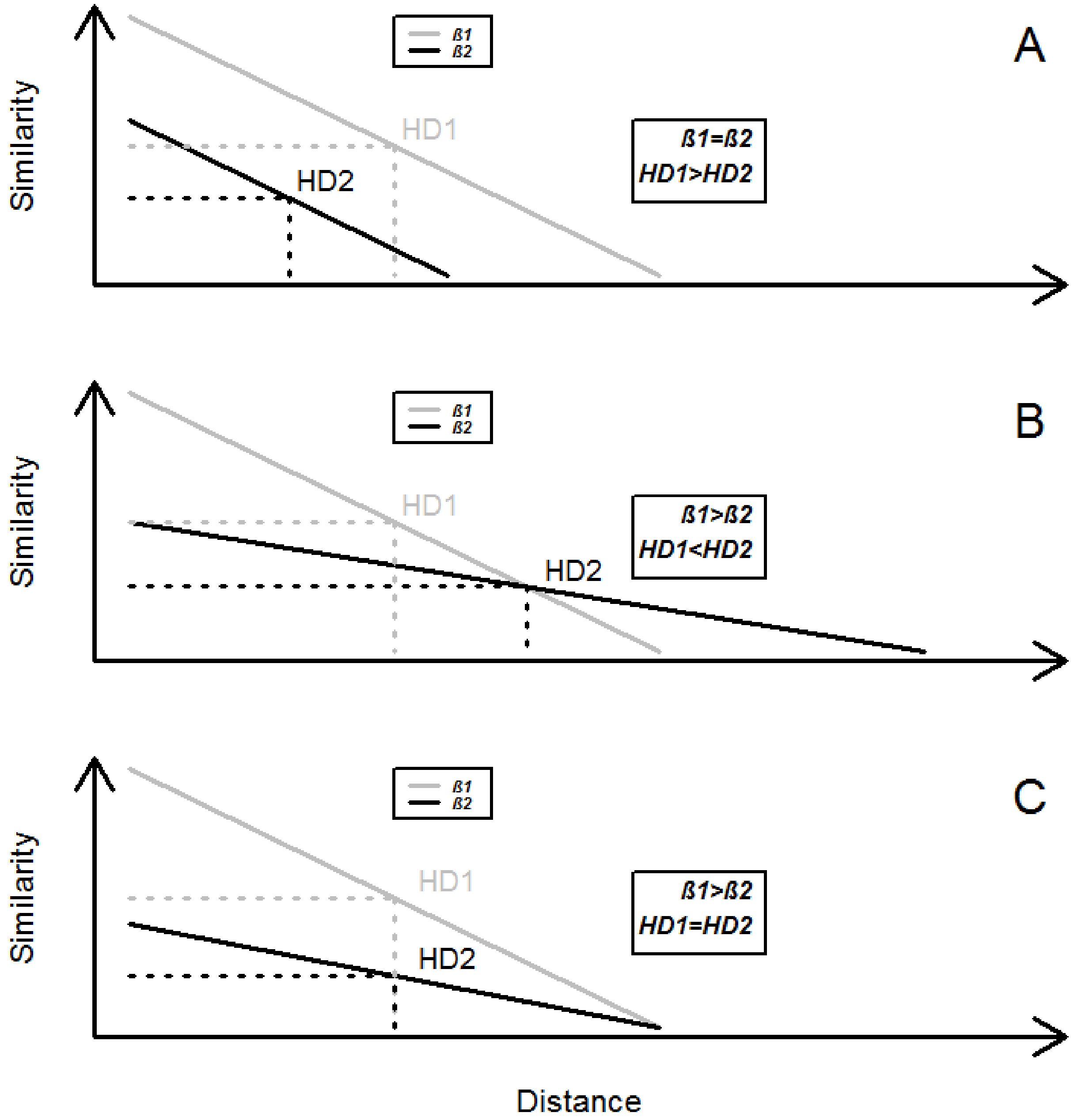


Figure 3.3 Conceptual figure denoting the similarity decay along distance in 3 different cases: A) Two equal distance-decay slopes ($\beta_1 = \beta_2$), but different Halving-Distance ($HD_1>HD_2$). B) Two different distance-decay slopes ($\beta_1 \neq \beta_2$), but different Halving-Distance ($HD_1>HD_2$). C) Two different distance-decay slopes ($\beta_1 \neq \beta_2$), but equal Halving-Distance ($HD_1=HD_2$).

We have also included an analysis of distance-decay relationships for buoyant micro-plastics[378], grouped into 16 colors, providing a neutral, passively dispersed “test community”, with no dispersal limitation and no life traits. The analysis of buoyant micro-plastics also provides a test of the particle dispersal models used.

3.2.4 Correlations of species turnover with currents and environmental predictors

Mantel correlation[261] between species dissimilarity and surface ocean transit times, and environmental distance, have been performed for causal modeling and inferences of marine connectivity . Partial Mantel tests have also been used to determine the relative contribution of surface ocean transit times and environmental distance in accounting for species composition similarity, using the *vegan* [263] package in R. Indeed, distance-decay patterns may also result from the relationship between species composition and environmental niche factors[180,261]. Multiple Regressions on distance Matrices (MRM) were also used to apportion the variability in species composition among different components (Figure 3.3).

Table 3.3 (A) Mantel correlations and Multiple regression on distance matrices (MRM) between β diversity (i.e. community variation), environmental distance, and current connectivity between pairs of sampling sites; and (B) Mantel partial correlations after controlling for the effects of environmental distance, in significant cases. The statistical significance of comparisons was assessed using Mantel and partial Mantel tests based on Pearson's product moment correlation using 9999 permutations (* = < 0.05 ; ** = <0.01).

(A)

Group	**Mantel test**			**MRM**
	N pairs	**Transit time**	**Env.distance**	**Transit time + environment**
MES - Small H. flagellates	112	0.30**	0.04	0.24
MES – Green Algae	112	0.27**	0.04	0.1
MES - Fungi	112	0.11**	0.04	0.06
Prokaryotes	120	0.28**	0.023	0.21
Microbial eukaryotes	120	0.14**	0.08	0.09
MES - Parasites	112	0.23**	0.002	0.05
MES - Cercozoa	112	0.10**	0.05*	0.03
MES – Large flagellates	112	0.19**	0.08	0.09
Coco. 0-160m	133	0.28**	0.01	0.22
Dino. 0-160m	133	0.21**	0.004	0.17
MES – Dino.	112	0.11**	0.04	0.05
Diatoms 0-160m	133	0.21**	0.02	0.13
MES - Diatom	112	0.15**	0.03	0.06
Meso-zooplankton	36	0.4**	NA	NA
Gelatinous zooplankton	89	0.09**	0.001	0.09
Macro-zooplankton	92	0.23**	0.09*	0.22
Myctophids	95	0.32**	0.32**	0.33

(B)

Group	**Mantel test**		
	N pairs	**Transit time**	**Env.distance**
MES - Cercozoa	112	0.07**	-
Macro-zooplankton	92	0.07*	-
Myctophids	95	0.09**	-

Many community similarity studies often use the Mantel correlations between biological distances matrices and matrices of geographic distance among sites derived from spatial coordinates, to infer in spatial pattern of community assembly. The Mantel test, instead, should be restricted to questions that concern dissimilarity matrices, and not “raw data tables” of spatial coordinates, from which one can compute dissimilarity matrices[389]. In our study, the global time scales of ocean connectivity among sites are not vectors of raw data tables from which a dissimilarity matrix can be calculated; this is why mantel tests are suitable for our purpose.

3.2.4.1 Dispersal scales and species turnover

Distance-decay relationships have been calculated by fitting a Type 1 linear regression equation describing the relationship between log similarity (S) and log linear distance (D):

$$\log S = a + b \log D \qquad (2)$$

where a is the intercept and b is the slope of the distance-decay relationship which reflects the rate of species turnover per unit distance. Halving-distances ($D_{1/2}$) for each community have been then calculated as proxies of dispersal scales[388]. We have estimated the dispersal scale using a logarithmic decay model expressed as:

$$S = c \ln(t) + int \qquad (3)$$

where S is similarity at time t, c is the rate of time-decay, and int the intercept of the model. Assuming S = 1 when t = 0; the corresponding halving-time (t_H) is:

$$t_H = \frac{e^{\left(\frac{S_0}{2} - int\right)}}{c} \qquad (4)$$

where S_o is the initial similarity at the lowest transit time (100 days). The value of 100 days to obtain the S_o was imposed after analyzing the similarity-decay of each group along surface ocean transit times. Long halving-times, represented by shallow distance-decay slopes, indicate a slow species turnover, while short halving-times imply fast species turnover. The major advantage of the halving-time over any metric of distance-decay slope is that it can be calculated for any type of regression between similarity and distance, and offers, therefore, a useful and easily comprehensible metric to compare among-studies[388].

The hypothesis that dispersal scales decrease with body size has been tested through the correlation between halving-time and the characteristic size of each biological group, and was calculated using parametric linear models and bootstrap cross-validation techniques.

3.2.4.2 Spatial patterns of β–diversity

Network graphs have been used to explore spatial patterns of community assembly on each surface group, and their connectivity degree, to analyze to which extent populations are connected at each pair of sites, using the *igraph* package in R[390]. We have clustered the groups using hierarchical clustering according to Jaccard, using Analysis of similarities (ANOSIM), and testing for significant differences between two or more groups of sampling units[263]. The optimal number of clusters has been selected. Subsequently, network graphs have been drawn with nodes (sampling stations) proportional to the number of connections (i.e. the similarity between sites) and color-coded to represent its cluster membership. A minimum similarity threshold has been imposed allowing all nodes to have a given connectivity degree.

3.3 Results

The relative influence of the processes shaping plankton and micro-nekton community structure - oceanic surface transit time and environmental predictors - varied among groups (Mantel tests, Table 3.3A). Community β-diversity was significantly correlated with surface ocean transit times in all groups, and the correlations with the environmental distance were only significant in cercozoa, macro-zooplankton and myctophids. In these three groups, the correlation between β-diversity and surface ocean transit times, controlling for environmental factors, remained significant (Table 3.3B). In myctophids, both processes have similar contributions to structuring the spatial patterns of community (Table 3.3A), and the correlation was the highest among all groups. We also found low shared covariation between environmental distance and surface ocean transit times, indicative of the low spatial autocorrelation in oceanic factors. A large fraction of the β-diversity variance remained unexplained by the selected explanatory factors (Multiple Regression on distance Matrices, Table 3.3A). This reflects the complexity of the mechanism underlying spatial community assembly. In summary, the communities we tested are structured primarily by dispersal, as reflected in the finding that surface ocean transit time accounted for a much larger mean fraction of the variance (21%) in Mantel distance compared to environmental niche factors (5%) (Table 3.3).

