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Project Deliverable Report
A cross-system comparison of response traits and trait-environment relationships in European Seas

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FutureMARES Project

FutureMARES - Climate Change and Future Marine Ecosystem Services and Biodiversity is an EU-funded research project examining the relations between climate change, marine biodiversity and ecosystem services. Our activities are designed around two Nature-based Solutions (NBS) and Nature-inclusive Harvesting (NIH):
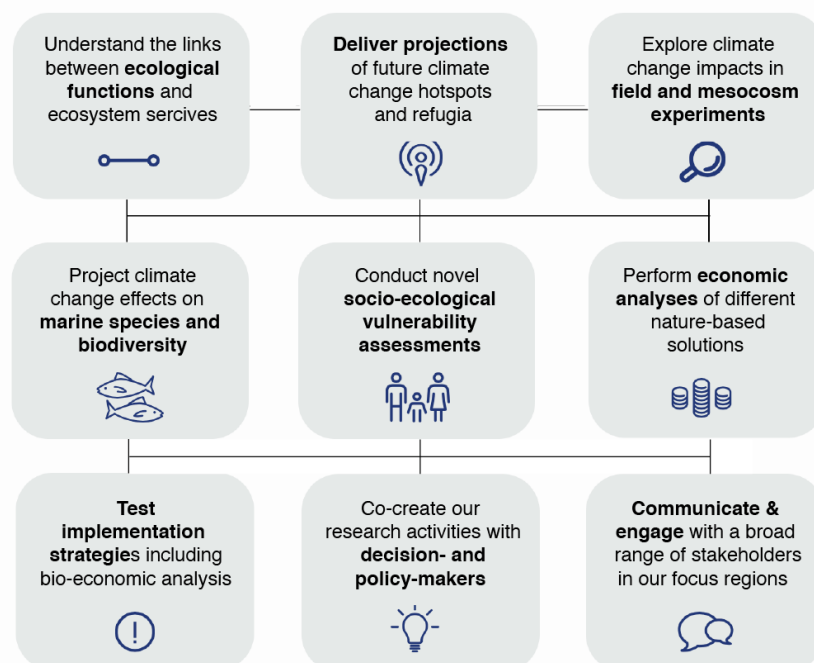
Effective Restoration (NBS1)

Effective Conservation (NBS2)

Nature-inclusive (sustainable) Harvesting (NIH)
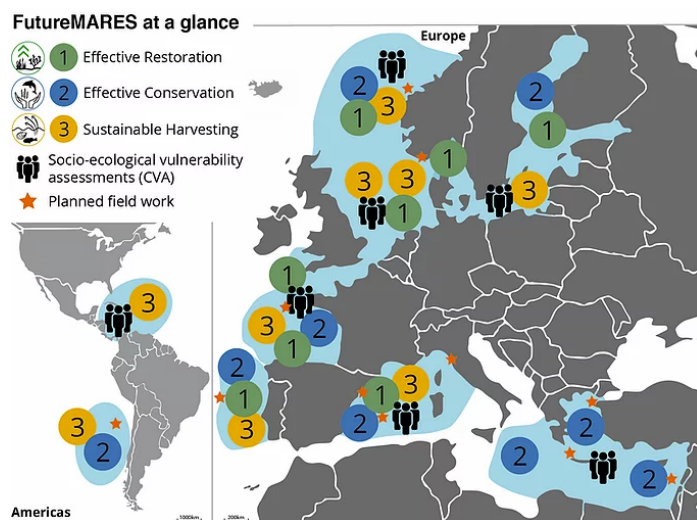
We are conducting our research and cooperating with marine organisations and the public in Case Study Regions across Europe and Central and South America. Our goal is to provide science-based policy advice on how best to use NBS and NIH to protect future biodiversity and ecosystem services in a future climate.

FutureMARES provides socially and economically viable actions and strategies in support of nature-based solutions for climate change adaptation and mitigation. We develop these solutions to safeguard future biodiversity and ecosystem functions to maximise natural capital and its delivery of services from marine and transitional ecosystems. To achieve this, the objectives of *FutureMARES* defined following goals:

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Table of content

List of symbols, abbreviations and a glossary

CC   Climate change

CWM   Community-weighted mean (trait)

DoA   Description of Action, a part of the project Grant Agreement describing the project work plan

EC   European Commission

EC GA   European Commission Grant Agreement – a contract between the European Commission and FutureMARES consortium

GA   Grant Agreement

GAM   Generalized Additive Model

HMSC   Hierarchical Modelling of Species Communities

JSDM   Joint Species Distribution Model

NBS   Nature-based Solutions

NIH   Nature-inclusive Harvesting

RF   Random Forest

SL   Storylines

Tn.x   Task – a sub-component of a work package where "n" is a number of the work package and "x" is a number of the task within this work package

WP   Work Package

Executive summary

Introduction

The primary objective of this deliverable is to report on activities in Task 1.2 aiming to investigate the role of organism traits in determining how marine organisms respond to change. More specifically, we provide results from a number of individual analysis, each representing one or several Storylines, where observational data on species abundances, traits and environmental conditions were assembled and investigated using a "hands-on" toolbox of statistical methods developed under Task 1.2. Finally, we provide a summary and synthesis of key traits and trait-environment relationships identified across different organism groups and areas at different spatio-temporal scales.

Defining the Challenge

Marine ecosystems worldwide are exposed to a multitude of natural and anthropogenic pressures, including overexploitation, habitat loss and CC. In order to take the necessary management and conservation actions, including NBS that seek to preserve natural ecosystems and their biodiversity, there is a need to anticipate future ecosystem changes through a better and more mechanistic understanding of the underlying responses of species and communities to pressures, including CC.

Approach

The overwhelming complexity of species and their individual responses to change can be simplified and described by a so-called "trait-based approach". Trait-based ecology is centred around the idea that individuals and species can be characterized by the key characteristics they carry, broadly representing characteristics in their feeding, growth, reproduction and survival. Traits may shed light on species' niches and ultimately determine community structure and the provision of ecosystem functions and services. The results and outcomes presented in this report were generated based on a set of univariate and multivariate methods for investigating trait-environment relationships. However, please note that the set of methods applied in each individual Storyline is conditioned on data availability. Hence, not all Storylines were able to consistently use all methods in the developed toolbox.

Contribution to the project

The results presented in this deliverable, including patterns and drivers of key traits across organism groups and areas fulfil the overall objectives of Task 1.2 aiming to provide a common knowledge base, while contributing to improved monitoring and development of operational trait-based indicators useful for management and conservation. Although the storylines differ in terms of the scale of the analysis, as well as the amount and resolution of input data, the results and outputs generated from our trait-based approach allows us to identify common and generally applicable outcomes in terms of the key traits, environmental conditions and trait-environment relationships of marine organisms in general. More specifically, a majority of storylines present a pronounced structuring in space and time for key life-history traits related to longevity, maturity, growth and body size (or complexity). In addition, most storylines identified temperature, or the degree of temperature seasonality as key determinants explaining the observed trait distributions. But, more local conditions specific to each area were also identified as important determinants. This indicating that a combination of both local and regional pressures may jointly determine the trait composition and responses of marine organisms to change. Taken together, our results suggest that there is a general and continuous gradient from species with more opportunist life-history traits being associated with environments characterized by higher temperature, degree of

seasonality and other forms of exposure, compared to species inhabiting colder, deeper, less seasonal and/or exposed environments. This is consistent with the "fast-slow" continuum of species life histories and supports "environmental filtering" as a primary assembly process determining community composition and diversity at large.

Finally, together with additional work on the Community Temperature Index (CTI) conducted within WP1 and reported in D.1.3, the identification of key traits and characterization of trait-environment relationships provide an important means to compare and contextualize findings from observational data across storylines with laboratory and mesocosm experiments conducted in WP3. Finally, both set of results provide information and knowledge for Storylines-specific risk assessments in WP5.

Dissemination and Exploitation

This deliverable report will be made publicly accessible to scientist and managers within and beyond *FutureMARES*. Furthermore, a number of scientific papers are in preparation for the individual Storylines which will contribute to disseminating the findings. Online Storyline summaries will also include the information. Last, but not least, the hands-on workshop and toolbox on trait-environment methods is available online and fit for uptake to scientist and managers (https://zenodo.org/record/6712534#.Y0fwduxBzb0).

1. Introduction and a brief review of concepts

1.1.   Background and aim of the deliverable

Marine ecosystems worldwide are exposed to a multitude of natural and anthropogenic pressures, including overexploitation, habitat loss and climate change (Millennium Ecosystem Assessment 2005; Halpern et al., 2015; IPCC 2019). In response to such pressures, notably global warming, many marine communities have already demonstrated shifts in species distributions and abundances (Perry et al., 2005; Last et al., 2011; Pinsky et al., 2013; Poloczanska et al., 2013; Freeman et al., 2018). Furthermore, the different rates of range shifts between species suggest a pronounced reorganization in community composition (See FutureMARES deliverable report from Task 1.1), as well as the structure and functioning of ecosystems at large (Poloczanska et al., 2013). In order to take the necessary management and conservation actions that seek to preserve natural ecosystems and their biodiversity, there is a need to anticipate these changes through a better understanding of the underlying responses of species and communities to pressures and change. The overwhelming complexity of species and their individual responses to change may be characterized and described by a so-called "trait-based approach" (McGill et al., 2006; Violle et al., 2007; Mouillot et al., 2013), because all individuals and/or species within the community are captured by only a few traits broadly representing their feeding, growth and reproduction that are based on evolutionary principles (Kiørboe et al., 2018). The primary objective of this deliverable is to embrace a trait-based approach and report on activities in Task 1.2 aiming to investigate the role of organism traits in determining how marine organisms responds to change. More specifically, we provide results from a number of individual studies (see section 3), each representing one or several storylines (Figure 1), where observational data on species abundances, traits and environmental conditions were assembled and analysed using a "hands-on" toolbox of statistical methods developed under Task 1.2 (see section 2 and Appendix 1 for more detail). Finally, we provide a summary and synthesis of key traits and trait-environment relationships identified across different organism groups and areas at different spatio-temporal scales (see section 4).
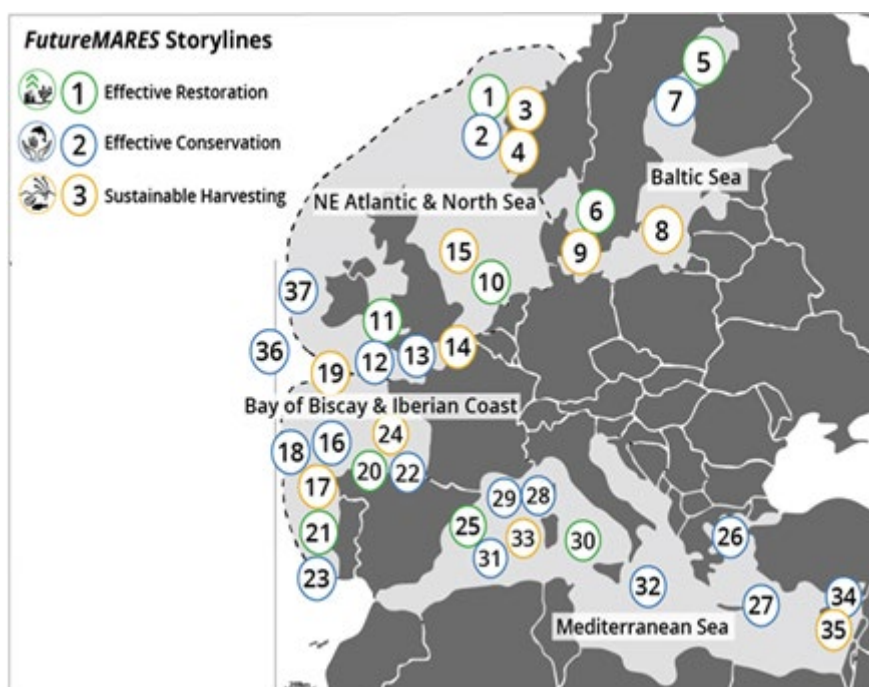

Figure 1 FutureMARES Storyline (SL) locations among four, broad regions where analyses were conducted in this deliverable (see section 3 for detailed results).

1.2.   The trait-based approach

Trait-based ecology is centred around the idea that individuals and species can be characterized by the traits that they carry (Figure 2). A trait is a characteristic of an individual that can be measured and is related to its physiology, behaviour, phenology, life history or morphology (McGill et al., 2006; Violle et al., 2007). Traits determine an individual's performance and ultimately its fitness through the three Darwinian missions in life: to survive, to feed and to reproduce (Violle et al., 2007; Litchman et al., 2013). Traits that are known to affect an organism's fitness are often called key traits or functional traits (McGill et al., 2006; Violle et al., 2007; Litchman & Klausmeier, 2008; Litchman et al., 2013). Since not all missions can be simultaneously maximized, individuals have to allocate the limited amount of energy available among the three processes, thereby leading to trade-offs. Traits can be used to quantify these trade-offs and to understand how individuals should allocate their energy to maximize their overall fitness (Westoby & Wright, 2006; Litchman et al., 2013; Kiørboe et al., 2018).
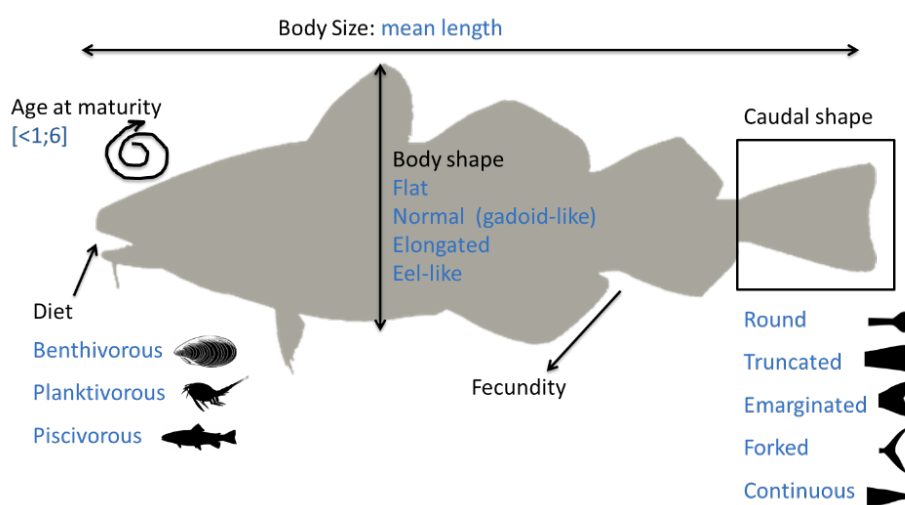

Figure 2 A schematic illustration of a trait-based approach aiming to describe an individual fish species on the basis of a set of key traits broadly representing their feeding, growth and reproduction. (Modified from a graphic provided by L. Pecuchet).

Besides identifying such trade-offs and the traits that drive them, explorations examine how trait values vary with environment or change in response to a disturbance, and how these changes affect organismal performance (McGill et al., 2006). Traits may also shed light on species' niches and with which other individuals or species they can coexist and interact with (McGill et al., 2006). Ultimately, trait-based ecology aims to understand and to predict how traits of individuals and species determine community structure and the provision of ecosystem functions and services (Díaz & Cabido, 2001; Lavorel & Garnier, 2002). A useful framework is the classification of traits as response and/or effect traits (Lavorel & Garnier, 2002; Suding et al., 2008), where response traits vary with a change in environment or an anthropogenic disturbance, while effect traits determine ecosystem functioning (Figure 3). Ecosystem functioning refers to the suite of properties and processes regulating the stock and/or flux of energy and organic matter through food webs (Jax, 2005; Solan et al., 2012). Consequently, effect traits are primarily associated with adaptations and characteristics affecting the speed and efficiency with which energy and organic matter is acquired, transferred, re-cycled or lost (e.g., diet, rates of metabolism, consumption, growth and reproduction, but also specific traits such as carbon fixation by primary producers, or bioturbation (nutrient mobilization) by benthic invertebrates.

This deliverable report will primarily focus on the identification of response traits for marine organisms by studying how traits of habitat-forming marine plants and animals, other invertebrates and marine

fish vary with environmental and anthropogenic pressure. The frequency of trait values within a community provides information about community structure in terms of traits. The abundance or biomass of each species adds additional insight and can be incorporated as a weight to each trait value. The most commonly used community-level trait metric, which is also the first central moment of a frequency distribution, is the mean. When trait values are weighted by abundance or biomass, this is referred to as the community-weighted mean (CWM). The CWM trait originally stems from the 'mass-ratio hypothesis' (Grime, 1998), which states that species with the highest biomass and the traits that they carry will have the strongest impact on ecosystem functioning. The CWM reflects the most common trait value and can thus considered to be the value most important for ecosystem functioning in an uneven community (Garnier et al., 2004; Violle et al., 2007). Gardarin et al. (2014), for instance, used CWMs of a set of plant traits in grasslands to identify the most important effect traits for digestibility – an ecosystem service related to the nutritious value that grasslands provide for herbivorous animals. CWMs are also commonly used to identify response traits that indicate community shifts in response to changes in environment or to an anthropogenic disturbance (Ricotta & Moretti, 2011; Mouillot et al., 2013). A shift in CWM trait values along an environmental gradient is interpreted as a shift in the optimal trait value, reflecting the optimal strategy (Figure 3). Van Der Sande et al. (2016) observed differences in the CWM traits of trees in five tropical rain forests that varied in soil fertility and rainfall. In forests with relatively little rain fall, the most common strategy observed was to have small leaves to reduce water loss during the dry season, whereas trees in the wettest forests invested in a high ratio of leaf area to leaf mass (called specific leaf area) in order to capture as much light as possible despite the high density of trees in such forests. Trends in CWM traits may thus help in identifying the optimal strategy under a given set of environmental conditions. CWMs have also been used to study changes in the structure of communities to detect the effects of a disturbance. For instance, declines in the mean size, age and length at maturity of a fish community in the North Sea were attributed to the intense size-selective fishing pressure on the community (Jennings et al., 1999a, b).
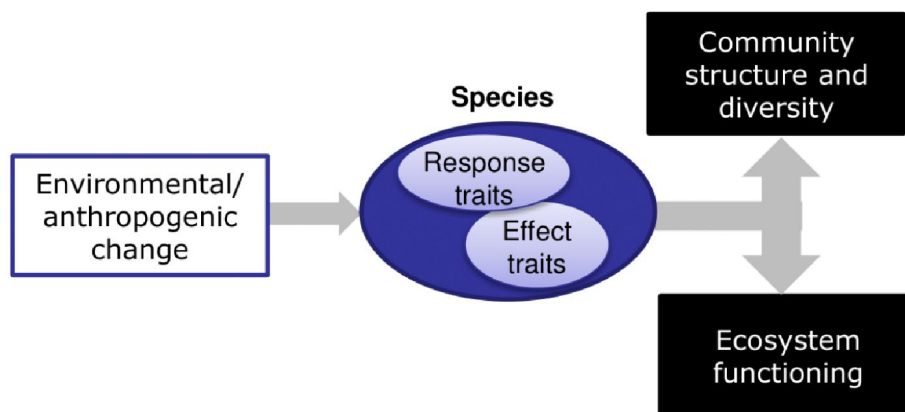
Figure 3 Representation of the response/effect trait framework. Figure adapted from Lavorel & Garnier (2002). The aim is to identify response and effect traits by which individuals or species can be characterized. A trait can be a response or effect trait at the same time. Knowing the response and effect traits of all species within a community allows for studying the effect of environmental or anthropogenic change or disturbance on the structure and diversity of the community, as well as the consequences for ecosystem functioning.

1.3. Trait-environment relationships

Biological traits are life history characteristics of species and can be applied to understand the structure and functioning of communities (Dolédec et al., 1996; Dray & Legendre, 2008; Dray et al., 2014), species distributions (Costello et al., 2015), and the underpinning biological mechanisms responding to environmental factors (Greenslade, 1983). Response traits characterize trait-environment relationships. They represent the performance of species in response to environmental variability and explain why a community is found in a specific habitat but not in another. The functional structure of a community is based on the distribution of trait values within that community. The survival of species in specific conditions and habitat occupancy patterns at both the community level and across species distributions result from response traits that indirectly characterize individual fitness (Violle et al., 2007). This response can be due to complex combinations of resistant forms and reproductive traits, e.g. reproductive allocation being strong in species resistant to abiotic stress, in contrast to species who have high resilience to disturbance (Beauchard et al., 2017).

Effect traits elucidate the impacts of organismal activity on the environment. Depending on factors such as body size, biomass, and metabolic rate, these traits can act at different degrees of magnitude and have both direct and indirect effects on ecosystem processes. Ecosystem functions such as habitat creation, food provision, bioturbation, and nutrient cycling can be driven by the expression of effects traits (Queriós et al., 2013; Beauchard et al., 2017) with subsequent impacts on ecosystem properties and services. Response and effect traits can often coincide, for example, traits conferring high resistance to stress also determine nutrient cycling (Diaz & Cabido, 2001). The implications of the effects of response and effect traits in ecosystem functioning also can include functional redundancy, when the loss of a species from a functional effect group causes no effect on ecosystem functioning, and functional insurance, where the long-term maintenance of ecosystem functioning is facilitated by a large variation in response traits across species from the same functional effect group (Diaz & Cabido, 2001). A conceptual response and effect framework can link species responses to environmental factors with subsequent effects on ecosystem functioning (Garnier et al., 2015).

Trait-based ecology for organisms other than terrestrial plants is not yet as advanced (explaining the high number of examples and references from plant ecology in this chapter), with a lack of data availability for marine species, even within well-studied ecosystems (Tyler et al., 2012). Recent progress has been made on identifying key traits and the exploration of trait-environment relationships also for marine organisms, with an aim of improving understanding of marine ecosystem functioning (Heip 2003; Lam-Gordillo et al., 2020). Aquatic scientists have studied trait biogeography of corals (Sommer et al., 2014; McWilliam et al., 2018) and plankton (Litchman & Klausmeier, 2008; Litchman et al. 2012; Barton et al., 2013; Litchman et al., 2013; Brun et al., 2016), with a recent study using key traits of zooplankton to calculate their effect on carbon cycling in the ocean an important ecosystem function in marine systems (Brun et al., 2019). For marine benthos and fish a strong focus has been on response traits to fishing and climate change (Jennings et al., 1998; Tillin et al., 2006; Fisher et al., 2010a; Greenstreet et al., 2012; Baudron et al., 2014; van der Linden et al., 2016; Beukhof et al. 2019), while for benthos also effect traits have been identified, e.g. the effect of burrowing species on oxygen and nutrient fluxes in the sediment (Mermillod-Blondin et al., 2004; Thrush et al., 2006; Norling et al., 2007; Bremner, 2008). A recent study investigated trait-environment relationships of fish in estuaries at a global scale (Henriques et al., 2017), whereas others showed fish community changes in multiple traits over time as a response to environmental change (Frainer et al., 2017; McLean et al., 2018; Beukhof et al., 2019).

Biogeography tries to understand the spatial and temporal distributions of species and ecosystems and the underlying mechanisms that explain them (Violle et al., 2014). Species-environment relationships are useful to model and predict species distributions (Guisan & Zimmermann, 2000). Joint species distribution models are now also available that consider multiple species simultaneously and can incorporate correlations between the abundance or occurrence of species (Clark et al., 2014; Pollock et al., 2014; Harris, 2015). Although such approaches are useful for predictive purposes and for identifying the drivers of species distributions, they cannot always provide a mechanistic understanding of why species occur where they do. Moreover, in a community or ecosystem context, a species-based approach does not easily allow for inferring consequences of environmental change on ecosystem functions and services. Trait-based approaches can address the fundamental challenge of determining why species are found in specific areas, and predict where they are likely to occur in the future, as traits determine which environments species can inhabit (Beukhof et al. 2019). Trait biogeography, including trait-environment relationships and modelling trait distributions in time and space, has the promise to improve our mechanistic understanding of species distributions and to incorporate knowledge on response and effect traits into models that can predict community structure and ecosystem functioning under different environmental conditions (Violle et al., 2014; Kiørboe et al., 2018). For example, the previously mentioned study by Gardarin et al. (2014) on plant traits important for digestibility of plants in grasslands was followed up by a study where they related the Community Weighted Mean (CWM) traits to the environment, and used these relationships to predict the spatial patterns of digestibility across France (Violle et al., 2015).

Trait-environment relationships are an important aspect of community assemblages and their functional composition. Environmental filtering can impact community assembly along an environmental gradient as the departure of a species from an optimum trait value results in lower abundances within that community (Beauchard et al., 2017), structuring the biogeographic distribution of a species. Two components are usually included: an optimal trait value or combination that facilitates maximum performance and higher abundance (Shipley, 2010), and a measure of how severe the decline in performance is from the optimal trait value, known as the intensity value (Denelle et al., 2019). Trait-gradient analyses focus on the impact of environmental filtering on community assembly along an environmental gradient, with the CWM and variance (CWV) of trait values expected to depict the optimum and intensity of filtering respectively (Denelle et al., 2019). Altered optimal values or the intensity of filtering results from changes in the functional composition of communities along environmental gradients (Ackerley & Cornwell, 2007). It is important to identify the different processes of local environmental filtering and those driving the functional composition of species pools at a larger scale and over a long term (Jiménez-Alfaro et al., 2018). An environmental gradient can be defined by local environmental filters imposing a gradient of distinct optima (Denelle et al., 2019). Regional trait range limits are more likely to occur in communities located at the extremes of environmental gradients, with regional trait range limits showing a decrease in local trait variance in communities located at environmental gradient extremes (Koch et al., 2004; Alpert, 2005; Denelle et al., 2019).

Trait-based analyses are becoming increasingly developed as a tool to examine changes in ecosystem structure and functioning under continued global change. To date, few studies have used trait-based approaches to predict ecological responses to anthropogenic changes, although over 2,500 morphological, physiological, behavioural, and life-history traits have been identified which respond to environmental parameters and influence the distributional range of species (Green et al., 2022). These have the potential to be of great use in predicting future global change on marine species and ecosystems. Multiple trait analyses identifying patterns within species and communities, and trait-gradient analyses that use functional trait distributions within communities to characterize

community-level responses along environmental gradients (Akerley & Cornwall, 2007; Garnier et al., 2016) are being increasingly used for marine management applications. In contrast to the focus on fundamental questions on life history theories and evolutionary concepts driving freshwater and terrestrial studies, multiple traits analyses in marine ecological research, data availability, and the development of statistical analyses have driven the increasing trend for biological traits analysis (BTA) in marine systems (Tyler et al., 2012; Beauchard et al., 2017).Many applications of multiple traits analyses have been identified for marine ecosystems (Bolam, 2013; Bremner, 2008; Rjinsdorp et al., 2016; Tillin et al., 2006), although few multivariate applications of biological traits have been developed for supporting environmental policies, with most being limited to individual or a few traits (Jennings et al., 1999; Greenstreet et al., 2012; Bolam et al., 2014; Rjinsdorp et al., 2016; Beauchard et al., 2017).

With the growing realization that we need to understand ecosystem responses in response to the rapidly changing environment, there is a recognized need for the development of ecological indicators for use in conservation programmes and marine directives. Given that traits link life-history to the habitat, multiple trait approaches could be developed to support marine management and governmental policies aimed at limiting human impacts on the marine environment (Beauchard et al. 2017). The application of multiple traits for this purpose has been recognized, with the need for them to be based on robust datasets and statistical tools (Bremner, 2008; Beauchard et al., 2017; Green et al., 2022).

This report uses the long-term and diverse biological datasets available in the *FutureMARES* project to develop robust methodologies for comparing response traits and trait-environment relationships in European Seas.