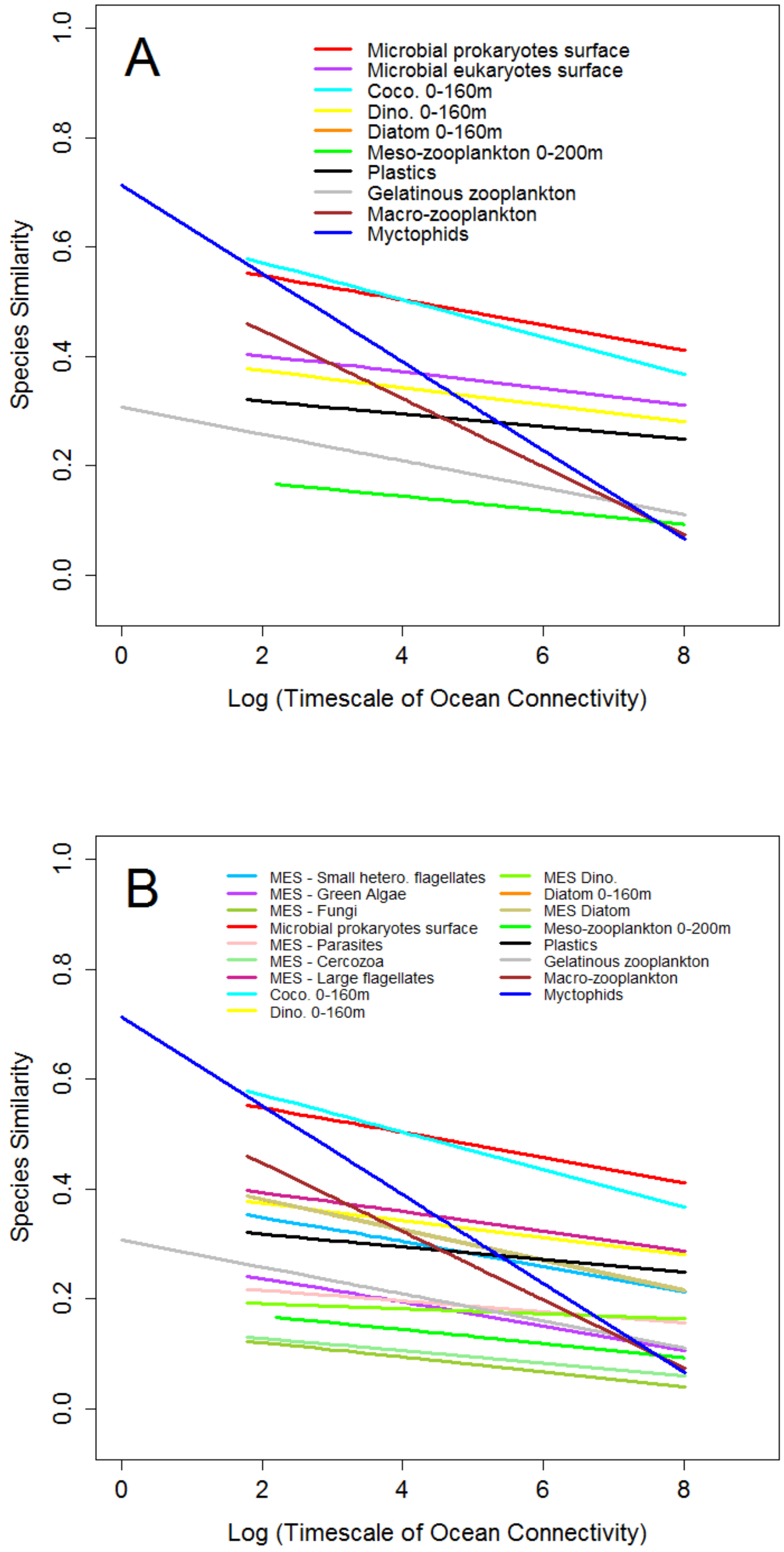
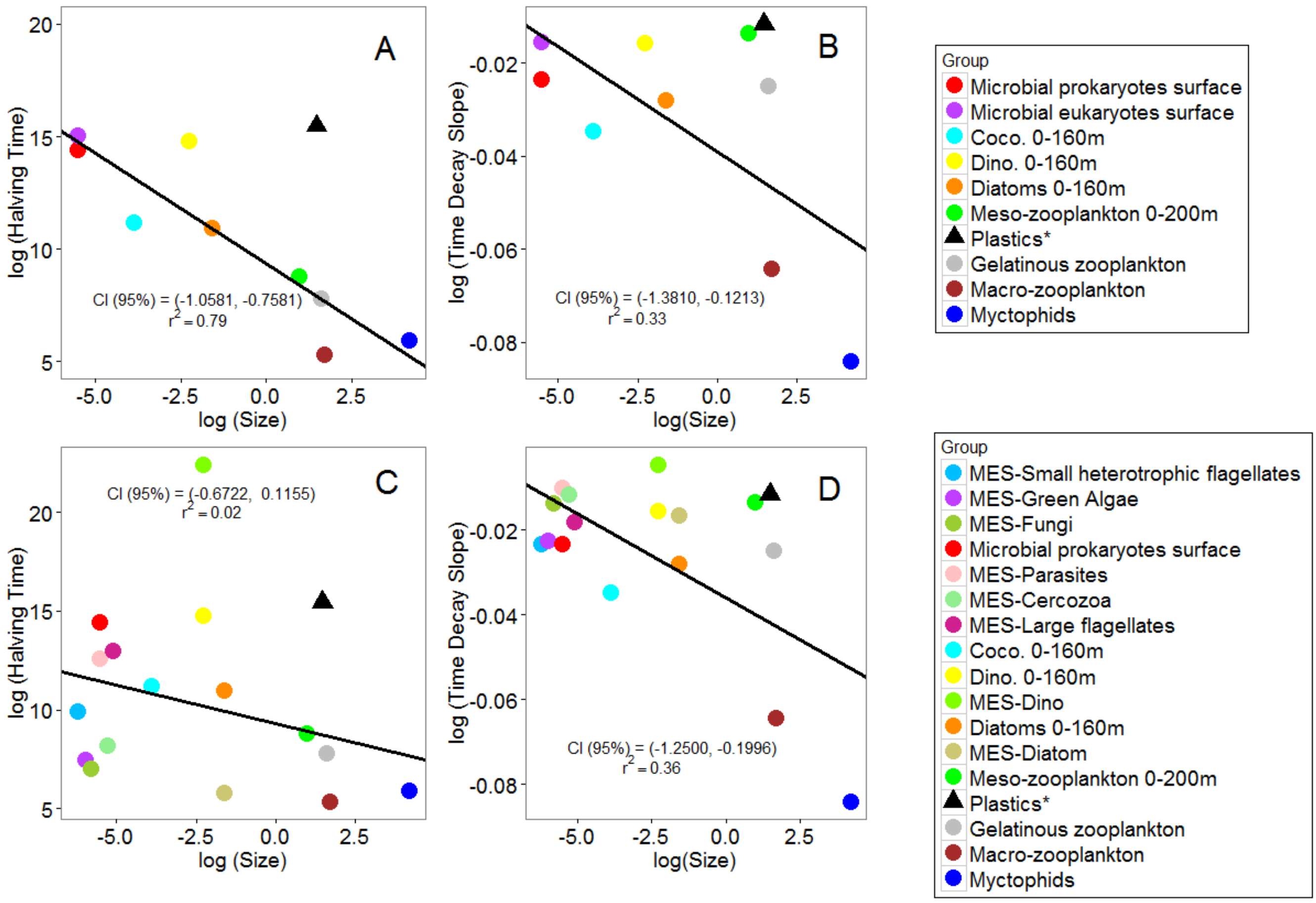


Figure 3.4 Time-decay relationship between species similarity (Jaccard) and oceanographic distance (days). 4A) Main - Groups. 4B) All - Groups.

That oceanic transit times are significantly correlated with the β-diversity of planktonic and micro-nektonic organisms, more so than environmental distance, lead us to estimate dispersal scales (halving-times) and spatial turnover rates (distance-decay slopes) for each group (Figure 3.4). In addition to the Mantel tests, the distance-decay slope and the community similarity halving-time reinforce the result that community similarity decreases with the logarithm of surface ocean transit times (Figure 3.4). For example, prokaryotes and microbial eukaryotes exhibit very long halving-times, $3.4x10^6$ and $1.85x10^6$ days, respectively. In contrast, gelatinous zooplankton (2476 days), macro-zooplankton (207 days) and myctophids (381 days) exhibit the shortest halving-times (Table 3.4). Likewise, the time-decay slopes are highest for large groups, such as myctophids, macro-zooplankton and gelatinous zooplankton (Figure 3.4A). Myctophids and macro-zooplankton show very high similarity between neighboring stations, denoting a high spatial-dependence in community structure compared to smaller organisms (Figure 3.4A, Table 3.3). The shallow time-decay slopes and long halving-times of prokaryotes and microbial eukaryotes indicate globally mixed distributions for these groups (Figure 3.4). Indeed, the hypothesized size-dependence of dispersal in planktonic and micro-nekton organisms is supported by a significant negative log-log relationship between the organism size and halving-time and time-decay slope (Figure 3.5, Table 3.5). In contrast, we observed no relationship between size and the scale of dispersal in micro-plastics, which have an intermediate "body" size, long dispersal scales and shallow time-decay slopes, similar to those of prokaryotes and microbial eukaryotes (Figure 3.5, Table 3.5).



***Plastics are not included in the regression line**

Figure 3.5 Relationship between the organism size (mm) and its realized dispersal in terms of oceanographic distance (days).

Spatially heterogeneous patterns in community similarity were observed in each size-group (Figure 3.6). Specifically, hierarchical clustering[33] of our estimates of community similarity revealed distinct spatial patterning of larger organisms (Figure 3.6), with clear biogeographic regions in the myctophid, meso- and macro zooplankton communities (Figure 3.6B and Figure 3.6C). In these communities, connectivity was highest in the Atlantic Ocean and the southern Indian Ocean. Network graphs also revealed an area of low beta-diversity for myctophids in the central Pacific Ocean (Figure 3.6C, pink points), where species connectivity is low due to limited mixing between neighboring communities. Marine communities in the Pacific and Atlantic oceans clustered into different groups, of course reflecting the barrier imposed by land (Figure 3.6). A possible oceanographic barrier is also detected in the Hawaiian archipelago, dividing communities in two different groups at either side of the islands (Figure 3.6C). In contrast to large-sized groups, small-sized groups showed many different clusters of various sizes, randomly distributed over the global ocean, for example as seen in diatoms (Figure 3.6A).

Table 3.4 Halving-distances derived from species similarity and (A) distance matrix with logarithmic decay models for each group. HT = Halving-Time (days). N= Neustonic; E = Epipelagic; M = Mesopelagic. So= Initial similarity, NA = Not Available. (** = <0.01).

Group	Logarithmic decay			Size range (mm)	Size mean	Sampling depth (m)	Habitat
	Slope (c)	S_0	HT				
Small H. flagellates	-0.0231**	0.34	20529	0.008-0.003	0.002	0	E
MES - Green Algae	-0.0222**	0.24	1731	0.008-0.003	0.0025	0	E
MES - Fungi	-0.0136**	0.11	1137	0.008-0.003	0.003	0	E
Prokaryotes	-0.0232**	0.52	1859497	0.0002-0.02	0.004	0	E
Microbial eukaryotes	-0.0154**	0.40	3418365	0.008-0.003	0.004	0	E
MES - Parasites	-0.0100**	0.22	292633	0.008-0.003	0.004	0	E
MES - Cercozoa	-0.0116**	0.11	3550	0.008-0.003	0.005	0	E
MES - Large flagellates	-0.0181**	0.39	443572	0.008-0.003	0.006	0	E
Coco. 0-160m	-0.0341**	0.52	72369	0.002-0.5	0.0205	0-160	E
Dino. 0-160m	-0.0156**	0.35	2673615	0.002-0.5	0.1025	0-160	E
MES - Dino.	-0.0046**	0.19	5450079988	0.008-0.003	0.1025	0	E
Diatom 0-160m	-0.0275**	0.27	57633	0.002-0.4	0.201	0-160m	E
MES - Diatom	-0.0164**	0.13	329	0.002-0.4	0.201	0	E
Meso-zooplankton	-0.0135**	0.16	6683	0.3-5	2.65	0-200	E
Plastics	-0.0116**	0.32	5201139	2-13	4.35	0	N
Gelatinous zooplankton	-0.0246**	0.23	2476	>5	5	0	N
Macro-zooplankton	-0.0622**	0.48	207	4-15	5.41	0	N
Myctophids	-0.0807**	0.47	381	20-110	65	0	M

3.4 Discussion

The oceanic connectivity of passively dispersing organisms depends both on physical transport by ocean currents and the ability to traverse environmental gradients[363,391]. In our analysis, the spatial arrangements of the sampled assemblages reveal that ocean connectivity (through our estimates of surface ocean transit times) explains a larger fraction of the variability in planktonic and micro-nektonic community similarity, relative to environmental factors. This indicates that passive dispersal with ocean currents, which is a neutral process similarly affecting all planktonic and micro-nektonic organisms, is a stronger determinant of community structure than niche-filtering factors[392].

Table 3.5 Evaluation of the log-log relationship between (A) group size and dispersal scale showing parametric models (all observation included) and bootstrap cross-validations.

(A)

MAIN GROUPS	Statistic	Parametric model	Bootstrap
log (HT) vs log (Size)	Confidence interval		(-1.0581, -0.7581)
	p-value	0.0008	< 0.001
	RMSE	1.717	
	Adjusted r^2	0.791	
	Formula	y=9.35+-0.98x	
log (Slope) vs log (Size)	Confidence interval		(-1.3810, -0.1213)
	p-value	0.06262	<0.02
	RMSE	0.02	
	Adjusted r^2	0.33	
	Formula	y= -0.039 +-0.004 x	

(B)

ALL GROUPS	Statistic	Parametric model	Bootstrap
log (HT) vs log (Size)	Confidence interval		(-0.6722, 0.1155)
	p-value	0.269	0.2
	RMSE	4.37	
	Adjusted r^2	0.02	
	Formula	y=9.30+-0.39x	
log (Slope) vs log (Size)	Confidence interval		(-1.2500, -0.1996)
	p-value	0.0081	<0.01
	RMSE	0.016	
	Adjusted r^2	0.36	
	Formula	y= -0.036+-0.003 x	

We also estimated dispersal scales and spatial turnover rates for numerous organismal groups, ranging in body-size. Results highlight that dispersal-limitation increase with body size in small (0.0002 to *ca* 10 mm) planktonic and micro-nektonic organisms. This is based on a trend toward steeper time-decay slopes and shorter halving-times with increasing body size. Notably, the large halving-times of marine microbial organisms imply that, when dispersing with ocean currents, it would take thousands of years of oceanic transport for such communities to halve their “similarity”. As a consequence, small organisms which have body sizes less than 2 mm and are probably sufficiently abundant, are likely to have a panmictic worldwide distribution[172,370], especially when compared to larger organisms which often exhibit stronger spatial patterning[173,393,394]. In contrast, larger organisms would need only a few decades, ~20 years at the most, to decline in similarity by half, with similar species at close sites and dissimilar far apart. These results highlight that patterns of β-diversity in open-ocean planktonic and micro-nektonic organisms are size-dependent[395]. However, we have also identified that body size is not the sole driver of dispersal, as confirmed by the dispersal patterns of micro-plastics. Micro-plastics have an intermediate size, but in contrast to organisms of the same size, display shallow distance-decay slopes and long dispersal scales. This suggests that large population densities and short generation times of micro-planktonic organisms, and not their size *per se*, leads to an over-dispersion of these organisms relative to passive tracers, and as consequence weak spatial structure[176,376,395,396]. In contrast, larger planktonic organisms have in general longer generation times and smaller population densities[375], and as a consequence are more sensitive to local extinctions, resulting in stronger spatial structure.

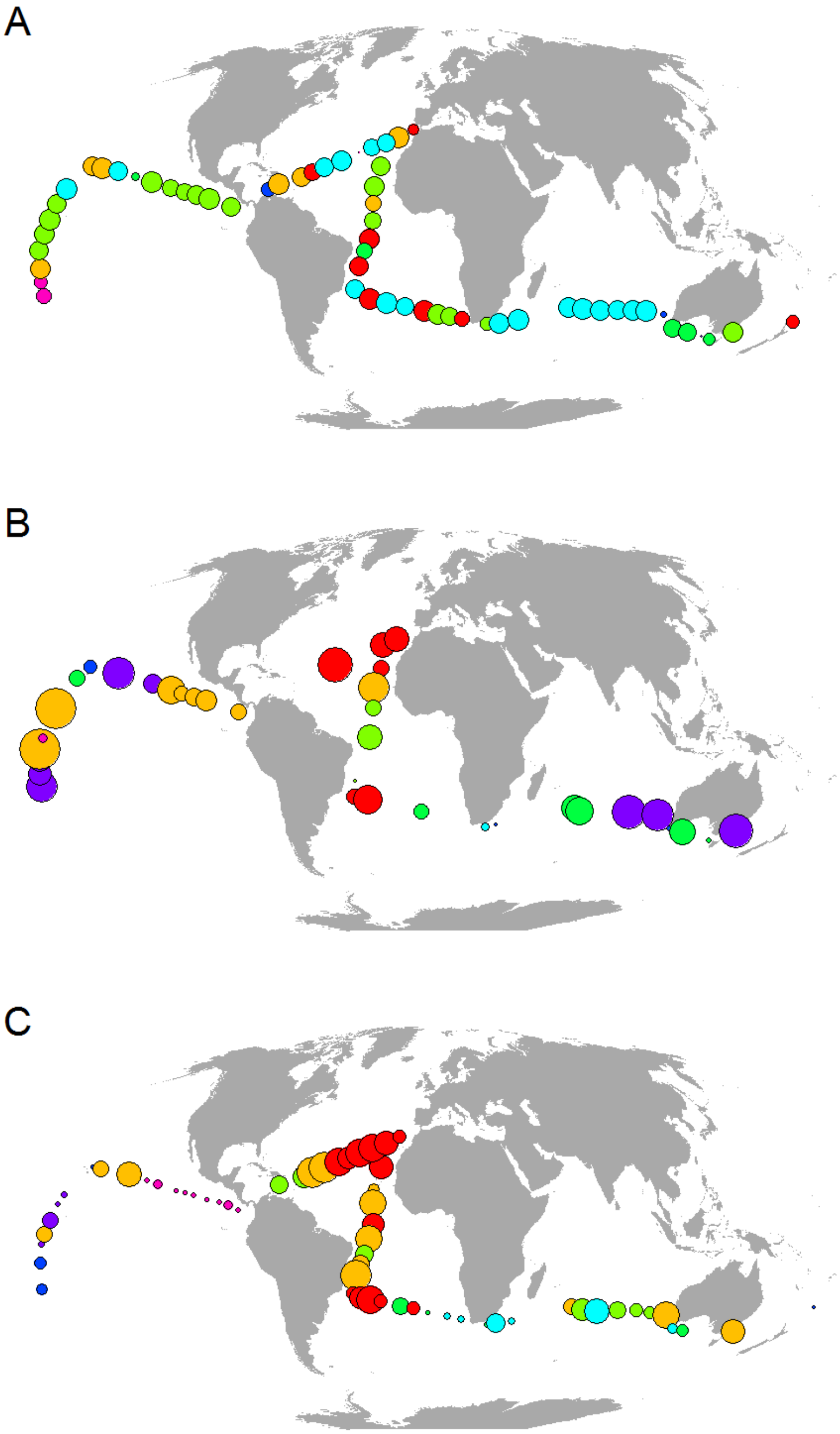


Figure 3.6 Hierarchical clustering based on the β_{sim} index for A) Diatom 0-160 m, B) Meso-zooplankton, and C) Myctophids. Colors = Cluster group. Size of stations = number of connections (i.e. similarity between sites). Some stations have been aggregated due to its proximity for clarity.

In addition to passively dispersed planktonic organisms, we also analyzed connectivity in myctophid fish communities (micro-nekton), which are active swimmers. The myctophid group showed short dispersal scales and a steep distance-decay slope comparable with those of other large bodied passive dispersers (i.e. gelatinous zooplankton and macro-zooplankton). This evidence of dispersal limitation for myctophids is likely a result of their migration patterns being mostly vertical (rather than horizontal), as they move daily between the mesopelagic to the epipelagic zone[397]. In contrast, numerous marine megafauna, such as large pelagic fish and marine mammals, actively move horizontally either foraging for food or to complete long-distance migration[398]. Indeed, previous research has demonstrated a positive relationship between dispersal distance and body size for such megafauna[399]. For myctophids, their horizontal movement occurs predominantly as larvae, being passively transported by ocean currents in epipelagic waters[397]. The observed similarity in dispersal patterns of myctophids and macro-zooplankton may thus arise from the same processes: passive horizontal dispersion of larvae, with movement as adults mainly devoted to diel vertical behavior. It is worth noting that contrasting results have been found in a study by Jenkins et al.[369] who suggested that body size controls the dispersal of active dispersers, but not passive dispersers like planktonic organisms. However, this analysis did not characterize the full range of body-sizes that we have studied, and as a consequence is limited in its scope.

The spatial distribution of community similarity, identified using hierarchical clustering, revealed distinct size dependent spatial patterns. In particular, we identified large-scale frontal zones as hotspots of β-diversity. These frontal zones act as barriers separating subtropical gyres, and are typically areas of relatively high primary production[17,400]. Indeed, recent studies have shown that there is a significant relationship between phytoplankton diversity and productivity and that this can be explained by dispersal[401-403]. In these studies, limited dispersal between distinct pelagic provinces has been shown to play a major role in plankton population differentiation, and the creation of strong genetic breaks and enhanced diversity in bridging regions. In the Malaspina survey, sample sites between subtropical gyres of the Atlantic, Pacific and Indian Oceans are extremely well connected (i.e. acting as bridges between ocean provinces) with relatively high biodiversity. In contrast, sample sites within these gyre systems are generally less productive; less connected by ocean currents, and as a consequence are characterized by low relative biodiversity.

In summary, we have shown that planktonic and micro-nektonic β-diversity declines logarithmically with ocean surface transit times, and that dispersal limitation, which is a neutral process, is a stronger determinant of community structure when compared to niche segregation. More importantly, we have identified that large-bodied plankton groups and mesopelagic myctophid fishes have shorter dispersal scales and higher species spatial turnover rates when compared to micro-plankton groups. Together, these results highlight that body size and ocean currents are key determinants of global patterns of biodiversity in marine planktonic and small-bodied pelagic communities.

4. Chapter 4: "Dispersal similarly shapes both population genetics and community patterns in the marine realm"

Chust G., **Villarino E.,** Chenuil A., Irigoien X., Bizsel N., Bode A., Broms C., Claus S., Fernández de Puelles M.L., Fonda-Umani S., Hoarau G., Mazzocchi M.G., Mozetič P., Vandepitte L., Veríssimo H., Zervoudaki S. & Borja A. (2016). "*Dispersal similarly shapes both population genetics and community patterns in the marine realm*". Scientific Reports, 6, 28730

Dispersal plays a key role to connect populations and, if limited, is one of the main processes to maintain and generate regional biodiversity. According to neutral theories of molecular evolution and biodiversity, dispersal limitation of propagules and population stochasticity are integral to shaping both genetic and community structure. We conducted a parallel analysis of biological connectivity at genetic and community levels in marine groups with different dispersal traits. We compiled large data sets of population genetic structure (98 benthic macroinvertebrate and 35 planktonic species) and biogeographic data (2193 benthic macroinvertebrate and 734 planktonic species). We estimated dispersal distances from population genetic data (i.e. F_{ST} vs. geographic distance) and from β-diversity at the community level. Dispersal distances ranked the biological groups in the same order at both genetic and community levels, as predicted by organism dispersal ability and seascape connectivity: macrozoobenthic species without dispersing larvae, followed by macrozoobenthic species with dispersing larvae and plankton (phyto- and zooplankton). This ranking order is associated with constraints to the movement of macrozoobenthos within the seabed compared with the pelagic habitat. We showed that dispersal limitation similarly determines the connectivity degree of communities and populations, supporting the predictions of neutral theories in marine biodiversity patterns.

4.1 Introduction

Dispersal plays a key role to connect populations, and contrastingly, its moderate limitation is one of the main processes to maintain species coexistence and promote regional biodiversity [112,404]. Knowledge of population connectivity and dispersal is relevant for determining the resilience of species to global change [405], the establishment of sustainable fisheries management strategies[406], the design of networks of functional marine protected areas [406-408], and other conservation issues, such as habitat restoration, population viability analysis, and invasive species monitoring[409]. However, difficulties associated with tracking and modelling the trajectory and fate of propagules and larvae have limited our knowledge of dispersal strategies and population connectivity of many marine species[410].

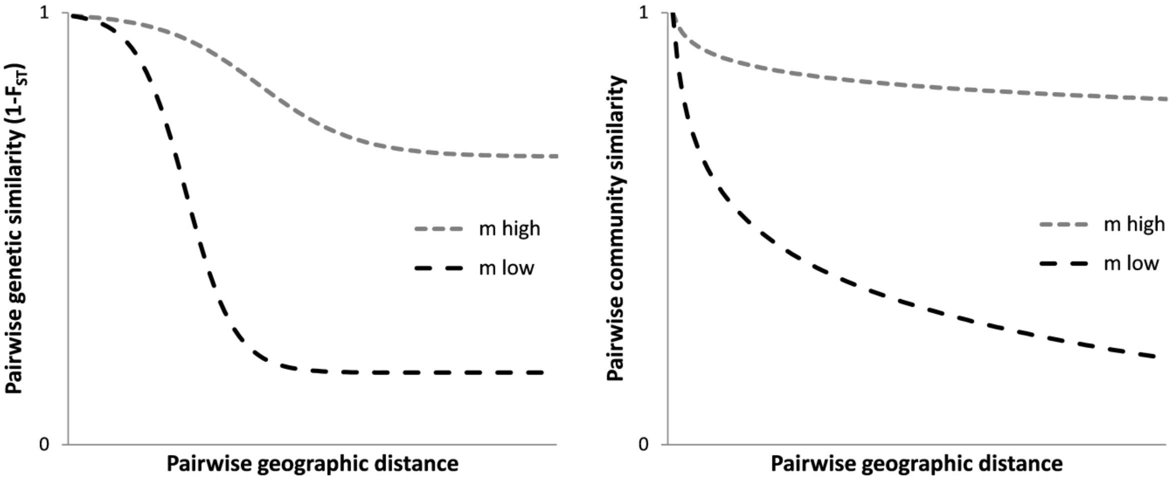


Figure 4.1 a) Decrease of genetic similarity (1-FST) with geographic distance under a stepping-stone model (isolation-by-distance plot). m is the migration rate among subpopulations in a metapopulation, modified from Selkoe and Toonen[145]. b) According to the neutral model of biodiversity, species cross-site similarity is predicted to decline logarithmically with increasing geographic distance as a function of migration rates. m is the migration among subcommunities in a metacommunity.