2. Methods

The results and outcomes presented in this report are based on analysis conducted across several Storylines, representing different organism groups and areas. The output was generated based on an online tutorial developed within *FutureMARES* to enable the analysis of trait-environment relationships (see Appendix 1 for more details). The tutorial was introduced and presented to partners during two dedicated workshops (fulfilling Milestone #13) and include training data and R code for initial data preparation, as well as for running a set of univariate and multivariate methods for investigating trait-environment relationships (see Figure 4). The set of methods are briefly presented below with further details provided under Appendix 1. Please note that the set of methods applied in each individual story line is conditioned on data availability. Hence, not all Storylines were able to consistently use all methods, even if in some instances a full comparison of outcomes is available for a given area.
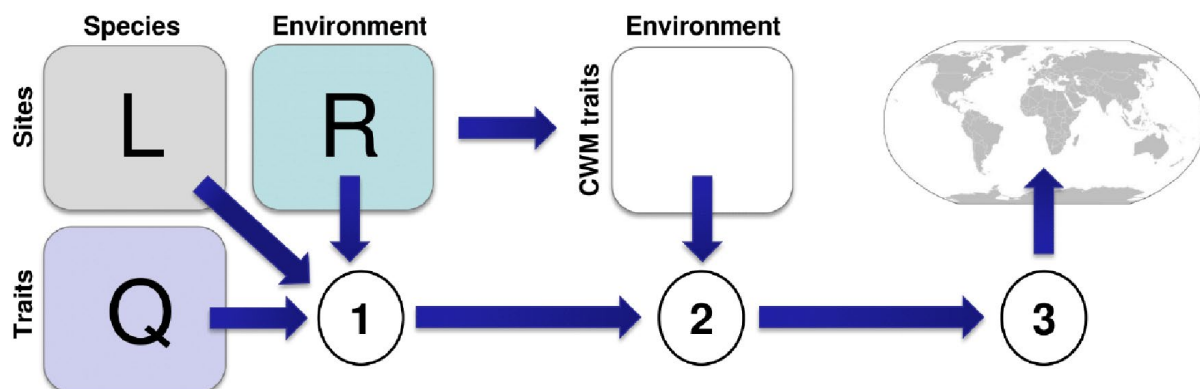

Figure 4 Overview of the data and methodological approach employed in this deliverable. In Step 1, all three datasets (species abundances per site (L), species traits (Q), and environmental variables per site (R)) are simultaneously used in the RLQ and fourth-corner analysis that explore the associations between traits and environment (i.e. the missing fourth corner). In Step 2, CWM trait values are calculated per site based on the species abundances, and their variation across environmental gradients is modelled using multiple random forests. In Step 3, the random forests are used to project the CWM traits across shelf seas worldwide.

2.1. The fourth corner problem – RLQ

The fourth-corner and RLQ analyses are two complementary approaches that are based on a species-occurrence or species-abundance matrix (L), a species-trait matrix (Q) and an environment-sites matrix (R). The fourth-corner analysis tests pairwise relationships between traits and environmental variables, whereas RLQ considers the inter-correlation of traits and environmental variables. RLQ analysis is a multivariate analysis and an extension of co-inertia analysis, which is an ordination method exploring the link between two matrices. The RLQ analysis explores the relationships between the three matrices R, L and Q, and the method and its mathematical background are described in detail by Dolédec et al. (1996) and Dray et al. (2014). First, a correspondence analysis on the relative abundance matrix L and principal component analyses on matrices Q and R is performed by using the scores of the sampling sites and species from the previous correspondence analysis on matrix L as weight of the rows. The RLQ analysis combines these three separate analyses and maximizes the cross-covariance between the environmental and trait ordinations, resulting in a co-

structure between the three matrices, which is quantified through so-called RLQ axes. The associations between species, traits and environmental variables along the RLQ axes represent the best compromise between traits and environmental variables through species abundances (Dray et al., 2014). Variables that have the highest positive or most negative score on the RLQ axes are contributing the most to the observed spatial patterns and trait-environment relationships, while variables with a score close to 0 do not contribute to the observed relationships. Similar to other multivariate analyses, the sign of the scores on the RLQ axes does not have a unit, and multiplying all scores by −1 would not change the interpretation of the results. The analyses were conducted using the "ade4" R package (Dray & Dufour, 2007).

2.2. *Community weighted mean traits: GAM and RF*

The community-weighted mean (CWM) of a trait is the average trait value in the community. It is based on the mass-ratio hypothesis, stating that dominant species are expected to have the largest impact on the structure and functioning of communities (Grime, 1998; Garnier et al., 2004). When a CWM trait changes in either time or space, it typically indicates that the community has shifted in its structure, often as a response to changes in the environment or sudden disturbances (Mouillot et al., 2013). CWM traits are thus useful detectors of changes in structure by summarizing the overall response of a community based on the underlying species dynamics (Ricotta & Moretti, 2011). Since the distribution of traits is often skewed the CWMs of each trait are often calculated as a geometric mean weighted by species abundance or biomass:

$$CWM = \left(\prod_{i=1}^{n} trait_i^{p_i} \right)^{1/\sum_{i=1}^{n} p_i}$$

where *n* is the number of species, *trait i* is the trait value of species *i*, and *pi* is the relative biomass of species *i*. To assess the effect and relative importance of environmental factors explaining the observed variation of any given CWM trait, whether in time, space or both, we applied Generalized Additive Models (GAMs) and random forests (RFs). The same set of candidate explanatory variables, reflecting the selected set of environmental factors potentially affecting the CWM trait expression for the specific organism group and area was used for both methods. The resulting statistical relationships and derived response curves between the set of covariates and the CWM traits were compared across methods to assess the sensitivity and robustness of the results to the choice of methodology. In terms of GAM, we used the following model formulation:

$$CWM_i = \alpha + s(env1_i) + s(env2_i) + s(envN_i) + \varepsilon$$

where the response variable CWM is the trait in question at each given sampling unit i (i.e., site, time, or site-time combination) and env1 to envN reflect the corresponding set of environmental conditions at each sampling unit. If needed to achieve normality and stabilize the variance, the response variable can be log(X+1) transformed prior to model fitting. The constant a is the overall intercept, s the thin plate smoothing function for each smooth term and ε the error term. Although the number of regression splines is optimized (and penalized) by the generalized cross validation criterion (GCV), the degrees of freedom of the spline smoother function (s) was further constrained to three knots (k=3) to allow for potential nonlinearities, but restrict flexibility during model fitting. Finally, to assess the importance of the predictors of the temporal and spatial models, the relative variable importance (RVI) was computed for each predictor in each model. The RVI ranges from 0 to 1 and represents the probability of a variable ending up in the best fitting model. First, a set of

models was generated based on combinations of all predictor variables. The RVI for each predictor was then calculated as the sum of Akaike weights of the generated models that included the variable of interest (Burnham & Anderson, 2002). The second method used, i.e., RF, is a machine learning tool comprising ensembles of decision trees that rely on bagging (i.e. bootstrap aggregation). RFs are capable of reproducing complex nonlinear shapes in single and multiple dimensions, making them suitable for ecological applications in which complex shapes are to be expected (Breiman, 2001). In addition, RF has fewer constraints and is able to capture interactions between variables that cannot easily be achieved with GAMs. Individual classification trees within the random forest are trained on randomly selected subsets of the data. The final forest prediction is obtained by averaging predictions across all trees in the forest. We used the same model setup in terms of response and explanatory variables as in the GAM. Once trained on the available data, we used the final RFs to estimate the relative importance of each predictor, as well as visualize the partial response curves of each individual explanatory variable. The analyses were conducted using the following R packages using the following packages: "mgcv" (Wood, 2017), the 'MuMIn' (Barton, 2016) for calculating RVI and "randomForest" (Liaw & Wiener, 2002).
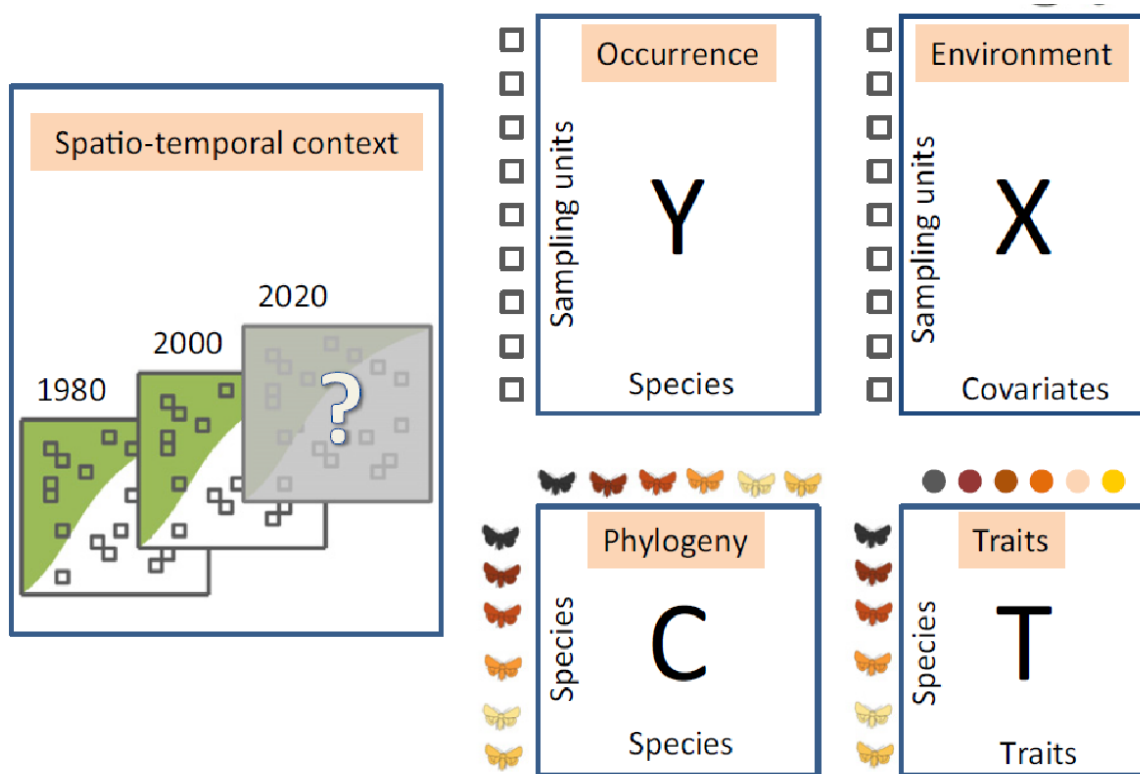

Figure 5 A schematic illustration of the key input data to the joint species distribution modelling approach using HMSC, which include: (i) abundance (or occurrence) data of species recorded in a set of temporal and/or spatial sampling units (Y); (ii) the environmental covariates measured over the sampling units (X); (iii) the set of traits measured for the species present (T); the phylogenetic dependencies among the species C). Finally, the spatiotemporal context, often introduced as random effects includes location and time information about the samples. (Modified from Ovaskainen et al., 2017).

2.3.   *Joint species distribution modelling (HMSC)*

In addition to RLQ and modelling CWM traits, we investigated potential trait-environment relationships using Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017). HMSC is a Bayesian joint species distribution model (Warton et al. 2015), including a hierarchical setup where species responses to environmental covariates are conditioned on their set of traits (Abrego et al., 2017). Although the methods are fundamentally different, the basic input data to HMSC is the same as for RLQ, including: (i) abundance (or occurrence) data of species recorded in a set of temporal and/or spatial sampling units; (ii) the environmental covariates measured over the sampling units; (iii) as well as the set of traits measured for the species present (Figure 5). However, HMSC may also account for phylogenetic dependencies among the species, as well as potential spatial/temporal random effects aiming to represent any residual variance not explained by traits and species responses to the environment.

The standard workflow of HMSC, as provided by the HMSC-R package constitute five key steps (Tikhonov et al., 2020a). The first step deals with defining the model structure and fitting it using either observed species presence-absences, or abundances/biomasses as response variables. The models were fitted to such data with Bayesian inference, using the posterior sampling scheme described in Ovaskainen et al. (2016), but extended to account for traits and phylogenetic constraints, if available. Where deemed appropriate, spatial random effects were included (that also model co-occurrence among species), either at the level of sampling station or aggregated into larger areas, using a latent factor approach (Ovaskainen et al., 2016). The above also accommodates specifying temporal random effects, representing time points, or various broader aggregations representing months, seasons or years. During model fitting the recommended HMSC default prior distributions were considered (see Abrego et al., 2017; Tikhonov et al., 2019). After model fitting, the convergence of the Markov chain Monte Carlo (MCMC) simulations are examined (step 2) and the model fit evaluated fit (step 3). More specifically, the explanatory power of the model is evaluated by computing the explained variance (R^2) for the individual species included in each of the implementations. In the event, presence–absence data was used as response the coefficient of discrimination (Tjur's R2) was calculated, defined as the difference between the average model prediction for successes and failures. The overall explanatory power of the model was summarized as the mean R2 across species. Additionally, a twofold cross-validation was performed to assess the predictive power of the model which includes setting aside a test data set not used for model fitting. Finally, the parameter estimates were explored (step 4) and predictions made (step 5).

After having fitted and validated the model we followed the approach by Ovaskainen et al. (2017) to partition the explained variation among the random and fixed effects, including each of the individual environmental variables, or grouped into broader categories (e.g., representing hydrography, nutrients, etc). Furthermore, the fitted and validated models include parameters (gamma) which measure the influences of the traits on the species-specific responses to the environmental covariates (Ovaskainen et al., 2016). It is therefore possible to measure the portion of the among-species variation of responses to environmental covariates attributed to traits. These in turn, represent the trait-environment relationships at the level of the community which facilitates a comparison between methods, at least in a qualitative manner pointing to the existence and sign of relationships.

3. Results

3.1. European fish communities (SL8)

3.1.1. Study organism and area

The study area encompassed demersal (bottom-living) marine fish communities inhabiting European marine ecosystems ranging from the Barents Sea and Icelandic seas in the north to the more southern shelf areas surrounding the Iberian peninsula (e.g., Bay of Biscay), as well as the Gulf of Lions in the Mediterranean Sea. Consequently, the areas cover a large latitudinal gradient with pronounced differences in environmental conditions structuring the diversity and composition of fish communities (Wiedmann et al., 2014; Pecuchet et al., 2016; Dencker et al., 2017). The aim of this study is to identify the key response traits of demersal fish species allowing them to occupy their respective habitats and areas and investigate their links to potential environmental characteristics, illustrating the trait-environment relationships. Although the focus was the Baltic Sea (SL8), the analysis covers and therefore applies to several Storylines across Europe.

3.1.2. Data description

We compiled available data from scientific bottom-trawl surveys in the North-East Atlantic (see global review of surveys by Maureaud et al., 2021). To ensure a similar temporal coverage and a consistent sampling period across surveys we selected the period from 2005 to 2015. The surveys exclusively use bottom trawls and identify catches to the finest taxonomic resolution possible, yet the surveys differ slightly in terms of the type of gears and sampling protocols used. Hence, we standardized the abundance data by the duration or swept area (in km^2) of each respective haul, depending on which meta-information that was available. Furthermore, abundances were log-transformed to reduce the influence of outliers. Thereafter, we converted these into relative abundances by dividing each species abundances by the sum of all individuals caught in a given haul. The taxonomy of the reported taxa was verified and whenever needed updated according to the World Register of Marine Species (WoRMS) (https://www.marinespecies.org/). All non-fish were discarded and species from the following classes were retained in the analysis: Actinopterygii, Elasmobranchii, Holocephali, Myxini and Petromyzonti. Finally, we restricted the analysis to mean relative abundances of species across years for each of the 169 1°x1° grid cells.

To represent the general ecology and life history of the species in terms of their feeding, growth, survival and reproduction the following 7 traits were selected. The trait information was obtained from an available trait online data base (Beukhof et al., 2019).

- Trophic level
- K: the growth rate (calculated as Von Bertalanffy growth coefficient in year−1)
- Lmax: maximum body length in cm
- Lifespan (in years)
- Offspring.size_log: egg diameter, length of egg case or length of pup in mm
- Fecundity_log: number of offspring produced by a female per year
- Age.maturity: in years

Trait values for fecundity and offspring size were log-transformed to reduce the influence of outliers.

To characterize the environmental conditions and human impacts caused by fishing we collected data for the following variables representing hydrography, habitat, food availability and anthropogenic pressures, which are known to affect the distribution of fish species:

- Depth: depth in meter, directly measured during the survey.

- SBT: monthly sea bottom temperature in °C from the Global Ocean Physics Reanalysis (GLORYSs2v4)
- SBS: monthly sea bottom salinity from the Global Ocean Physics Reanalysis (GLORYSs2v4)
- Chl: Chlorophyll a concentration (in *mg.m*–3) as a proxy for primary production and food availability from the GlobColour database.
- SBT_sea: seasonality of sea bottom temperature, calculated as the difference between the warmest and the coldest month of the year.
- Chl_sea: seasonality of chlorophyll a concentration, calculated as the difference between the highest and the lowest primary production in the year
- Fishing: the cumulative demersal fishing pressure in 2013, estimated globally by Halpern et al. 2015, DOI 10.1038/ncomms8615.

3.1.3. Patterns and drivers of CWM traits

This section presents an investigation of the patterns and underlying environmental drivers of fish CWM traits, i.e., characterizing the mean trait value of each community (i.e., grid cell) weighted by the relative abundances of species. Since methods in the following sections are capable of jointly investigating and illustrating multiple trait-environment relationships this section will report on individual response of CWM traits (here using trophic level as an example) to the selected set of environmental predictors using both GAMs and RF (see section 2 for details regarding methods).
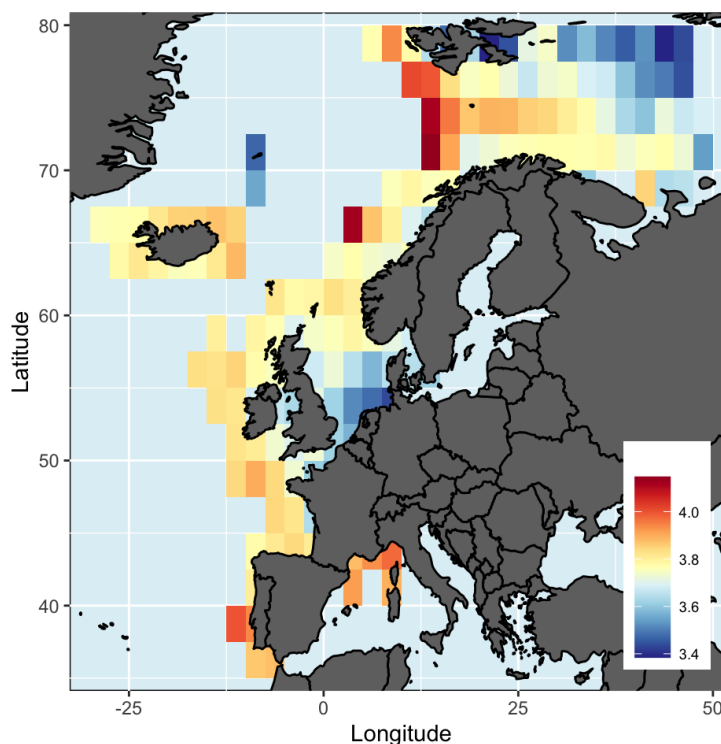
Figure 6 Map of CWM trophic level of demersal fish communities across the study area.

The spatial patterns of CWM trophic level show pronounced spatial variability throughout the study area (Figure 6). In general, we found higher values primarily around the shelf breaks in both the north and south, while lower values were found in the shallow areas of the southern North Sea and the eastern Barents Sea. This indicates a higher prevalence of species feeding lower in the food-web in the latter areas, including flatfish species preying exclusively on benthos, while in the other areas a higher relative abundance of piscivorous species (such as large gadoids) are found.
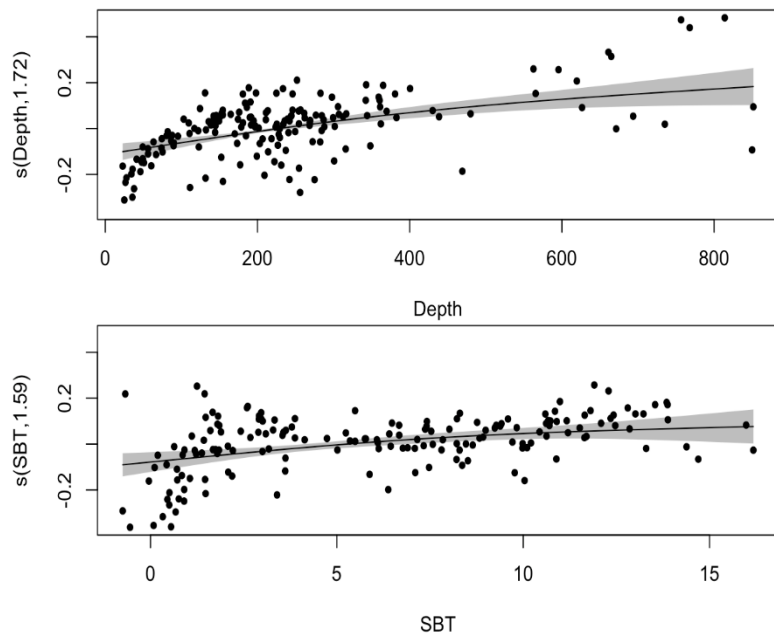
Figure 7 Partial smooth based on the final GAM demonstrating the statistical relationships between CWM trophic level and depth (top) and sea bottom temperature (bottom). Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

After a formal model selection routine comparing all combinations of predictors, the final GAMs (demonstrating the lowest AIC) identified depth and sea bottom temperature as the main predictors contributing to explain the spatial patterns in trophic level. The model explained 35.5% of the deviance and demonstrated significant (p<0.001), non-linear increasing relationships between trophic level and both predictors, reflecting the trait-environment relationships (Figure 7). The complementary analysis using RF largely confirmed the GAM results but identified also sea bottom salinity and temperature seasonality as important predictors, i.e., all these predictors would result in a ~25% increase prediction errors (Figure 8).
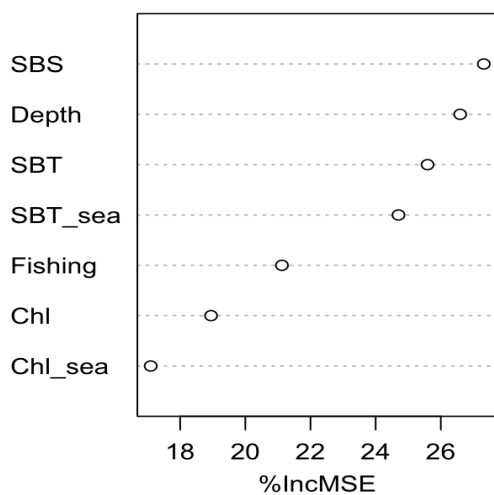
Figure 8 Variable importance of all predictors in RF illustrated by the increase in mean squared errors (MSE) of model predictions (if a given predictor is left out of the model).

The RF model explained a considerably higher degree of variance (65.6%) compared to the final GAM. However, note that no exclusion of predictors was undertaken. The derived response curves largely corroborate the GAM findings, showing positive non-linear relationships between trophic level and depth and sea bottom temperature (SBT), but also a positive saturating response to sea bottom salinity (SBS) and a non-linear negative relationship with seasonality (Figure 9). Taken together, the derived trait-environment relationships indicated a dominance of lower trophic level species in shallow, seasonal environments with a higher degree of fresh water input (e.g., from rivers of ice such as in the southern North Sea and North-eastern Barents Sea).
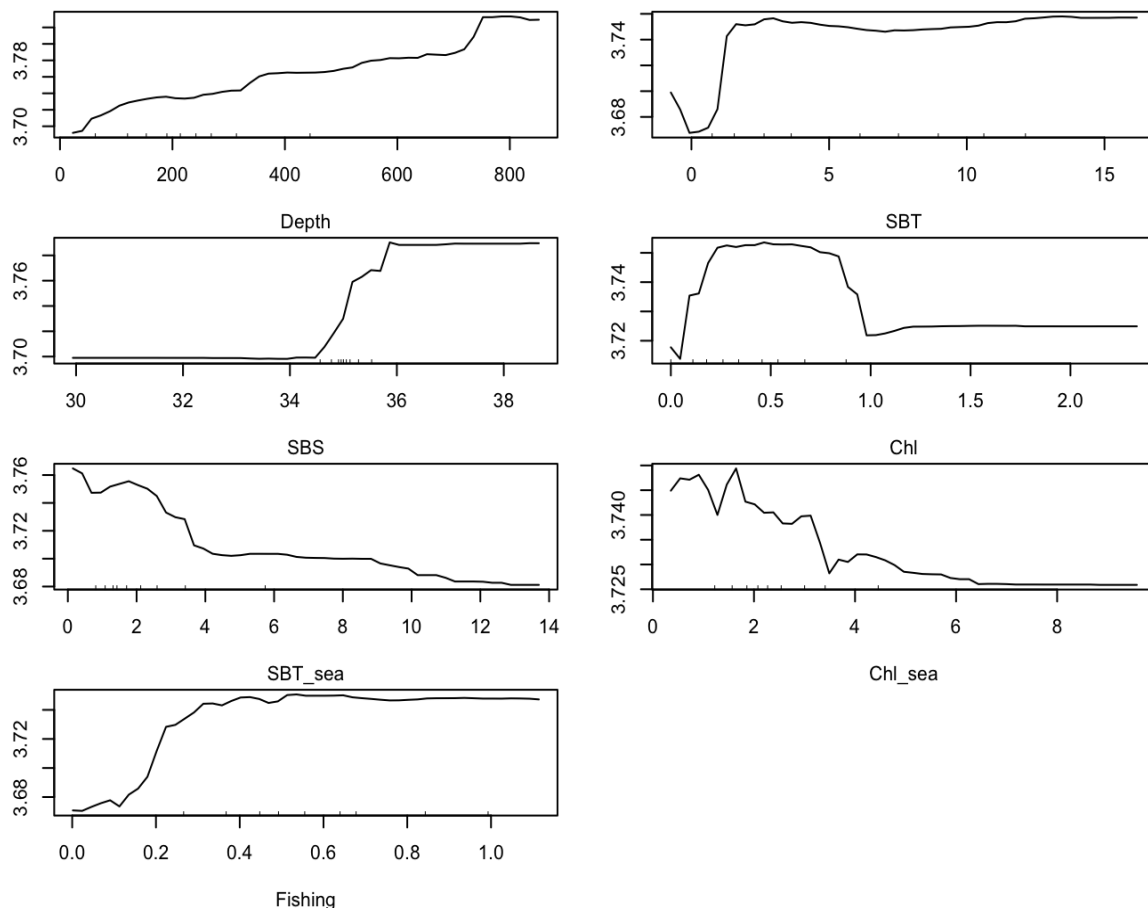
Figure 9 Partial dependence plots based on the RF demonstrating the predicted responses of CWM trophic level to changes in each of the predictors, while maintaining all other predictors at their mean levels.