Dispersal limitation of propagules and larvae and their demographic stochasticity (i.e. resulting from random events of individual mortality and reproduction, and not from environmental variance which can also induce population fluctuations) are neutral processes that shape both genetic structure and community composition. Due to finite number of individuals in a population or community, the relative frequencies of alleles or species will to some degree change stochastically[411]. Recently, studies have been motivated to identify similarities between processes underlying patterns of species diversity and those underlying genetic diversity[157,412-416]. In neutral theories, alternative forms of a gene (alleles or haplotypes) in a population are analogous to species in a community, random genetic drift in populations is analogous to ecological drift (random fluctuations in species relative abundances[392]) in communities, and spatially structured populations (i.e. metapopulations) are analogous to metacommunities[417]. The neutral theory of molecular evolution[418] states that most evolutionary changes at the molecular level are the result of random genetic drift acting on neutral alleles (those that do not affect fitness). When the number of migrants that disperse over short distances is higher than that over long distances, the isolation-by-distance (IBD) theory predicts that pairwise genetic variation (for instance, the Wright's fixation index F_{ST}, the sample pairwise genetic differentiation) will increase with the geographic distance between a pair of populations[418-420]; see Figure 4.1. Quantitative IBD predictions consider neutral alleles and populations to be at equilibrium between dispersal and genetic drift [146]. The slope of IBD varies with migration rate (i.e. the proportion of individuals that leave the natal site and successfully reproduce at another site) (Figure 4.1A) and is commonly used for estimating dispersal distance (i.e. geographic distance travelled between source and settlement sites) with genetic markers.

In ecology, whether the regional distribution of species arises from limitations to dispersal[176] or niche adaptive processes[421] has been a long-standing debate and the emergence of the concept of neutrality[392] has appeared more recently than it has in population genetics. In a neutral community, all individuals are assumed to have the same prospects of reproduction and death. According to the neutral model of biodiversity, species cross-site similarity (i.e. the opposite of β-diversity) is predicted to decline logarithmically with increasing geographical distance when migration rate is low [392,416] (see Figure 4.1B). This pattern, named distance decay, has been observed for a variety of biomes and taxa: trees of the rainforest [422,423], coral reefs[392], marine bacteria[424], and plankton[180] (but see[425]). Neutral theories of macroecology have synthesised spatial patterns in species diversity and genetic diversity that postulate that stochastic processes (migration, genetic/ecological drift, and mutation/speciation) act similarly at all taxonomic scales down to the level of individuals [413]. However, parallels in biological connectivity between population genetics and community ecology have been nearly exclusively restricted to theoretical studies[414,426] that have been validated with field observations in only a few terrestrial and freshwater groups [412,413,415,417,427,428]; none of which represent the marine realm.

Our aim is to evaluate whether dispersal traits in marine species determine the connectivity degree among communities and among populations within species. In particular, we hypothesise that planktonic species will have a higher dispersal distance than macrozoobenthic species at both the genetic and community levels. We base this prediction on constraints to movement in adult macroinvertebrates within the seabed, which are only partially compensated for by their larval stage. In comparison, pelagic plankton experience higher seascape connectivity. To test this hypothesis, first, we conducted a meta-analysis based on a literature survey of the genetic population structure (98 macrozoobenthic species and 35 planktonic species) and collated a large data set on community composition (2193 macrozoobenthic species and 734 planktonic species). Subsequently, we estimated dispersal distances at the genetic level derived from IBD slopes (i.e. F_{ST} vs. geographic distance) and compared them with those at the community level derived from β-diversity analysis.

Table 4.1 Values for the isolation-by-distance (IBD) slope and dispersal scale (km) for each group. N_{sig} = Number of species with significant IBD slopes. N_{total} = Total number of species analysed. NDL= Non-dispersal larvae. DL = Dispersal larvae. A correction factor was applied to the IBD slope for mitochondrial cases.

Group	Mean of IBD slopes	Dispersal scale (km)	N_{sig}	N_{total}
Macroinvertebrates			66	98
Macro-NDL	0.005168	0.31	15	17
Macro-DL	0.000835	1.92	51	81
Plankton			9	35
Phytoplankton	0.000082	19.53	3	13
Zooplankton	0.000018	88.99	6	22

4.2 Methods

4.2.1 Genetic population analysis: definitions of biodiversity components and data compilation

We selected three biological marine groups: phytoplankton, zooplankton, and benthic macroinvertebrates (hereinafter called macrozoobenthos). In this study, phytoplankton included diatoms, dinoflagellates, and coccolithophorids; zooplankton included Annelida, Arthropoda (euphausiids, mysids, copepods, and Crustacea), Chaetognata, Cnidaria, Ctenophora, and Nematoda (i.e. all available taxa with a pelagic adult stage), and excluding benthic macrozoobenthic larvae (i.e. meroplankton); and benthic macrozoobenthic taxa included Annelida, Arthropoda (Crustacea), Bryozoa (Cheilostomatida), Chordata (Tunicata), Cnidaria, Echinodermata (spinosulida, ophiurida, camarodonta), Mollusca (Gastropoda), platyhelminthes, and Porifera (dictyoceratida). Macrozoobenthic species were divided into two main groups according to their larval dispersing strategy [429]: (i) dispersing larvae (DL; including both planktotrophic and lecithotrophic larvae characterised by a long (>12 weeks) to short (1 day-12 weeks) pelagic phase); and (ii) nondispersing larvae (NDL; direct developers, brooding, characterised by a larval stage with very low dispersal potential).

We conducted a bibliographic survey of IBD slopes derived from population genetics data to test differences in dispersal scale among marine groups. Inclusion criteria for the selected studies included the availability of (i) either IBD slope or differentiation F_{ST} statistics [419]; (ii) geographic distances among populations or raw genetic data (e.g., haplotypes, molecular markers); and (iii) more than three sites per case study. We used abstracts obtained from the Web of Science (Reuters 2014) (1997- 2014), using pairs of combinations of the following keywords as search strings: *genetic, structure, isolation by distance, diversity,* and *population* with *phytoplankton, zooplankton*, and *macrobenthos*. We also included some unpublished data in the analysis. Overall, we analysed 290 papers about plankton (zooplankton and phytoplankton) and 220 papers about macrozoobenthos. Studies were excluded if they included invasive species with recent (i.e. years to decades) invasions to new areas or did not include the geographic locations of sampling points. For those studies that did not include correlation and significance of IBD correlations, we tested the significance of their IBD slopes using reported F_{ST} values and the geographic coordinates of the sampling sites (see next section). We used GENEPOP (http://genepop.curtin.edu.au/) to estimate pairwise F_{ST} values from haplotype frequencies for the few studies that included haplotype frequency matrices.

4.2.2 Analysis of dispersal scales based on IBD

We compared differences in dispersal scales between macrozoobenthic and planktonic groups. To address this, we searched IBD values for species whose F_{ST} and geographic coordinates were provided. We used *marmap*[430] package in R to calculate the least-cost distance between sampling points surrounding land and Mantel tests[431] with a Spearman correlation coefficient and 1000 permutations to assess the significance of the correlation between the sample pairwise genetic differentiation, F_{ST}, and geographic distance for each species. We used a four-fold correction factor on the IBD slope for mitochondrial genetic markers rather than the two-fold correction used in Kinlan and Gaines[432] because the effective size of mitochondrial genomes accounts for the number of females (i.e. a quarter of the number of nuclear genomes assuming a 1:1 sex ratio for diploids). This approach was based on linear regressions of F_{ST} versus distance.

To estimate dispersal distance from IBD slopes at the group level, we applied the method used by Kinlan and Gaines[432] to our data set based on simulations under a particular stepping-stone model[433]. We used a power function model (dispersal distance = 0.0016 (IBD slope)$^{-1.0001}$) to estimate dispersal distances established in Palumbi[433]. Dispersal estimates represent the equivalent mean dispersal distance required to generate the observed F_{ST}/distance slope under the model's assumptions (stepping-stone model and assumption of a deme size of 1000; see Palumbi[433]).

Because molecular marker choice for determining F_{ST} can affect the outcome of population genetics studies[434-437], several precautions were taken when comparing studies using distinct genetic markers. Microsatellites have much higher mutation rates than other markers, in particular compared to allozymes [438], but mutation rates should not influence IBD parameters under the neutrality hypothesis. However, allozyme polymorphisms are expected to depart from the neutral hypothesis more often than microsatellites, which are noncoding DNA regions, and differences in IBD values could eventually result from this because of the influence of selection on allozyme diversity. Mitochondrial DNA markers represent another case regarding the selective regime (more genetic drift, leading to a lower efficiency of natural selection) and always represent a single locus since the mitochondrial genome does not recombine (high stochasticity). Hence, we tested the effect of the main molecular marker types (allozymes, mitochondrial, and microsatellites) used for each species on the IBD slope for each biological group, including the molecular type as a factor in the statistical test (see below).

Subsequently, we compared differences in dispersal scales between macrozoobenthic and planktonic groups using two approaches. In the first approach, we tested for differences in the mean values of IBD slopes among biological groups using a two-way ANOVA (after normalising data using a logarithmic transformation), one factor for the biological group and the other for the molecular marker type, and a Tukey's test for pair-wise comparison. To retrieve F_{ST} from studies taking $F_{ST}/(1- F_{ST})$, we performed the corresponding transformation and fit a linear regression taking into account F_{ST} maximum and minimum values, the intercept, and the IBD slope.

The second approach was based on a meta-analysis that integrated the quantitative findings from separate but similar studies and provided a numerical estimate of the overall effect of interest, by taking into account different weights assigned to the different studies to estimate the pooled effect [439]. Studies with smaller standard error and larger sample size were given more weight in the calculation of the pooled effect size. In particular, we conducted a weighted mixed effect model meta-analysis [440] to test the effect of the predictor variables (marker and group) on the IBD slope by means of the restricted maximum-likelihood estimator. The null hypothesis was that there were no differences in test statistics among groups or markers. The meta-analyses were conducted using the *metafor* package in R [440]. Because this analysis required the variance of the IBD slope, this statistic was estimated from the fit of IBD between the geographic and F_{ST} data, and hence, the number of cases was limited to those where all data was available (i.e. n = 60 out of 138). As in the previous approach, two factors were included in the two-way ANOVA (biological group and molecular marker type).

4.2.3 Definitions of community data sets and compilations

We analyzed the species composition of communities of phytoplankton, zooplankton, and soft-bottom macroinvertebrates to quantify the dispersal scale of organisms for each group. The data set detailing information on these species and information on dispersal modes are given below. In all cases, we restricted the data set to marine samples (inner estuarine areas were excluded) and to individuals identified at the species level, removing all taxa identified at higher (e.g., genus) and lower (e.g., subspecies) taxonomic levels to minimize the effect of different taxonomic resolutions used in each study.

We compiled an inventory of phytoplankton from 36 stations (33 were fixed stations and 3 were considered small areas where data were compiled from different studies). Stations included the Atlantic Margin and North Sea[441], the southeastern Bay of Biscay[442], the Kattegat strait, the southwestern Baltic Sea[443], and Sinop Bay and the Gulf of Trieste (North Adriatic[444] and the Sea of Marmara) and Izmir Bay (eastern Aegean Sea) from the Mediterranean Sea. We restricted the data set to three phytoplankton groups (diatoms, dinoflagellates, and coccolithophorids) and overall 555 species were identified.

We compiled an inventory of zooplankton (restricted to copepods as representative of zooplankton communities because they are the most diverse and are commonly identified at the species level) using data from 27 fixed stations from the Atlantic Margin, the North Sea, the Norwegian Sea (NMFS-COPEPOD global plankton database)[445], the Bay of Biscay[446,447], the Kattegat strait, and the southwestern Baltic Sea (unpublished data); and the Gulf of Trieste[448], the Gulf of Naples[449,450], Saronikos Gulf, and southwest of Mallorca island[451,452] from the Mediterranean Sea. We checked species names using WoRMS[453] to avoid synonyms and duplicates. The overall data set resulted in 179 species of copepod.