3.1.4. Trait-environment relationships using RLQ

This section presents the results of the RLQ analysis aiming to investigate the unknown 4th corner (i.e., the trait-environment relationships) using the three matrices R (the environment), L (the species abundances), and Q (the species traits) as input. The total amount of co-inertia explained by the RLQ amounted to 0.599 with the first dimension (i.e., RLQ axis) contributing to 79.4% of the explained covariance. Hence, we will only present the scores of the first axis (but similar visualization could be carried out for subsequent axis). In terms of traits (Figure 10A), RLQ1 demonstrate positive scores for traits and species associated to slow life history (high age at maturity, large offspring, large size and high life expectancy) and negative score for traits associated to fast life history (fast growth). In terms of environmental variables, RLQ1 show a gradient between shallow-warm and deep-cold waters (Figure 10B). This is illustrated by positive scores for environments characterized by high depth, but low and constant temperature, as well as low primary production. Conversely, sites with negative

scores have high average temperature and high seasonal fluctuation of temperature, as well as high primary production and low depth. Please note that fishing also loaded highly on RLQ1, but with a positive score. Hence, rather than reflecting a negative fishing impact this likely indicates a spatial co-occurrence of high fishing effort in areas with large and commercially valuable species (such as gadoids).
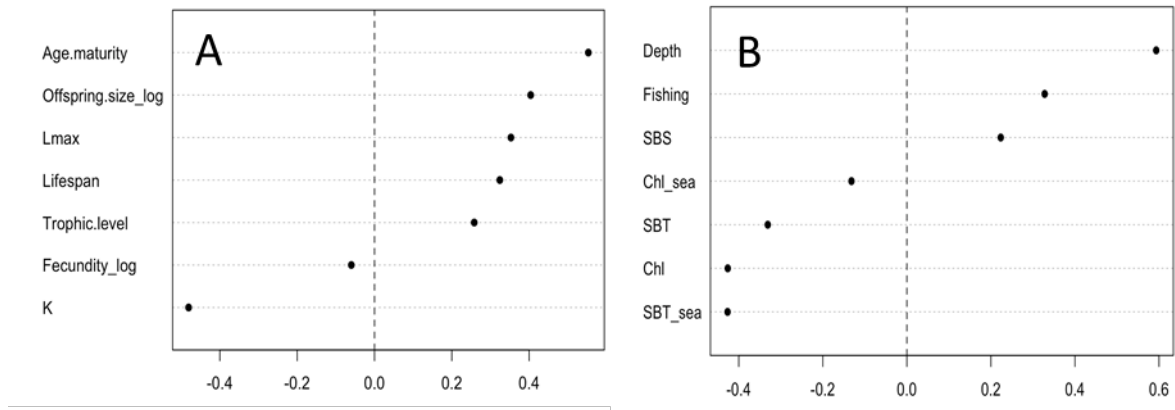

Figure 10 Loadings of traits (A) and environmental variables (B) on RLQ1. Positive and negative values show the associated scores.

Taken together, the association between trait and environment identified by RLQ analysis can be summarized as a map of site scores for each of the grid cells of the study area (Figure 11). Cells with green colour (representing negative scores) are shallower and have higher and more fluctuating water temperature. They host species that are faster, especially with a fast growth coefficient K, low age at maturity, small offspring and overall smaller and shorter-lived species. On the contrary, cells with pinkish colour are deeper with constantly cold water temperature, which host a fish community with, in average, slower growth and maturity, larger offspring, size and longer lived species.
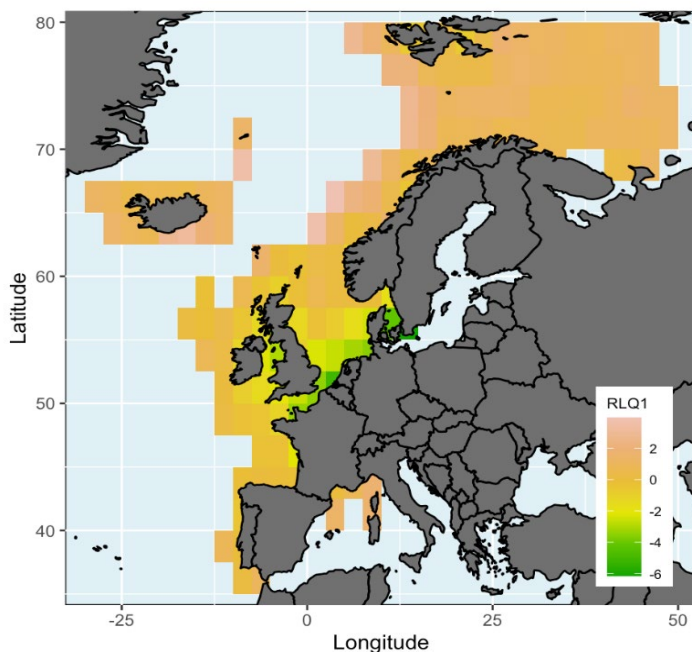
Figure 11 Site scores on RLQ1 showing the association between trait and environment identified by RLQ.

3.1.5. Trait-environment relationships using HMSC

This section presents results of joint species distribution model runs using HMSC aiming to investigate species response to the environment conditioned on their traits (see section 2 for more details regarding the method). The model required the same basic input as in the RLQ analysis (i.e., the three matrices of species abundances (or occurrences), traits and environmental variables per grid cell), but also use a matrix of pair-wise species relatedness (here derived based on taxonomy, rather than phylogeny), as well as spatial random effects (here grid cells). The model was setup, fitted and cross-validated using either species abundances, or species presence-absence as input. Below we present results only for the presence-absence analysis (using a probit link function).

The fitted model demonstrated a good performance (mean AUC = 0.96) with an average explained variance of observed species occurrences amounting to 62.2%. A variance partitioning analysis show that roughly half of the explained variance (55%) could be attributed to the random spatial effects (i.e., grid cells), while the remaining part was attributed to the set of environmental predictors, albeit with differences between individual species (Figure 12). The main environmental drivers were sea bottom salinity, seasonality in primary production (Chl_sea) and sea bottom temperature.
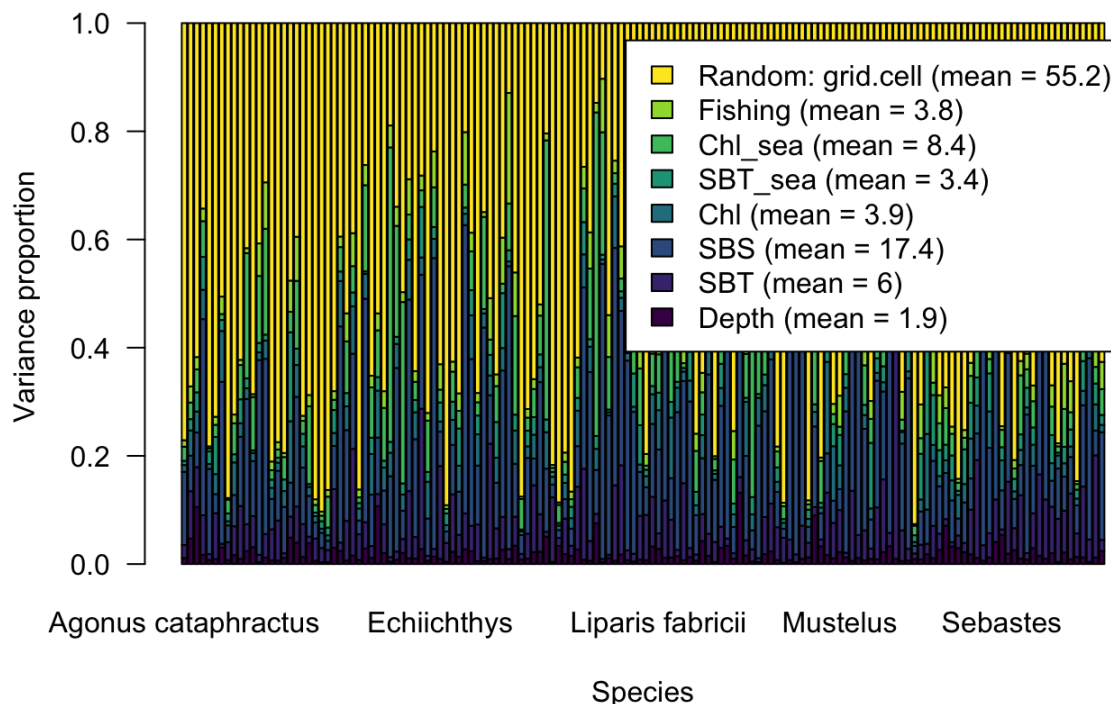
Figure 12 Variance partitioning of fixed and random effect on species occurrences, as well as the associated mean values across species for each predictor (see insert).

 Interestingly, the traits contribute substantially to the variation in species occurrences. This is reflected by a number of pair-wise relationships between traits and environmental variables with high statistical support, such as between sea bottom temperature and seasonality (in temperature and Chl a) with age at maturity, lifespan, length and growth coefficient K (Figure 13). Similar to RLQ, the analysis also identifies a potential relationship with fishing effort, here illustrated by a positive interaction with offspring size and fecundity and a negative interaction with growth coefficient K. As argued in the previous section, this likely reflects a co-occurrence and spatial allocation of fishing effort in areas with species characterized by relatively high fecundity, but slow growth (such as gadoids) that are also commercially valuable and targeted by the fishery.
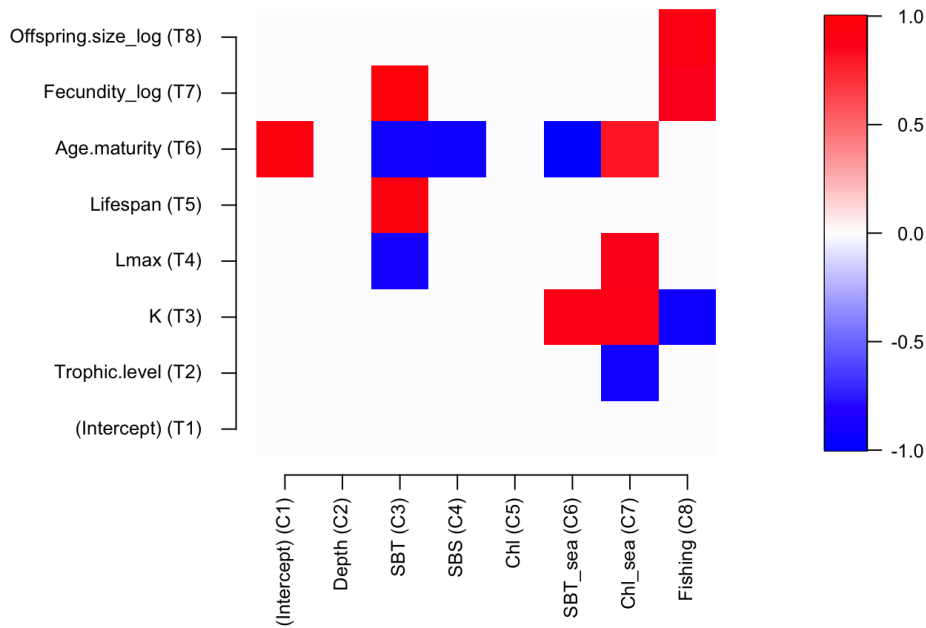
Figure 13 Pair-wise relationship between traits and environmental variables, illustrated by the mean posterior estimates of the gamma parameters with a support level p>0.9. Red and blue colours indicate positive and negative parameter values, respectively.

The realized trait-environment responses show similar relationships as observed using GAM/RF and RLQ, such as a positive and non-linear saturating relationship between trophic level and lifespan with sea bottom temperature (Figure 14).
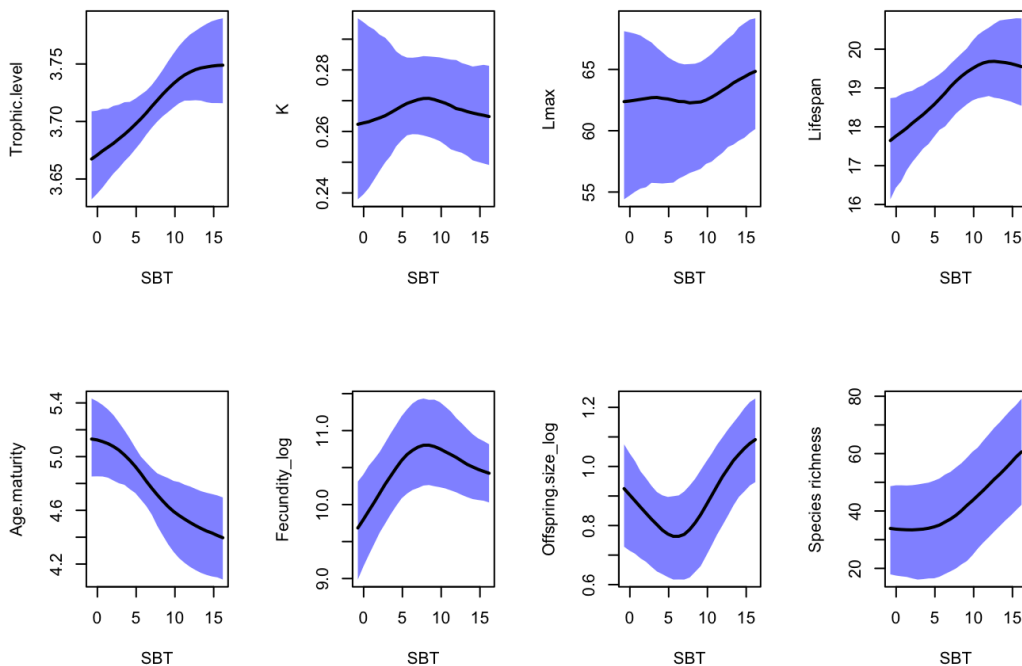

Figure 14 Predicted community trait values across the entire range of observed environmental conditions using sea bottom temperature (SBT) as an example. Black lines and blue shaded areas show means and 95% confidence intervals of model predictions, respectively.

3.1.6. Summary of main findings

- The investigation of trait-environment relationship for marine demersal fish throughout European continental shelf seas show broadly consistent results across the three methods, indicating that patterns and findings seem robust to model choice.
- The primary traits explaining the spatial occurrence and/or abundance patterns of species are mainly associated with age at maturity, lifespan, body size and fecundity, indicating that these are the primary "response" traits of marine fish.
- The key environmental variables explaining the distribution of species are primarily associated with depth, bottom temperature and the degree of seasonality in temperature and primary production.

- Our results are consistent with the "fast-slow" continuum of species life histories (Stearns 1983; Reich 2014) and supports "environmental filtering" as a primary assembly process determining community composition and diversity at large (Keddy 1992; Pecuchet et al. 2016).

3.2. Reef fish communities in the Aegean and Ionian Sea (SL26)

3.2.1. Study organism and area

The study area encompasses all shallow territorial waters of the Aegean Sea and Ionian Sea, situated in the north-eastern Mediterranean Sea (Figure 15). The Aegean Sea is divided into the North and the South Aegean basin, which are characterized by distinct oceanographic conditions, with the South Aegean Sea being more oligotrophic. The Ionian Sea is located in the west of the continental Greece and surrounds the southernmost Hellenic continental coast, hosting the deepest basins of the Mediterranean Sea (Lykousis et al., 2002). Mediterranean shallow rocky reefs are very productive and diverse ecosystems providing important provisioning, regulating and cultural ecosystem services (Salomidi et al., 2012). However, they are exposed to multiple stressors, including overfishing (Sala et al., 2012), pollution (Tornero & Hanke, 2016), invasive species (Katsanevakis et al., 2014), destructive fishing practices (Guidetti, 2011), and climate change (Rilov, 2016). The associated rocky reef fish assemblages are also of high ecological importance, since they play a fundamental role in the functioning of reef ecosystems by regulating food web dynamics and nutrient releases, thus securing ecosystem stability and resilience, and the flow of respective services to humans (Holmlund & Hammer, 1999). Moreover, reef fish have an intrinsic economic value for artisanal fisheries and underwater tourism, greatly supporting coastal economies (Badalamenti et al., 2000).

The aim of this study is to identify the key response traits of demersal fish species and investigate their links to potential environmental characteristics, illustrating the trait-environment relationships.
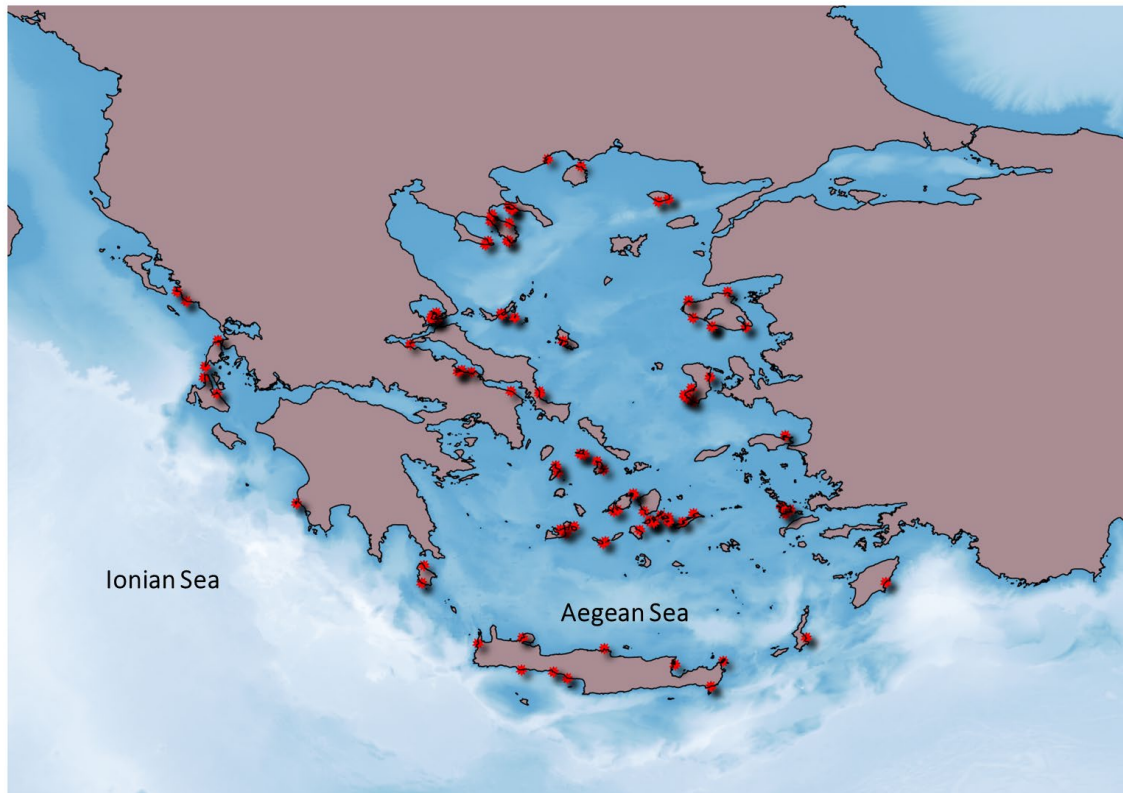
Figure 15 Study area with sampling stations (red circles) of reef fish communities sampled along the Aegean and Ionian Sea.

3.2.2. Data description

Abundance and biomass data were acquired from the ALAS – INVASION project (https://alas.edu.gr/?lang=en) and Sini et al. (2019). Data were collected through underwater visual surveys, performed by SCUBA diving at two distinct depth zones (5 and 15 m), at 158 sampling stations, distributed along the Aegean Sea (Fig. 3.2.1). Abundance data were reported for 64 fish species, 56 native and 8 invasive species.

To represent the general ecology and life history of the species, in terms of their feeding, growth, survival and reproduction, the following 8 traits were selected. The trait information was obtained from the available online database of Fishbase.

- Growth performance index phi (Φ)
- Maximum body size in cm
- Reproductive guild (non-guarder, guarder)
- Trophic level
- Substrate type (benthic-benthopelagic/pelagic)
- Biogeographical status (native/neo-native/invasive)
- Undertake of seasonal migrations (no/yes)

For the trait-environment relationships, we selected environmental variables relevant to the climate and topography, such as sea temperature, temperature of the coldest and warmest month, temperature seasonality (extracted from the E.U. Copernicus Marine Service Information at respective depths for each sampling station; 5.465m and 13.3184m), chlorophyll concentration, salinity, current velocity and depth, as well as human pressures, such as fishing.

- Average sea temperature
- Temperature of the coldest month
- Temperature of the warmest month
- Temperature seasonality
- Average chlorophyll concentration
- Average salinity
- Average current velocity
- Depth in meter
- Small-scale fishing pressure

We selected the average tri-annual values of the variables, for the locations of the 158 sampling stations. We estimated the tri-average conditions for periods of 2014-2016 and 2018-2020, as samplings took place in 2016, 2020-2021. Environmental data were acquired from the E.U. Copernicus Marine Service Information - CMEMS-MED-PUM-006-004 (https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1). Spatial data on small-scale fisheries pressure were derived from Kavadas et al. (2015) this dataset was produced following a multi-criteria decision analysis. All analyses were realized in R studio and ArcGIS 10.1.

3.2.3. Patterns and drivers of Community Weighted Mean (CWM) traits

Community Weighted Mean (CWM) offers an approach to average the values of traits across species in a community, weighted by the relative abundances of species. A comparison of CWM traits over different regions or sites could allow to detect trait patterns over the entire communities, across space.

For the reef fish communities studied here the spatial patterns of CWM longevity and growth parameter phi showed pronounced spatial variability throughout the study area (Figure 16), following a north to south pattern. In general, we found higher values of growth performance index in the central and southern Aegean Sea, while lower values were found in the northern sampling stations. Longevity followed the inverse pattern, with higher values in the northern sites and lower values in the southern Aegean Sea. The same pattern was observed also for the community weighted trophic level, with marine communities of lower trophic level (e.g., grazers, omnivores) mainly distributed in the central and southern seas. Thus, the northern Aegean Sea represents a marine area of reef fish communities with fish of higher longevity and trophic level compared to the central and southern seas of Aegean and Ionian, which consist of marine communities with higher growth parameters.
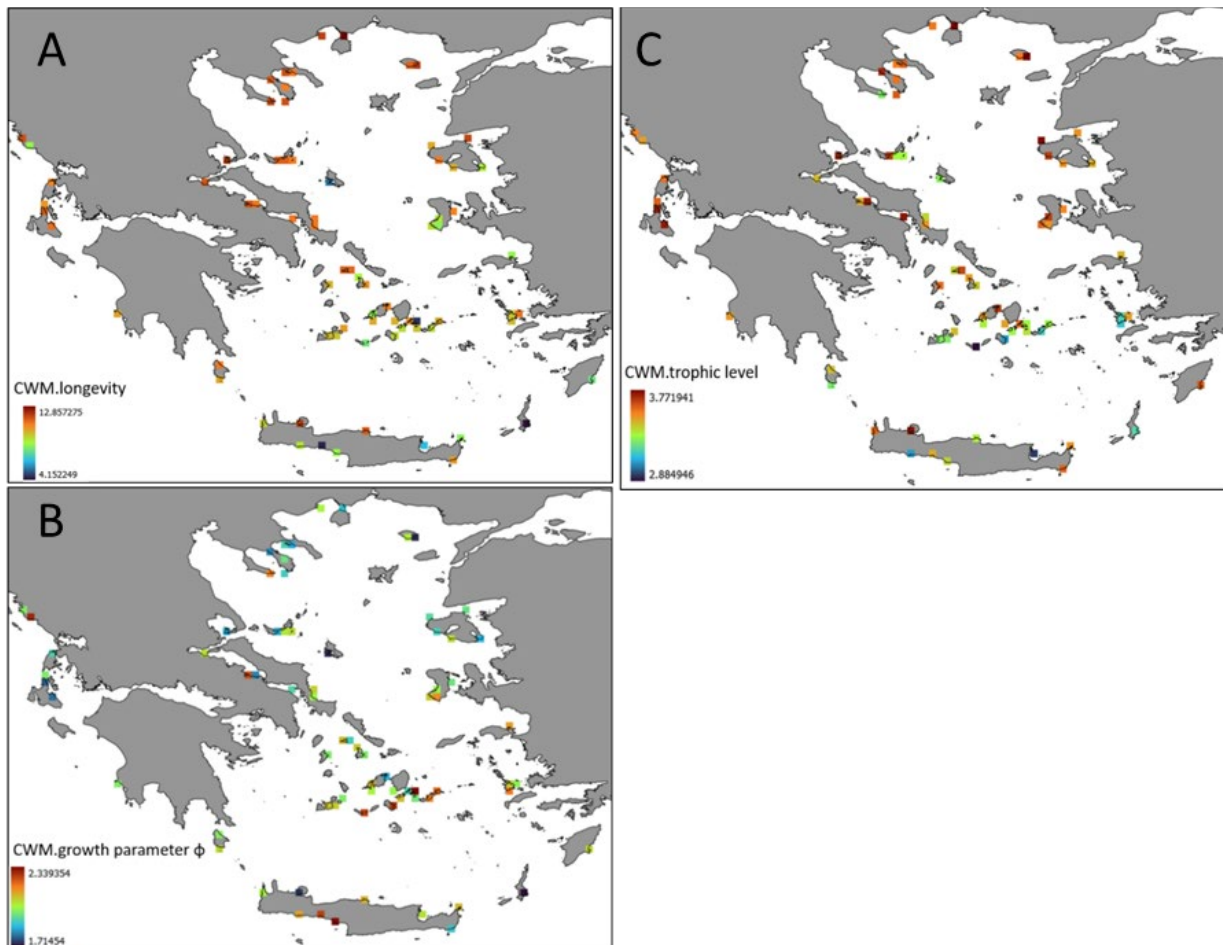
Figure 16 Map of CWM trophic level (A), Growth parameter phi (B) and Longevity (C) of reef fish communities across the study area.

As predictors of the CWM traits (CWM.trophic level, CWM.growth parameter index, CWM.longevity), we used sea temperature (sst1), sea temperature seasonality (sst4), max temperature of warmest month (sst5), min temperature of coldest month (sst6), salinity, currents and chlorophyll concentration. In order to statistically investigate trait-environment relationships, we modelled with GAMs and random forest the trait responses at the community level (using CWM). Comparing all combinations of predictors, the GAMs that obtained the lowest AIC, identified temperature seasonality (sst4) and currents velocity, as the main predictors of longevity. The model explained 34.4% of the deviance and demonstrated significant (p<0.001), non-linear increasing relationships between longevity and temperature seasonality (p<0.1 for currents) (Figure 17B).
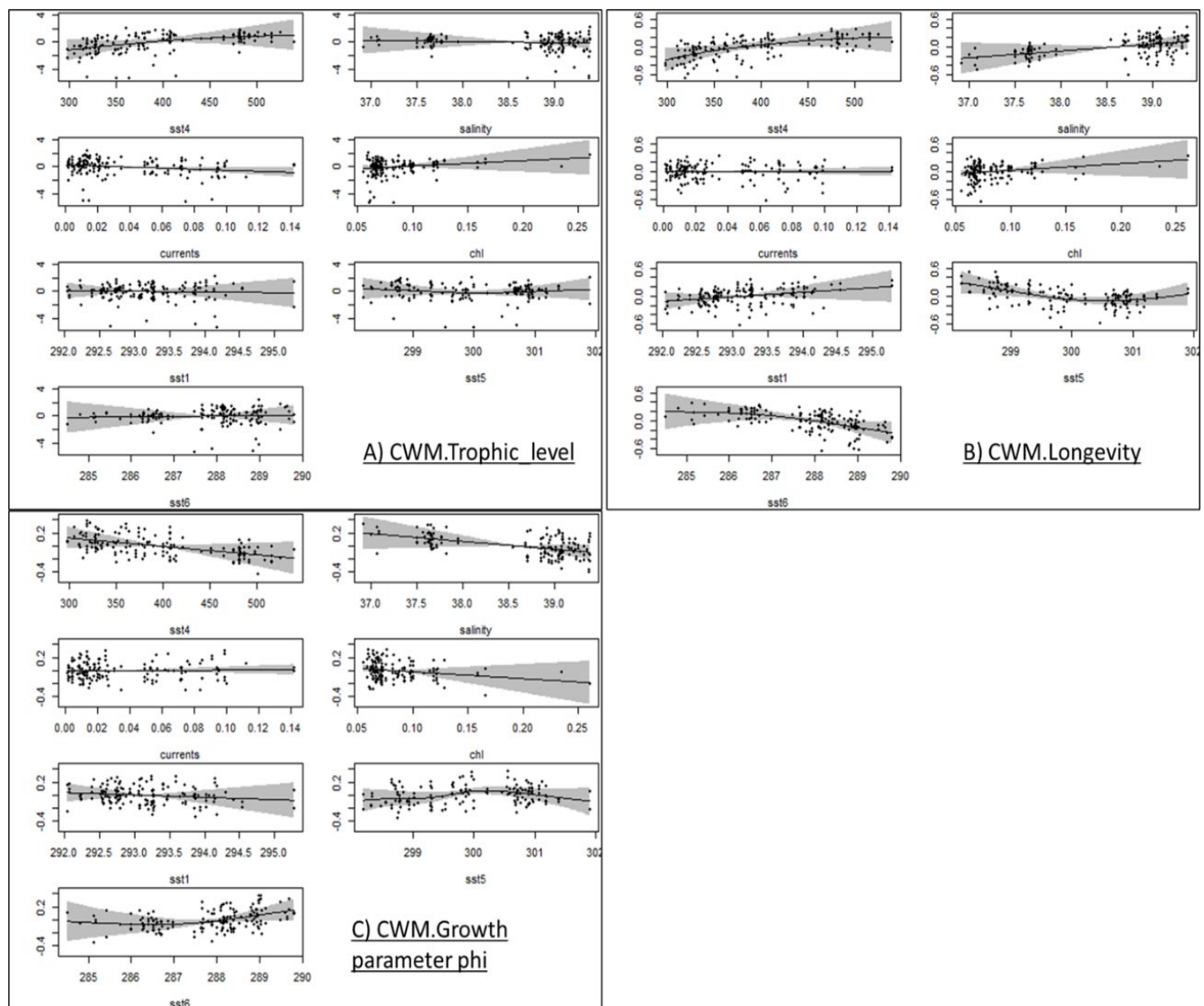
Figure 17 GAM partial smooth demonstrating the statistical relationships between CWM trophic level (A), longevity (B) and Growth parameter phi (C) and chlorophyll, salinity, currents velocity, sea temperature, max temperature of warmest month, min temperature of coldest month. Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval

The complementary analysis using RF largely confirmed the GAM results (except for currents) but identified also chlorophyll concentration and min temperature of coldest month (sst6) as important predictors, i.e., all these predictors would result in a ~25% increase prediction errors (Figure 18). For CMW.trophic level, the final GAMs identified the min temperature of coldest month (sst6), salinity and temperature seasonality (sst4) as the main predictors. The model explained 20.3% of the deviance and demonstrated significant ($p<0.001$), non-linear increasing relationships among trophic level and both min temperature of coldest month and salinity ($p<0.1$ for temperature seasonality) (Figure 17A).
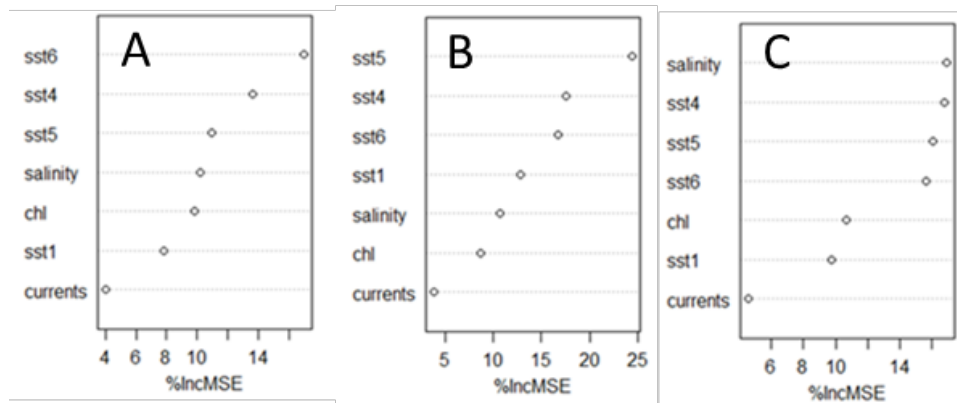
Figure 18 Variable importance in RF illustrated by the increase in mean squared errors (MSE) of model predictions (if a given predictor is left out of the model) for longevity (A), trophic level (B) and growth parameter phi (C). Predictors represent sst1: mean sea temperature, sst4: temperature seasonality, sst5: max temperature of warmest month, sst6: min temperature of coldest month.

For CMW.growth parameter phi, the final GAMs identified sea temperature seasonality (sst4), salinity and min temperature of coldest month (sst6) as the main predictors. The model explained 14.2% of the deviance and demonstrated significant (p<0.01), non-linear relationships among growth parameter and sea temperature seasonality (sst4) and salinity both min temperature of coldest month and min temperature of coldest month (p<0.1 for temperature seasonality) (Figure 17C). The complementary analysis using RF largely confirmed the GAM results, with the exclusion of salinity and the addition of maximum temperature of warmest month (sst5) (Figure 19C).
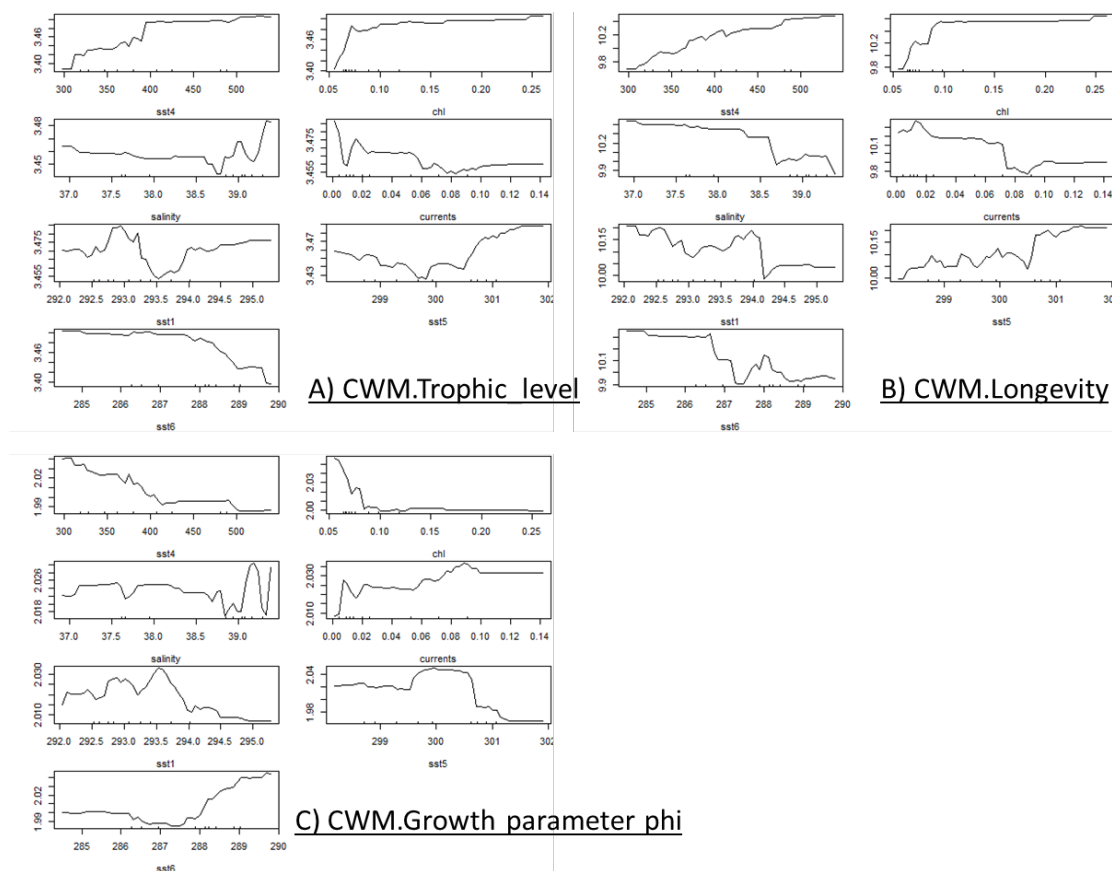
Figure 19 Partial dependence plots based on the RF demonstrating the predicted responses of A) CWM trophic level, B) CWM longevity and C) Growth parameter phi to changes in each of the predictors, while maintaining all other predictors at their mean levels

The final GAM model explained a considerably higher degree of variance compared to the RF both for longevity (34.4% vs 6.53%) and trophic level (20.3% vs 1.6%). However, findings from both modelling approaches show similar results. Taken together, the derived trait-environment relationships indicate a dominance of higher trophic level species in environments of higher sea temperature seasonality, with colder winters and dominance of longer-lived species in seasonal environments. Fish of faster growth are found in less seasonal waters with warmer winters.

3.2.4. Trait-environment relationships using RLQ

The total amount of co-inertia explained by the RLQ amounted to 0.365 with the first dimension (i.e., RLQ1 axis) contributing to 92% of the explained covariance. Hence, we will only present the scores of the first axis (but similar visualization could be carried out for subsequent axis). In terms of traits, RLQ1 demonstrated negative scores for traits and species associated to slow life history (high trophic level, high longevity) and positive score for traits associated to fast life history (fast growth – increased parameter growth phi) (Figure 20.A). In terms of environmental variables, RLQ1 show a gradient between waters of higher seasonality to waters of higher sea temperature that experience warmer winters (Figure 20.B). This was illustrated by positive scores for environments characterized by higher minimum temperature of coldest month and high sea average temperature. Conversely, sites with negative scores have high temperature seasonality, as well as high chlorophyll concentration. Fishing did not score highly on RLQ1, however positively, showing a small potential co-occurrence of high fishing effort in areas with reef fish of faster growth.
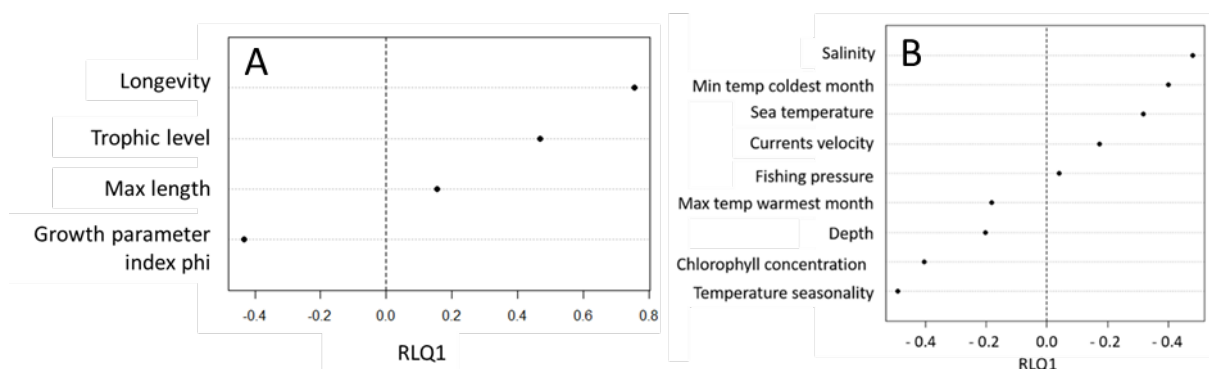
Figure 20 Loadings of traits (A) and environmental variables (B) on RLQ1. Positive and negative values show the associated scores.

Taken together, the association between trait and environment identified by RLQ analysis can be summarized as a map of site scores for each of the grid cells of the study area (Figure 21). Following a colour gradient, there exists a strong pattern between northern and southern sampling stations for the Aegean Sea. Cells representing negative scores (i.e., blue colour) have stronger temperature seasonality and higher chlorophyll concentration. They host species with higher longevity and trophic level position. On the contrary, cells with reddish colour have higher salinity and are characterised by warmer winters hosting fish communities with, in average, higher growth parameter phi.
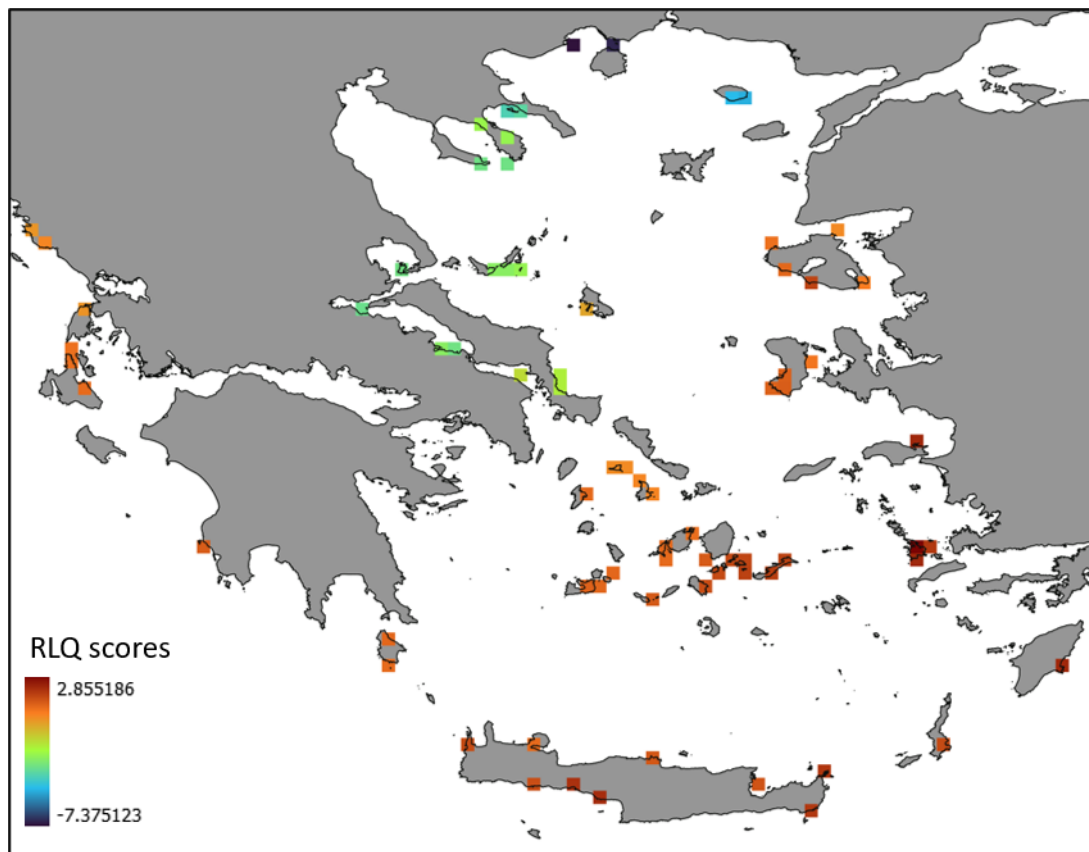
Figure 21 Site scores on RLQ1 showing the association between trait and environment identified by RLQ.