We compiled an inventory of soft-bottom macrozoobenthic species from three data sources: (i) the pan-European MacroBen database[454] (available at EMODnet Biology portal (http://bio.emodnet.eu/portal), covering the Irish Sea, the North Sea, the Norwegian Sea, Barents Sea, and the Gulf of Lion (eastern Mediterranean), including 1814 sampling locations that were spatially (~10 by 10 km) and temporally aggregated into 305 stations. (ii) The Basque water quality network (19 fixed coastal stations were sampled during 2003-2008 and were spatially and temporally aggregated into 17 stations; see Borja et al.[455]) covering the Basque coast (the southeastern Bay of Biscay). (iii) A Danish data set covering the Kattegat strait and the southeastern Baltic Sea[456] (1415 sampling locations were sampled during 1990-2013 and were spatially and temporally aggregated into 271 stations) (http://www.dmu.dk/en/water/marinemonitoring/mads/plankton/). Macrozoobenthic taxa were sampled with a grab within 0.04 to 1 m^2 of the surface of soft-bottom sediment, where most occupied 0.1 m^2. We restricted stations sampled between 0 and 450 m depth (all stations without depth information were removed), between 1990 and 2013 (to reduce heterogeneity in temporal changes), and at a minimum of 10 km between samples (those closer were aggregated). With these filtering criteria, the overall data set comprised 593 stations and 2276 species. The macrozoobenthic group was divided into two sub-groups according to dispersal types of 2193 species: 1345 species belonged to the dispersing larvae group and 848 belonged to the nondispersing larvae group.

4.2.4 Environmental data for community analysis

We obtained environmental data from the records of each biological station and took an averaged of those points with multiple samplings; in the case of unavailable data, we sourced Bio-Oracle [457] and NOAA ETOPO1[305]. For phytoplankton, we analysed seven environmental variables: sea surface temperature (SST), surface salinity, dissolved oxygen, Secchi depth, ammonium-nitrogen (NH_4-N), total nitrogen, and total phosphorus. For zooplankton, we analysed six environmental variables: depth, SST, salinity, dissolved oxygen, chlorophyll-*a*, and the diffuse attenuation coefficient. For macroinvertebrates, we analysed seven environmental variables: depth, SST, surface salinity, dissolved oxygen, nitrate ([NO_3] and [NO_3+NO_2],), phosphate (ortho-phosphate concentration [HPO_4^{-2}]), and a diffuse attenuation coefficient at 490 nm (m^{-1}).

4.2.4.1 Community species similarity

We computed pairwise species similarity among sites for each group separately (macrozoobenthic, phytoplankton, and zooplankton). We used a narrow sense dissimilarity index that focused on compositional differences independent of species richness gradients [385]: β_{sim} [458]. This expresses the proportion of shared species with respect to the minimum number of species of the two sites as:

$$\beta_{sim} = 1 - \frac{a}{\min(b,c) + a} \qquad (1)$$

where *a* is the number of species shared between the two sites and *b* and *c* are the total number of species that occur in sites 1 and 2, respectively. The aim of this index is to prevent problems related to the number of species at each site, which differs mainly because of different sampling efforts. For macroinvertebrates, some sites were sampled only once, while others were sampled 2 to 30 times. For phytoplankton, sites were sampled between 19 and 316 times and for zooplankton; sites were sampled between 12 and 787 times.

The geographic distance matrix was defined as the minimum path distance (km) between two pairs of sites across the sea, circumventing the terrestrial zone; this was computed using *unicor*[459] software and *marmap*[430] package in R. *Unicor* applies Dijkstra's shortest path algorithm to individual-based simulations. We assigned a resistance value of 1 to all marine pixels; thus, the distance matrix is given in distance (km) units. Because of computational limits, the resistance layer (i.e. binary map marine/land) had a spatial resolution of 10 km for macroinvertebrates, 3.3 km for phytoplankton, and 14 km for zooplankton.

We performed Mantel correlation tests and partial Mantel tests[431] between species similarity, geographic distance, and environmental distance for causal modelling and inferring marine connectivity. Because distance decay may also result from the relationship between species composition and environmental niche factors[157,180,460], firstly, we performed partial Mantel tests to determine the relative contribution of geographic and environmental distances in accounting for species composition similarity. Pairwise environmental distances were computed using the Euclidean distance. To test the correlation between species similarity and environmental distance, we first selected the best subset of environmental variables, such that the Euclidean distance of scaled environmental variables would have a maximum correlation with community dissimilarities; this was done using the *vegan* package[461] implemented in R We then compared the possible $2^p - 1$ models, where p is the number of environmental variables for each community group. Subsequently, we undertook a partial Mantel test to determine the relative contribution of environmental (after model selection) and geographic distances in accounting for species variation.

We inferred dispersal scales and compared among species groups by estimating halving distances as a measure of the distance-decay rate (i.e. species similarity decay with (geographic) distance[413]) using two approaches. (i) The logarithmic decay model, expressed as $1\text{-}S = c \ln(d)$, where S is similarity at distance d and c is the rate of distance decay, assuming $S = 1$ when $d = 0$; the corresponding halving distance, at which the similarity is half its initial value is $d_H = e^{0.5/c}$. (ii) The exponential decay model expressed as $S = S_0 e^{-cd}$, where S_0 is the initial similarity[147] and the corresponding halving distance is $d_{HD} = -(\ln(0.5))/c$. Additionally, we used the fit of distance decay curves with local polynomial regression functions[462] to identify thresholds in those curves using breakpoint detection from generalised linear models with piecewise linear relationships[463].

We performed network graphs that show spatial patterns of community groups and the degree of connectivity among them with *igraph*[464] package in R language. First, we aggregated the number of stations (593 for macrobenthos and 36 for phytoplankton) into limited, representative areas according to their proximity (14 groups for macrobenthos and 11 for phytoplankton). Second, we regrouped species matrices using hierarchical clustering into groups according to the β_{sim}[458]. Subsequently, we generated network graphs specifying the following parameters: vertices (i.e., sites) denoted locations where size was proportional to the number of connections (i.e. the similarity between sites), colour represented clustered groups, edges (i.e. connections) had widths that were proportional to the degree of dissimilarity (thicker and thinner edges represent more or less similar, respectively). We removed connections with dissimilarities larger than 0.6 for clarity.

4.3 Results

4.3.1 Population genetic analysis

Our literature search for studies of population genetic analysis found 12 on phytoplankton (addressing 13 species), 42 on zooplankton (22 species), and 110 on macrozoobenthos (98 species). From these 98 macrozoobenthic species, 81 species have dispersing larvae (DL) and 17 species have nondispersing larvae (NDL); 62 species live on hard bottoms and 36 species live in mixed- or soft-sediment habitat.

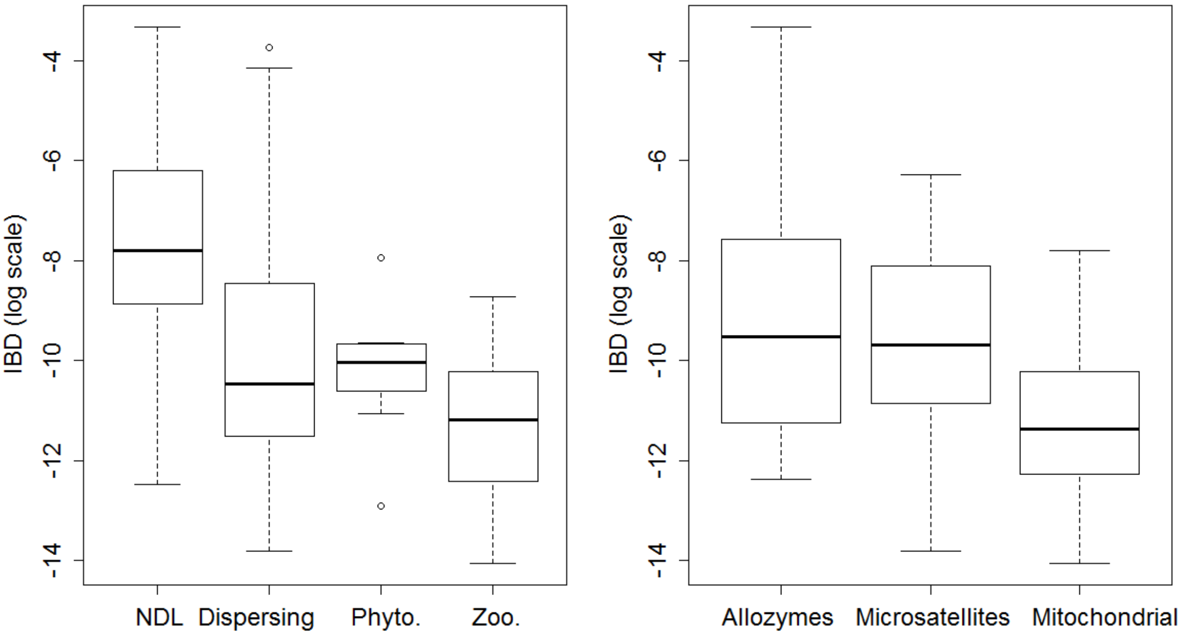


Figure 4.2 Boxplots of IBD slopes according to biological group or molecular marker type. NDL= macrozoobenthos Non-Dispersing Larvae, Dispersing: macrozoobenthos Dispersing Larvae.

The mean IBD slopes for each biological group or marker type are shown in Table 4.1 and Figure 4.2. The two-way analysis of variance (ANOVA) indicated significantly different IBD slopes among groups for both factors ($p < 0.0001$ for the biological group, $p = 0.009$ for marker type, and $p = 0.012$ for their interaction using the logarithm of IBD slope to normalize distribution (Kolmogorov-Smirnov $p = 0.194$)). Biological group was the main factor explaining variance (17.4%, compared with 6.0% by marker type and 9.4% by interaction). A Tukey's post-hoc test showed that significant differences exist between the IBD slopes of NDL and DL macrozoobenthic species, between those of zooplankton and DL macrozoobenthic species, and between those of zooplankton and NDL macrozoobenthic species (Table 4.2). These results indicate that IBD slope is significantly higher for NDL, moderate for DL and lower for zooplankton (Figure 4.2). Potentially the small sample size of studies limited the differentiation of phytoplankton from any other group. However, when phytoplankton and zooplankton are clumped into a single group (i.e. plankton), its IBD slope was significantly larger than that of NDL ($p < 0.0001$) or DL ($p = 0.035$). Using the power function model established in Palumbi[433] (see methods), we inferred dispersal scales for each biological group from their IBD slopes. The inferred dispersal scales were as follows: NDL macrozoobenthic species (0.31 km) < DL macrozoobenthic species (1.92 km) < phytoplanktonic species (19.5 km) < zooplanktonic species (88.9 km) (Table 4.1).

Table 4.2 Tukey's test for the log IBD values for pairwise comparison among biological groups and among molecular marker types. NDL= macrozoobenthos Non-Dispersing Larvae, DL: macrozoobenthos Dispersing Larvae.

		Difference	**p-value**
Biological group	NDL-DL	2.421	**0.0038**
	Phytoplankton-DL	-0.216	0.9968
	Zooplankton-DL	-1.773	**0.0258**
	Phytoplankton-NDL	2.637	0.1165
	Zooplankton-NDL	-4.194	**<0.0001**
	Zooplankton-Phytoplankton	-1.556	0.5169
Molecular marker type	Microsatellites-Allozyme	-0.585	0.5835
	Mitochondrial-Allozyme	-1.562	**0.0187**
	Mitochondrial-Microsatellites	-0.977	0.2577

In the meta-analysis, which takes into account different weights assigned to the different studies, the test of moderators indicated significant differences among biological groups ($QM_{(df = 5)} = 17.48$, $p = 0.0037$); in particular, species of NDL had significantly higher logarithmic IBD slopes ($p = 0.0004$) compared with the overall mean. In contrast, no molecular marker type was significantly different in terms of logarithmic IBD from the others ($p > 0.06$).

Table 4.3 Mantel (rM) and partial Mantel tests between species similarity and geographic distance surrounding land and environmental determinants for each taxonomic group and for each approach (logarithmic decay where S declines with ln of distance, and exponential decay expressed as S = Soe-cd). NDL= macrozoobenthos Non-Dispersing Larvae, DL: macrozoobenthos Dispersing Larvae.

		Phytoplankton		Zooplankton		Macrozoobenthos		Macrozoobenthos DL		Macrozoobenthos NDL	
Model	Variable	r_M	p-value	r_M	p-value	r_M	p-value	r_M	p-value	r_M	p-value
Logarithmic decay	Geo.distance	0.77	0.0001	0.63	0.0001	0.69	0.0001	0.69	0.0001	0.56	0.0001
	Environment	0.49	0.0001	0.36	0.0001	0.49	0.0001	0.50	0.0001	0.37	0.0001
	Geo.distance, out env.	0.72	0.0001	0.63	0.0001	0.62	0.0001	0.61	0.0001	0.49	0.0001
Exponential decay	Geographic distance	0.64	0.0001	0.39	0.0001	0.35	0.0001	0.34	0.0001	0.24	0.0001
	Environment	0.42	0.0001	0.21	0.0001	0.32	0.0001	0.31	0.0001	0.22	0.0001
	Geo.distance, out env.	0.57	0.0001	0.39	0.0001	0.29	0.0001	0.28	0.0001	0.19	0.0001

4.3.2 Community analysis

Similarity in species composition decreased with the logarithmic distance for all groups (Table 4.3), showing a strong decay in the first 1000-2000 km and a flat decay beyond that threshold (Figure 4.3). For all groups, the Mantel correlation between species similarity and the logarithmic geographic distance was higher than that between species similarity and environment (Table 4.3). Therefore, halving distances were estimated according to the two fits (logarithmic and exponential), but more reliability was given to the logarithmic value.

Halving distances using both logarithmic and exponential decay as surrogates of dispersal scales were lowest in the NDL macrozoobenthic community (64 km and 1346 km for logarithmic and exponential decay, respectively), followed by DL macrozoobenthic (101 km, 1603 km), phytoplanktonic (826 km, 4051 km), and zooplanktonic (1444 km, 7280 km) communities (Table 4.4). Break-point detection analysis over geographical distances showed that phytoplanktonic communities were pan-dispersed for threshold distances below ~168 km, while macrozoobenthic community similarities decreased faster up to ~205 km. In general, a strong decay was observed in the first 1000-2000 km and a smooth decay was observed beyond that threshold.

4.4 Discussion

Estimates of dispersal scales derived from population genetic data sorted the biological groups as follows: NDL macrozoobenthic species < DL macrozoobenthic < plankton. This is supported by the ANOVA of the overall data set. These results support why plankton-related studies cover in average a much larger area than do those of macrozoobenthic species (mean sampling range for plankton = 4121.8±2023.8 km and for macrozoobenthos = 1477.3±563.4 km). The specific weight meta-analysis of the data subset also indicated lower dispersal scales for NDL, although no differences were evident between DL and plankton groups. This could be related to the limited amount of data available for this specific analysis (n = 60, out of 138). In particular, the scarcity of IBD studies for phytoplankton (possibly caused by difficulties related to strain isolation and/or monoclonal culture) limited the power of the statistical analysis when compared with other groups.

Marine invertebrates with direct development often display relatively strong genetic population structure in comparison to species with planktonic larval stages [465,466], and strong differences linked to their development mode can be evidenced even within a single cryptic species complex [467]. Nevertheless, factors other than the pelagic duration of larvae, such as the ability to tolerate environmental stress[468], habitat fragmentation[469], effective size, and generation time[470], can explain the genetic structure observed in the populations of these organisms[471]. Even within a development mode and within a cryptic species complex, significant differences in realised connectivity can be observed [472], suggesting that contingency, such as demographic history, has a potentially strong influence. Furthermore, we estimated the distance between populations using the geographical distance surrounding land without taking into account the hydrodynamics, which can also play an important role in connectivity patterns [363,473,474].

Table 4.4 Halving distances from logarithmic and exponential decay models for each species group.

	Logarithmic decay $1\text{-}S = c\ln(d)$		Exponential decay $S=S_0e^{-cd}$		
	Slope (c)	Halving distance (km) $d_{HD}=e(0.5/c)$	Slope (c)	S_o	Halving distance (km) $d_{HD}=-(\ln(0.5))/c$
Macrozoobenthos	0.1111	90.1	4.334e-04	0.25	1599.3
- NDL	0.1202	64.1	5.150e-04	0.06	1345.9
- DL	0.1084	100.7	4.325e-04	0.25	1602.6
Phytoplankton	0.0744	826.1	1.711e-04	0.65	4051.1
Zooplankton	0.0687	1444.3	9.520e-05	0.54	7280.9

At the community level, similarity in species composition decreased with the logarithm of distance for all groups, with a strong decay in the first 1000-2000 km and a flat decay beyond that threshold. For all groups, moreover, the Mantel correlation between species similarity and the logarithm of geographic distance was higher than that with environment, supporting the assumptions of the neutral theory of biodiversity and enabling the inference of a dispersal scale. The dispersal scale ranked the biological groups in support of our hypothesis: NDL macrozoobenthic (64 km) < DL macrozoobenthic (101 km) < phytoplanktic (826 km) < zooplanktonic (1444 km). This was the same as they were ordered for the genetic population analysis. In terms of absolute values, different estimates of dispersal between the two methods are probably due to the use of different similarity indices, sets of localities, and species analysed. The larger halving distance of zooplankton than of phytoplankton might be related to their slightly longer life span and the diel vertical migration of zooplankton, which allows them to use different currents in the water column to their dispersal advantage. This indicates that prevailing habitat (strict pelagic, i.e. phyto- and zooplankton; strict benthic, i.e. NDL macrozoobenthos; or multihabitat, i.e. DL macrozoobenthos) determines the degree of community connectivity.

Results from break-point detection analysis over geographic distances showed that phytoplanktonic communities were “pan-dispersed” for threshold distances lower than ~168 km, while macrozoobenthic communities’ similarity decreased faster until ~205 km. In general, a strong decay was observed in the first 1000-2000 km and a smooth decay was observed thereafter, which may be associated with a spatial choke point where two main regions (e.g., Mediterranean and Atlantic phytoplanktonic populations, Figure 4.4) connect through the Strait of Gibraltar. Shorter distance thresholds identified at logarithmic scales (170-200 km) could be related to individual or propagule dispersal distance because they are of the same order of magnitude as several of the species reported in the analysis of population genetics[114].

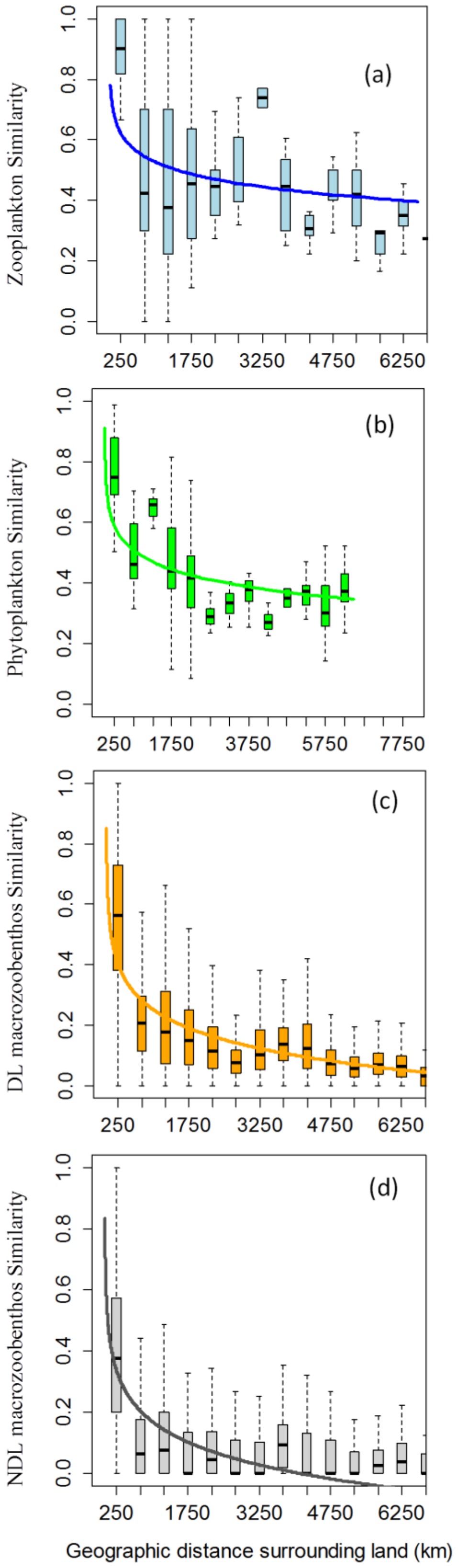


Figure 4.3 Community similarity vs. geographic distance for planktonic and macrozoobenthic groups. Community similarity is fitted with the logarithmic decay model. Boxplots depict data variability at each distance interval. NDL= macrozoobenthos Non-Dispersing Larvae, DL: macrozoobenthos Dispersing Larvae.

By comparing planktonic and benthic macroinvertebrate assemblages, we show relevant links between community and population genetics. Similarity decreases in both population genetics and community composition with geographic distance, whereby, for communities at least, this is not a resulting pattern of environmental distance. Thus, this appears to be a pattern associated with dispersal limitation for an important number of species and communities. Moreover, both genetic and community analyses show that macrozoobenthic NDL species have lower dispersal scales than do macrozoobenthic DL, and both have lower dispersal scales than do plankton, in agreement with neutral theory expectations. Here, we highlight the similar patterns obtained at both genetic and community levels regardless of the following differences: (i) the use of different similarity indices and sets of localities and species analysed (hence, characterised by different biogeographic histories); (ii) processes such as ecological and genetic drift might act at different time scales; and (iii) limits in the parallels between population genetics and community ecology; for instance, many aspects of the evolutionary process, such as epistasis, pleiotropy, inbreeding, and recombination, have no parallels in community ecology[411].

The IBD model was well supported in macrozoobenthic groups, but supported by only 3 out of 13 species of phytoplankton tested. To balance the particularities in genetic diversity of individual taxa, such as population similarity reflecting historical rather than contemporary gene flow in some species[406], a multi-taxon approach is required. Recent developments in sequencing technologies[475] are now allowing for a much finer resolution of subtle population genetic structures, which will be useful especially for planktonic species.

Beyond the particularities of each species, similarity decreased in population genetics and in species composition consistently with geographic distance for a considerable number of species, where the rate of decline is associated with dispersal limitations. At the genetic level, dispersal scales sorted the groups in the same order as they did at the community level: NDL macrozoobenthos < DL macrozoobenthos < plankton, in agreement with expectations of the neutral theory. Since there are six (i.e. 3x2x1) possible rankings of three elements, the probability of obtaining this ranking, predicted by dispersal ability at both levels of organisation by chance is 1/6 x 1/6 = 0.028. This statistically significant value provides the first evidence of relevant links between community and population genetics among marine planktonic and benthic macroinvertebrate assemblages. Implications of this finding in terms of how dispersal might affect local species richness and speciation in pelagic *versus* benthic habitats remain to be studied. A practical consequence for biodiversity conservation is that population genetics data from only a few species may help to predict community connectivity patterns, and conversely, β-diversity knowledge may provide useful a priori information to infer single-species connectivity, taking into account differences in dispersal estimates between the two methods.

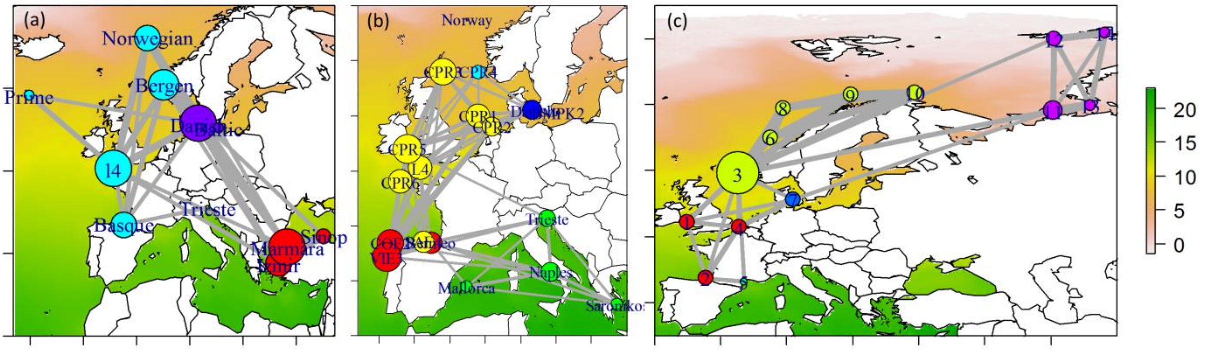


Figure 4.4 Hierarchical clustering based on the β_{sim} index for (a) phytoplanktonic, (b) zooplanktonic, and (c) macrozoobenthic communities (colours of stations indicate different cluster groups). Size of stations indicates the number of connections (i.e. the similarity between sites). Width of connections indicates the degree of similarity (thicker or thinner for more or less similar, respectively). Connections with similarities below 0.6 were removed. Previous to the analysis, some stations were aggregated according to their proximity for clarity. Network graph maps were generated with *igraph*[390] package in R.

5. General Discussion

The following section integrates and synthesizes the most important findings in relation to the topic, the limitations encountered, and the implications and lessons learned on climate-related plankton global biogeographical patterns.

5.1 Part I:Climate change and habitat-modelling of plankton

Broadly, Part I describes the undergoing (**Chapter 1**) and future (**Chapter 2**) climate change impacts on the biogeography of the North Atlantic zooplankton communities using habitat-modelling techniques. A number of studies have revealed that impacts of global warming are affecting the whole pelagic ecosystem from plankton to higher trophic levels[111,222,225,476]. These include poleward movements in range distributions, shifts in the seasonal cycles and changes in abundance and community structure. To avoid extinction, organisms exposed to a changing climate can respond by adapting to the new conditions within their current range or by tracking their climatic niches in space (distribution shifts) or time (phenological shifts). Although the evolutionary potential for marine organisms to cope with climate change remains uncertain[477], distribution shifts are already widely observed[111,244,478,479] and are likely to become increasingly important, given the expected intensification of current rates of climate change[480].

The significant sea warming trend identified in the North Atlantic[237-240] and Mediterranean Sea[241] during the last decades has fostered our interest to explore how warming affects temporal and spatial patterns of marine planktonic communities. In the last decade, a set of advances in habitat and climate modelling has allowed us to reduce uncertainties of climate change impacts on species distribution. To understand what drives distribution in ecological communities and shape the biogeography patterns we need to recall on a core concept in ecology - the ecological niche. Because species have distinctive niche-ranges[248,249], species response to climate change is not uniform and shifts in their distributions occur at widely different rates[94,110,282].

In **Chapter 1**, we have characterized the thermal niche of coastal zooplankton species, and we have explored the mechanism driving temporal patterns of community assembly (temporal turnover), across three time series in the North Atlantic and Mediterranean Sea. An ecologically important functional trait in the context of climate change is the thermal tolerance that determines species' propensity to respond to climatic variation. Species responses to climate change are in large part determined by their ecological niche, which is unique for each species. Within this context, we have analyzed if sea warming is altering the abundances of coastal zooplankton species according to their ecological niche boundaries. The correspondence between zooplankton abundance and sea surface temperature trends may be due to random processes, or because the species are changing its abundance according to their thermal niche. We found strong links between zooplankton abundance and climate variability; most of species (91%) have shown significant changes (increase or decrease in abundance) with time due to sea warming. Such shift is associated to changes in sea surface temperature; the expected copepod abundance trends following its thermal niche agreed significantly with observed values. Previous niche model related studies[91,481] in zooplankton have also shown that temperature is the main driver limiting distribution.

Recent meta-analyses have shown that beta-diversity through space (i.e. variability in species composition) is driven by factors related to species functional traits, geographical gradients and ecosystem properties[388]. Spatial variation in species assemblages is one aspect of beta-diversity and has been deeply discussed in Chapter 3 and Chapter 4. The second component is variation in assemblages through time (temporal β-diversity, i.e. temporal turnover), which has been the second objective of Chapter 1. In this study, we examined the decrease of assemblage similarity in time in relation to environmental gradients. By doing so, we have shown that the sea surface temperature is the most important variable limiting the ecological niche of the zooplankton communities, which support the hypothesis that environmental selection rather than time-derived stochastic processes dominates the zooplankton temporal community structure. In addition, this finding is in line with the species level analysis, where we found relevant links between the variability of zooplankton abundance and the variability of temperature trends. In a recent study, Rivero-Calle et al.[244] have also reported changes in the relative abundance of certain planktonic groups in response to global warming. Similarly, niche descriptors dominating temporal patterns of plankton community assembly has been also well reported in the North Atlantic[180] and globally[158].

Some planktonic species exhibit local adaptation[210,276,277] or have mechanism that help species to adapt to changing conditions, for example, through phenotypic plasticity or evolutionary (genetic) changes[104,352,482]. However, we have found significant similarity decay with time in the zooplankton community at all three sites (Objective 2) and therefore we suggest that the community is changing with time because the species are following their thermal niches. With ongoing warming, locations that are historically too cold for survival will become increasingly suitable for colonists. In our study, we observe community similarity decay with time that does not correspond to the expectations of an adaptation process. A lack of species thermal adaptation has been also reported in Hinder et al.[209] for two key calanoid species (*Calanus finmarchicus* and *C. helgolandicus*) in the North Atlantic using Continuous Plankton Recorder data. Similarly, Helaouet & Beaugrand[483] found strong support of niche-conservatism in *C. finmarchicus* at multidecadal scale using the same dataset along the North Atlantic. Rapid plankton biogeographic shifts have also been reported in Beaugrand et al[283]. Hence, it seems that climatic changes results in zooplankton community shifts and the species population shift their distributions following their thermal niche.

In **Chapter 2** we scaled up in space from local time series in coastal stations (Chapter 1) to a basin-wide scale at the North Atlantic. Once we learned from Chapter 1 that temperature is key driving temporal distribution of zooplankton, as well as to characterize the ecological niches, we explored the future biogeography of zooplankton. We addressed the climate change effect on the zooplankton communities, by comparing present and future scenarios of environmental change, using a unique database (the CPR) covering more than 34 years of monthly sampling over the North Atlantic. The North Atlantic climate regime shift[322,484,485] served us to perform a temporal validation of the habitat models usually neglected in climate change projection studies: the habitat model built in the cold period (1970-1986) was validated in the warm period (1987-2004). Further, using coupled hydrodynamic and biogeochemical models, we focused on the biological effects of latitudinal range shifts, seasonal cycles and community composition that are driven by climate.

Undergoing changes in the abundance, diversity and composition of plankton in marine pelagic ecosystems may have pronounced consequences for higher trophic levels and therefore require to be investigated. Interpretation of both temporal and spatial variability of planktonic species abundance is complex; mainly because of the difficulty to identify the main variables that drive species distribution. For example, SDMs, in which each environmental variables represent n-dimensions of the ecological niche *sensu* Hutchinson[40], are a useful tool to determine the range of environmental conditions a species is able to cope with. By applying SDM to key species of the North Atlantic, we have shown that there is a strong response of zooplankton to climate change. The modelling approach enabled us to gain knowledge on which are the main climate drivers affecting copepod distribution and determine their future biogeographical boundaries. We found that sea surface temperature, is, as in copepod time series studied in Chapter 1, the environmental driver explaining most of the variance of species occurrence in the plankton community.

The compilation of information reported in Chapter 2 represents a step toward modelling the plankton community distribution, following the ecological niche theory of Hutchinson[40], to quantify their future response to climate change over the North Atlantic. The SDM-based maps suggested that we can expect a marked change in the North Atlantic copepod community consisting in a (1) prevailing poleward shift, (2) high species turnover (local colonization and extinction) near the Oceanic Polar Front, and an (3) overall earlier seasonal peak along driven by the ocean warming trend.

1. Poleward shift. The expected rapid pace of climate change[224,225] means that range shifts might be the dominant impact on ecosystem function and structure[226,227,486]. Our models projected a plankton community shift of 9 km decade^{-1}, which is within the range of shift estimated by Cheung et al.[58] for marine fishes and invertebrates (1.4-28 km decade^{-1}), but substantially lower than the shift projected by Sorte et al[232] for 129 marine species (190 km decade^{-1}). At species level, range shift projected in *C. finmarchicus* (3.7 km decade^{-1}) is considerably lower than the shift suggested by Helaouët & Beaugrand[487] for nearly the same area, period and scenario (111 km decade^{-1}). Future distributional shifts of zooplankton reported here are not surprising and fall within the range of shift reported by the other studies focusing in only one species [291].

2. Species turnover. Marine communities at the extreme limits of their ecological niche are especially sensitive to local extinction due to the eco-physiology of animals[347]. In this study we have projected an important species turnover area of colonization and extinction, located in the oceanic polar front, splitting the biogeographical boundaries of the northern and southern species assemblages. Reygondaeu and Beaugrand[291] also found that the future spatial distribution of northern species assemblages (*C. finmarchicus*) is mainly located above the oceanic polar front. These areas with high turnover of species coincide with a large predicted sea surface temperature increase by the end of century, where warm species assemblages could benefit to settle their populations there, while the southern limits of the cold subarctic and arctic species assemblages will retract. In the marine environment, boundaries to species distributions may also be generated by current circulation patterns[488]. Ocean currents could facilitate distributional shifts by advection of planktonic larvae to new suitable habitats[489]. Large-scale frontal zones as hotspots of biodiversity have also been

reported in Chapter 3. These frontal zones act as barriers separating subtropical gyres, and are typically areas of relatively high primary production[17,400]. Many authors have drawn attention that species and ecosystems are more influenced by climate over transitional systems[358]. These projected species turnover change have a cascade effect and may propagate through higher trophic levels[234,286], having an ecosystem-wide effect on the North Atlantic.

3. Phenology changes. Our models predicted an advance in the annual peak of 12–13 days between present time and the end of the 21st century for *C. finmarchicus* and *C. hyperboreus*, due to sea warming. Mackas and colleagues[490], in a review of phenological shifts with historical observations, also proposed temperature as the main driver playing a significant role. Our phenology shifts results are a bit higher compared to a recent meta-analysis study carried out by Thackeray et al.[215] where mid-century climate change projections estimate an advance in the timing of seasonal events of *ca* 3 days for secondary consumers. Fastest rates of spring advancements have been reported for pelagic animals (zooplankton 11.6±2.9 days/decade, and larval bony fish 11.2±1.7 days/decade)[111], with historical data. The main differences between the distribution shift- and phenological-change related papers and ours are the taxa assemblage analyzed and model algorithm used. A recent study reveal that methodological differences between the studies explained more of the variation in range shifts and phenology, compared to the variation explained by ecological traits[491].

SDM limitations

In spite of their utility to help in our understanding of plankton biogeography, SDMs developed in this thesis do not account for three major ecological processes which can be important in defining the plankton distribution[95-97]: (1) the role of dispersal and its limitation, (2) biotic interactions, and (3) intraspecific variability. Failure to explicitly include these factors can affect the predictive performance of SDMs[64,98,99]. The relative importance of these processes in shaping planktonic species' ranges has yet to be explored[158,492]. Each of these points is discussed briefly below:

1. Sea currents control marine plankton dispersal. Despite barriers to dispersal are fewer in the marine realm compared to the terrestrial one[493], the coupling of particle tracking models with niche models may provide more realistic

information on ocean connectivity. Source-sink dynamics may arise frequently because of the advection of water masses[295,494] that can introduce species to unsuitable regions[46], potentially biasing SDMs.

2. A number of studies have reported an increasing need to biotic interactions (mainly predation and competition) when predicting species distributions[495,496]. The exploration of the plankton *'interactome'*[497] allows describing how biotic interactions occur across trophic levels and relate the environmental conditions and ecosystem functioning, with a number of new symbiotic interactions identified[492].

3. SDMs may ignore the adaptive potential of species[352]. However, some planktonic species are able to adapt as seen in Chapter 1, instead of following their ecological niche. This has been documented for small and spatially isolated zooplankton such as *Calanus helgolandicus* in the Mediterranean and Black Sea[353], or chaetognats in the NE Atlantic[354], but not in the North Atlantic population of *C. finmarchicus* [498] . In this sense, we assumed in Chapter 2 that zooplankton has limited evolutionary response to climate change following several authors[291,357,487], and according to what is suggested from Chapter 1.

One of the main requirements of SDM is the necessity of determining precisely the limit of the niche. The niche should be determined on the basis of the whole spatial distribution of species, which is often larger than expected. If the niche is not well characterized by the models, projections might be strongly biased. Published studies indicate that species distribution models can perform quite well in characterizing the natural distributions of species particularly when well-designed survey data and functionally relevant predictors are analysed with an appropriately specified model[289]. In such a setting, models can provide useful ecological insight and strong predictive capability. In plankton, a major problem with SDMs is the scarcity of occurrence data, which can lead to an incomplete niche description and/or biased models. However, after reviewing the limitations of the SDMs, we argue that it remains one of the most powerful tools currently available to appraise the future effects of climate-induced temperature changes on plankton at species level.

5.2 Part II: Connectivity and biogeography of plankton

During the past few years, there has been intensive debate on whether unicellular organisms exhibit biogeographic patterns different from those of macro-organisms[171]. The traditional view holds that, being small and extremely abundant, unicellular organisms are ubiquitous dispersers, flourishing wherever they find a suitable environment ('everything is everywhere, but the environment selects'). Thus, unlike most macro-organisms, they lack well-defined biogeographic patterns[172-174]. This generalization has now been challenged by a growing body of evidence showing that many microbial organisms have restricted distributions with well-structured spatial patterns of assemblage composition[148,175]. Regressing community similarity against environmental and spatial distance provides an effective means to determine the relative roles of local environmental structuring versus regional control of community composition[148,166]. Dispersal is also a key component of the ecological niche of the species, which in turn drives distribution and structures marine communities[102,145,180]. To address dispersal, within Chapter 3 and Chapter 4, dispersal scales and distance-decay patterns of community assembly have been analyzed for a number of planktonic and macro-benthic groups, at global scale.

In **Chapter 3** we have analyzed large scale ocean connectivity patterns for a broad range of taxa as a function of body size, converging two unique datasets: (1) global estimates of timescales of ocean connectivity[132] and (2) biological data globally distributed with samples taken during the Malaspina circumnavigation expedition[25].

The spatial arrangements of the studied assemblages reveal that dispersal limitation explains a larger fraction of the variability in planktonic and micro-nektonic community similarity, relative to environmental factors. This indicates that passive dispersal with ocean currents, which is a neutral process similarly affecting all planktonic and micro-nektonic organisms, is a stronger determinant of community structure than niche-filtering factors[392].

Our main finding in this study is that the organism body size is a key determinant shaping the global spatial patterns of community assembly, with large bodied plankton showing significantly lower dispersal scales compared to small bodied plankton. The hypothesized size-dependence of dispersal in planktonic and micro-nekton organisms is supported by a significant negative relationship between the organism size and halving-time and time-decay slope. In fact, species with elevated dispersal have rapid gene flow that slow down adaptation to local condition, so it is rare to observe spatial structure between populations separated by thousands of kilometers. Large population densities and short generation times of microplanktonic organisms have led to an over-dispersion, and as consequence have shown weak spatial structure[176,376,395,396]. In contrast, larger planktonic organisms have in general longer generation times and smaller population densities[375], and as a consequence are more sensitive to local extinctions, resulting in stronger spatial structure, compared to microplankton. Our work contrasts with recent publications comparing distance-decay patterns of micro- and macro organism and its relationship with body size [3,4]. Contrasting results have also been found in a study by Jenkins et al.[369] who suggested that body size controls the dispersal of active dispersers, but not passive dispersers like planktonic organisms. However, Jenkins et al. did not characterize the full range of body-sizes that we have studied, and as a consequence is limited in its scope.

In **Chapter 4**, we carried out a parallel analysis of biological connectivity at genetic and community levels in marine groups with different dispersal traits: coastal macro-benthos and marine plankton. We learned from Chapter 3 that dispersal is a key trait limiting planktonic distribution. In fact, the neutral theories of molecular evolution (Kimura et al.[144]) and biodiversity (Hubbell et al.[126]) suggest that dispersal limitation of propagules and population stochasticity are common neutral processes shaping both genetic structure and communities, respectively. The average dispersion distances of marine larvae have generally been poorly described, despite the central role that larval dispersal plays in the demographic connectivity of populations across geographic space. In addition, the parallels between dispersal pattern in population genetics and community ecology are inexistent, to our knowledge, in the marine realm and across taxa. In Chapter 4, we compared the dispersal scales of plankton *vs* macro-benthos to test if dispersal shapes similarly the population genetic and community composition of marine plankton and macro-benthic communities.

Our study strongly suggests a direct link between dispersal traits and the patterns found in population and community structure. Results reveal that dispersal distances ranked the biological groups in the same order at both genetic and community levels, as predicted by organism dispersal ability and seascape connectivity: macro-benthic species without dispersing larvae, followed by macro-benthic species with dispersing larvae and plankton (phyto- and zooplankton). This ranking order is associated with constraints to the movement of macro-benthos within the seabed compared with the pelagic habitat. We showed that dispersal limitation of individuals is a key factor that determines similarly the connectivity degree of communities and populations, supporting the predictions of neutral theories in marine biodiversity patterns.

There are few works in the literature reporting similarities between the processes underlying patterns of species diversity and genetic diversity[152,157,177,499]. In one of these studies, Baselga[499] provide evidence of emergent bridges between the neutral theory of molecular evolution and the neutral theory of biodiversity in freshwater beetles: in neutral theories, alleles, which are the different variants of a particular gene in a population, are analogous to species in a community, in the same way that random genetic drift in populations is analogous to ecological drift[126]. Neutral processes thus emerge as a unifying principle of ecology and evolution, which has deep implications in biodiversity assessment and conservation.

5.3 Link part I and part II

Climate change impact on the diversity patterns and processes at regional to global scales have now started to be investigated. A global redistribution of species is occurring, widely recognized as a fingerprint of climate change, with species tracking environmental warming, most often by moving towards the poles[94,479,500], and advancing the timing of their seasonal cycle[31,215], which often lead to changes in the structure of the communities (Chapter 1 and Chapter 2). In the context of ecological responses to climate change dispersal is also a central process because it determines the spread potential and rate of a population as well as the process by which genes are moved between populations (Chapter 3 and Chapter 4). The capacity of species to track or adapt to climate change depends on their dispersal capacity and connectivity and the heterogeneity of the environments they occur[157,501]. During this thesis we have compared dispersal distances of groups with varying dispersal traits, holo-plankton and macro-benthos. We have shown that the development mode influences the spatial extent of larval dispersal, which in turn affects species spatial distribution and genetic variation among populations. Climate change can affect dispersal by altering the spatial distributions of sink and source habitats, the environmental cues for dispersal or settlement, and the environment in which individuals disperse. The potential for dispersal related phenotypes to acclimatize or adapt to these changes may often determine the impacts of climate change on population structure, adaptation and range shifts. For example, most marine animals disperse as larvae in the plankton, and their potential dispersal distance and survival are influenced by their size[173,369], and morphology [502], as we have seen in Chapter 3. The duration of the marine larval period is temperature dependent, and there is very little variation among taxa in this effect[115,118]. Warming accelerates development and shortens the larval period, potentially reducing dispersal distance and population connectivity[118,503]. In other cases, plasticity in pelagic larval duration phenotypes can increase potential dispersal to suitable habitats, accommodating climate-driven change in the spatial arrangement of critical habitat. In the marine environment, boundaries to species distributions may also be generated by current circulation patterns[488].

Dispersal will be particularly important for organisms with sessile or sedentary adults, including marine algae, and many invertebrates and fish (Chapter 4). On the other hand, species characterized by high dispersal potential are likely to migrate rapidly with little adaptive change. For example, pelagic groups such as plankton have rapid generation times and offspring production is very high making its populations' size huge[375]. That makes planktonic species to show large distributional ranges[172,173]. Although some benthic species can develop directly on sea bottom (e.g. intertidal gastropods), the vast majority (e.g. corals, sea-urchins, crabs, worms) have a planktonic phase (mero-plankton), that ensure species propagule dissemination over several weeks (Chapter 3). However, the dispersal distance of benthic animals is lower compared to planktonic, due to the constraints to movement in adult benthic species within the seabed, making them more vulnerable to cope with climatic changes due to limited-dispersal, in relation to plankton. Therefore, species with poor dispersal ability are likely to either adapt or go extinct, and species that disperse widely are thought to be less susceptible to global extinction (Chapter 3 and Chapter 4).

We have shown in Chapter 1 that niche descriptors are more important than the time-derived stochastic replacement of individuals, driving temporal distribution of plankton at coastal zones. In Chapter 3, instead, we have revealed that the main spatial patterns of plankton are governed by dispersal limitation, more so than environmental drivers, globally. Methodological differences aside (presence-absence vs abundance), we conclude that distributional patterns of plankton community assembly are scale dependent: when time is considered, the species temporal patterns in a given place are driven mostly by its niche requirements (mainly seasonal variability); when space is considered, dispersal-limitation is the process driving spatial distribution. Further research will be required to establish whether this is due to the difference in the gradient of observed environmental conditions, to the choice of environmental descriptors or to the scale of the studies.

5.4 Implications and future perspectives

Climate change is having profound impacts on the phenology, abundance and distribution of a broad range of taxa across both marine[111,215,504] and terrestrial systems[111]. How these demographic processes will change in the future is a sound debate in ecology. Variability in phenological and biogeograhical responses to climate change can desynchronise ecological interactions, ultimately driving trophic mismatch and thereby affecting recruitment processes. To assess these threats, we must quantify the relative impact of climate change on species at different trophic levels. Identifying species dependent distinct biogeographical and phenological patterns would have substantial socio-ecological implications. Such knowledge would afford some predictability to future ecological outcomes and would help to identify sentinels species of climate impact, facilitating the development of indicators and estimates of vulnerability for conservation programs[505,506]. For example, habitat suitability models have been widely used to try and predict how species ranges might change in the future. In order to improve the predictions, habitat models should integrate dispersal limitation and population dynamics. We have learned from Chapter 3 that the body size is negatively correlated with dispersal; a good solution for the future can be to include the body size as dispersal proxy in the habitat-models. Another alternative to gain a mechanistic understanding of ecological processes is to develop Individual Based Models. However, these type of models require extensive computational resources and can only be applied when demographical, physiological, and life traits of species are well known (e.g. in *Calanus finmarchicus* or *C. helgolandicus* in Maps et al.[362] and Pepin et al.[507]; but see Melle et al.[344]. Since we addressed a number of species with different ecological requirements, the use of statistical models (GAMs) is a useful approach for the scope of our work: it shows the possibility to investigate the effect of climate change on multiple species, without requiring sophisticated and time-consuming mechanistic models.The niche-based approach developed here has been specifically designed on CPR data but it can also be applied to a wide range of pelagic species. Both the assessment and comparison of a large number of ecological niches may provide a new insight into ecosystem functioning.

The understanding of marine population connectivity is not only key to determine the resilience of species to global change, but to implement sustainable fisheries management strategies or for designing networks of marine protected areas (MPA) , which is useful for policy makers. A practical implication for biodiversity conservation is that population genetics from few species can help to anticipate community connectivity patterns, and the other way around, knowledge in β-diversity may provide useful information to infer single species connectivity.

Today, there is still a hot debate on the relative contribution of dispersal-limitation and niche processes on plankton spatial patterns[158,169,180]. In the last few years, global oceanographic campaigns such as the TARA Oceans and the Malaspina Expedition have provided an excellent opportunity to gather a unique inventory of plankton data and explore marine biodiversity. A new era of plankton data has flourished, that must help scientists to better understand the global structure of marine planktonic ecosystems and macro-ecological patterns. High-throughput omics data combined with traditional taxonomy and novel modelling tools offer great potential to do so. In addition, information on species occurrence has recently started to be gathered in global databases, where each institution can provide new data. A good example of these global databases is the Ocean Biogeographic Information System (OBIS), an initiative developed in the Census of Marine Life program.

6. Conclusions

1. We found strong links between zooplankton abundance and climate variability; most of species (91%) showing significant changes (increase or decrease in abundance) with time due to sea warming. Part of this shift is associated to changes in sea surface temperature because the expected copepod abundance trends following its thermal niche agreed significantly with observed values (46% of cases).

2. The zooplankton community is expected to respond substantially to climate change in the North Atlantic by the end of the century with changes consisting in a (1) prevailing poleward shift (9 km decade^{-1}), (2) high species turnover (local colonization and extinction) near the Oceanic Polar Front (43-79%), and an (3) overall earlier seasonal peak (14 days) along driven by the ocean warming trend. These changes might lead to alterations of the future North Atlantic pelagic ecosystem.

3. β-diversity of the plankton communities was significantly correlated with the timescales of ocean connectivity, and the correlation was more strong compared to the environmental distance. These results allow us to estimate the dispersal scale of each group and analyze relationships with its body size. Large-bodied groups showed shortest dispersal scales and stronger spatial patterning compared to small-bodied groups; hence the organism's body size has emerged as an important factor for distribution patterns of marine β-diversity.

4. Dispersal distances ranked the biological groups in the same order at both genetic and community levels: macrozoobenthic species without dispersing larvae, followed by macrozoobenthic species with dispersing larvae and plankton (phyto- and zooplankton). This ranking order is associated with constraints to the movement of macrozoobenthos within the seabed compared with the pelagic habitat. We showed that dispersal limitation similarly determines the connectivity degree of communities and populations, supporting the predictions of neutral theories in marine biodiversity patterns.

THESIS

We have studied broad scale macro-ecological patterns of plankton communities, from genes to community level, from coastal areas to global ocean, from historical trends to future projections, applying novel statistical and modeling tools in global datasets. We have shown that plankton is responding to climate change through range shifts in their spatial distribution and through an advance in the timing of their seasonal events, which may lead to changes in structure of the communities. We have also provided evidence that the mechanisms underlying plankton distribution are scale dependent: globally, dispersal-limited processes are ranking first, and locally, niche-filtering. Dispersal traits and body size might be instrumental to cope with climate change: populations from species characterized by high dispersal potential and reduced size (small plankton), showing generally wide distributions, could shift rapidly, compared to species with poor dispersal ability and larger size (large plankton and macro-benthos), which tend to have narrow distributions and are likely to either adapt or go extinct.

7. References

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