3.2.5. Summary of the main findings

- The primary traits explaining species spatial occurrence patterns are mainly associated with longevity and growth parameter index phi.
- The key environmental variables explaining the distribution of species are temperature seasonality and minimum temperature of the coldest month, playing a key role in species' traits.
- Results show a North-South spatial pattern, with higher longevity and high trophic level fish communities found in the North, where marine environment is characterised by stronger sea temperature seasonality, colder winters and higher chlorophyll concentration, while fish communities of higher growth species are found in the South, characterised by less seasonal waters, warmer winters and higher salinity.

3.3.   Fish communities in the Gironde estuary (SL16-17)

3.3.1. Study area

The study area encompasses the median part of the Gironde estuary. This estuarine area is located SW France (Figure 22). It is one of the largest European estuaries (Lobry et al., 2003) with a surface area of approximately 625 km^2 at high tide. Between the ocean (seaward of a transect drawn between Pointe de Grave and Pointe de Suzac) and the upstream salinity limit (Bec d'Ambes), it is 76 km long. The watershed covers 81,000 km^2 and the mean annual rate of freshwater discharge is now around 800 m^3.s^{-1} (Chevillot et al., 2019; Girardin et al., 2006).
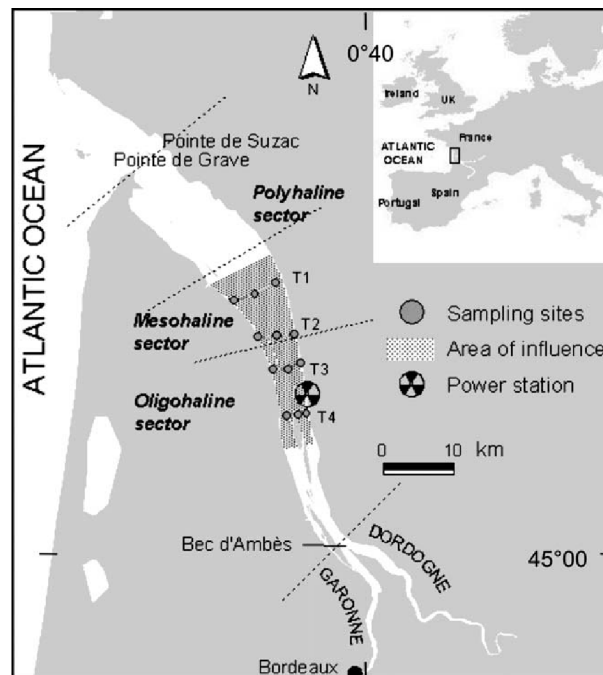
Figure 22 Location of the sampling stations in the Gironde estuary. Sampling sites are represented by circles that are aligned along fictive transects (T) historically numbered from 2 (T2) to 4 (T4) from downstream to upstream. Previous studies concluded that this ensemble of 4 transects is representative of the median part of the whole estuary (represented by the dotted zone named Area of influence). From Lobry et al. (2006).

This study is a first attempt to (1) describe the key ecological traits of the Gironde estuarine fish community, (2) investigate the main patterns of the traits-environment relationships in relation with the estuarine longitudinal gradient (i.e. from the river to the sea) and (3) identify potential effects of global changes on this trait assemblage for further investigations.

3.3.2. Data description

The dataset comes from the Blayais Power Plant monitoring program. In the frame of this program, fish sampling surveys are conducted monthly since the late 1970s. For the purpose of this analysis, we selected data from 1985 from which the sampling protocol is considered stable and standardized. Three sampling sites are located along four transects (Figure 22). On each site, simultaneously, one fishing sample is made near the surface and one near the bottom. Surface samples are taken using two 4.0 x 1.0 m rectangular frame nets fitted both sides of the boat. The subconical nets have a stretched mesh size of 18 mm in the main section and 2.8 mm in the terminal section. For the benthic samples, a 2.0 x 1.2 m frame is used with runners keeping the frame 0.2 m above the bed. The net meshes are identical to those used for surface samplings. A sampling lasts five to seven minutes and is performed in daytime, between the halfway stage of the flood tide and high tide slack, with the gear being towed against the current. Details in the sampling protocol can be found in Lobry et al. (2006) or in Chevillot et al. (2017). The monitored fauna consists mainly of small fish species and juveniles of larger species. 40 species are considered in the analysis. Fish abundances are expressed in number of individuals per filtered volume (ind.1000m^{-3}).

Fish traits were compiled from (Teichert et al., 2017; Nils Teichert et al., 2017; Teichert et al., 2018) that investigated patterns of fish functional diversity and life history traits for a set of European estuaries. Thirteen qualitative and quantitative traits were retained for the study (Table 1). In particular, some of these traits classically allow to discriminate two types of life history strategies: fast

life history (mainly low LT_mat, low A_Mat, high spawn_freq, no parental care, high Fec_max…) and slow life history (mainly high LT_mat, high A_Mat, low spawn_freq, parental care, low Fec_max…).

Several *in-situ* measurements of environmental conditions are available for each sampling occasion, including the following: temperature (°C), turbidity (mg L^{-1}), height of the water column (m), oxygen concentration (mg.L^{-1}), oxygen saturation (%), conductivity (μS cm^{-1}) and salinity. Both fish and environmental data were averaged over all years and by sampling station.

Table 1 Fish traits compiled in the analysis. Note that some categories might not be relevant for estuarine fishes.

Code	Trait	Definition
Use_guild	Ecological guild	Define the habitat use of the species. FW: Freshwater species; CA: Diadromous species; MA: Marine adventitious species; ER: Estuarine resident species, MS: Marine seasonal species; MJ: Marine juvenile species
Pos_guild	Position guild	Representative position of the species in the water column. P: pelagic, D: demersal, B: benthic
trophic_guild	Trophic guild	Defined by the dominant food item in the species' diet. IB: Bentic invertebrate feeder, IS: Supra benthic invertebrate feeder, Z: zooplankton feeder, O: Omnivorous, F: Piscivorous (including parasitic species), V: Herbivorous
Trophic_level	Trophic level	Quantitative estimate of the species' trophic level (mainly at adult stage; from fishbase.org)
LT_mat	Size-at-maturity (cm)	Total length at which 50% of females become sexually mature
A_mat	Age-at-maturity (year)	Age at which 50% of females become sexually mature
LT_max	Maximum length (cm)	Maximum total length reported in literature
A_max	Maximal life span (year)	Maximum age reported in literature
repro_guild	Reproductive guild	Defined by five states reflecting the level of parental investment; Op: oviparous species with pelagic eggs; Ob: oviparous species with benthic eggs; Ov: oviparous species with adhesive eggs laid in a specific substrate; Og: oviparous species with post-fertilisation parental care of eggs guarding them externally; Os: ovoviviparous species with post-fertilisation parental care of eggs by sheltering them in a part of their body; W: Ovoviviparous
spawn_freq	Spawning frequency	Defined by three states; (1) semelparous species characterized by a single reproductive episode throughout their life; (2) iteroparous species where female spawn one time a year and/or reproductive season extend less than three months; (3) iteroparous species where female are multiple spawners and/or reproductive season is longer than three months.
parent_care	Parental care	Define if the species has or not a parental care comportment
Fec_max	Absolute maximum fecundity (number of eggs)	Maximum number of eggs spawns by a female during a reproductive event.
Egg_size	Maximal egg size (mm)	Maximum diameter of oocyte at the end of the maturation process or before fertilisation
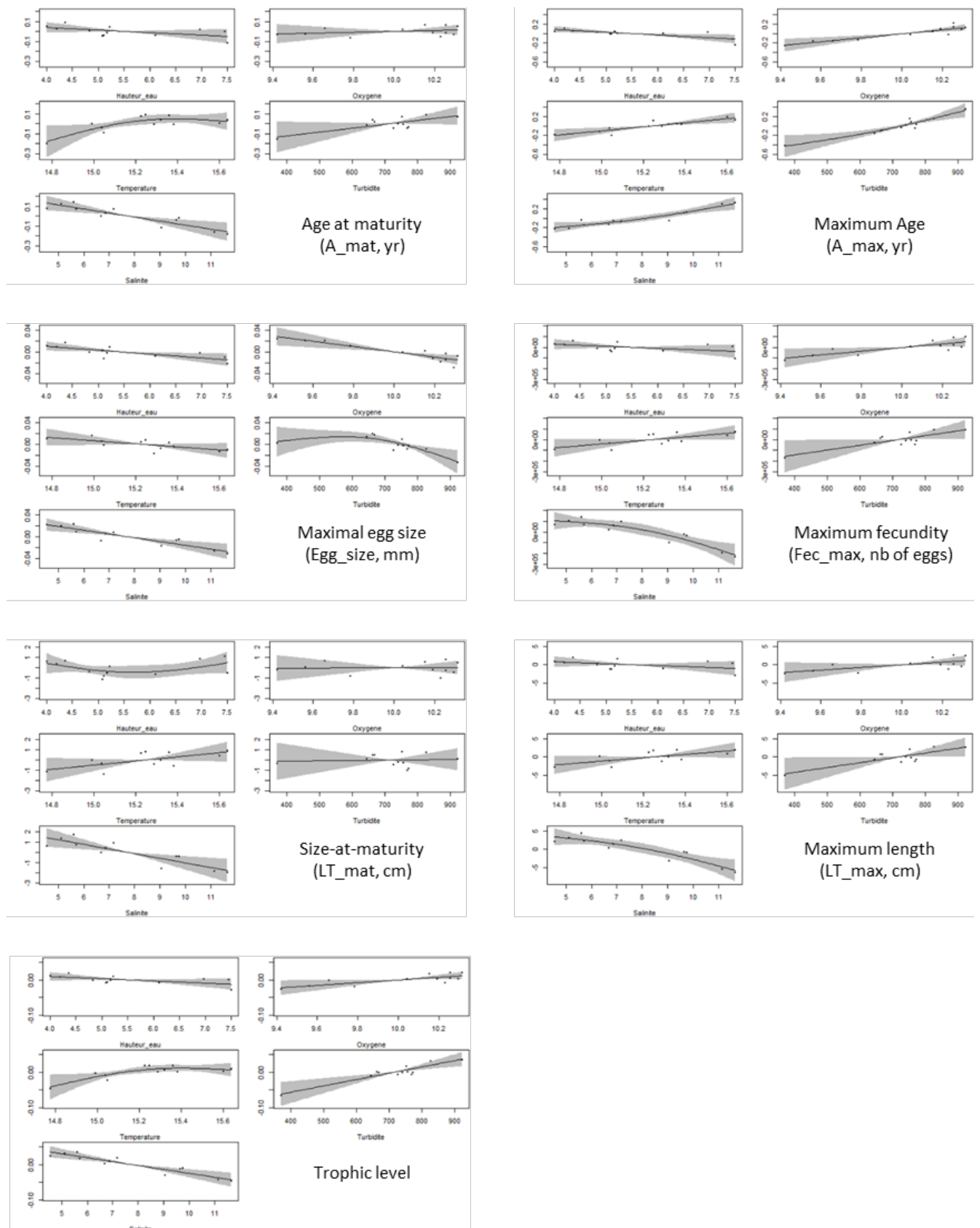
Figure 23 GAM partial smooth illustrating the statistical relationships between selected quantitative fish traits and selected environmental factors measured during sampling. Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

3.3.3. Patterns and drivers of CWM traits

In this section we compare CWM traits over different sites along the estuarine longitudinal gradient in order to identify trait-environments patterns and potential environmental drivers of the community. Only quantitative traits were retained for the CWM analysis: A_mat, A_max, Egg_size, Fec_max, LT_mat, LT_max and trophic levels. In addition, as oxygen concentration (mg L^{-1}) and saturation (%) and conductivity (μS cm^{-1}) and salinity are highly correlated, we only retained 5 environmental parameters for the CWM analysis: temperature (°C), turbidity (mg.L^{-1}), height of the water column (m), oxygen concentration (mg L^{-1}) and salinity. All implemented GAMs were significant (p<0.001) and explained between 87% (for LT_mat) and 96.7% (for TL) of the total deviance. Salinity was demonstrated significant (p<0.05) in all models and highly significant (p<0.01) for most of them. It was the only significant factor in 4 models (A_mat, Fec_max, LT_mat, LT_max) out of 6, whereas all factors were significant (p<0.05) in the model for A_max. Oxygen and turbidity were demonstrated significant for Egg_size and TL respectively. The GAM partial smooth illustrating the statistical relationships between selected quantitative fish traits and selected environmental factors presented (Figure 23), including primarily linear positive and negative relationships, but also a few non-linear declining or saturating responses, such as the fitted relationships between temperature and age-at-maturity and trophic level.

3.3.4. Trait-environment relationships using RLQ

The A RLQ analysis was implemented to investigate the trait-environment relationship in a complementary way. First, we kept the same quantitative traits as in the previous analysis. The total amount of co-inertia was quite low (0.069). The first dimension (RLQ1 axis) contributed to 92% of the explained covariance. Hence, we will only present the scores of the first axis.
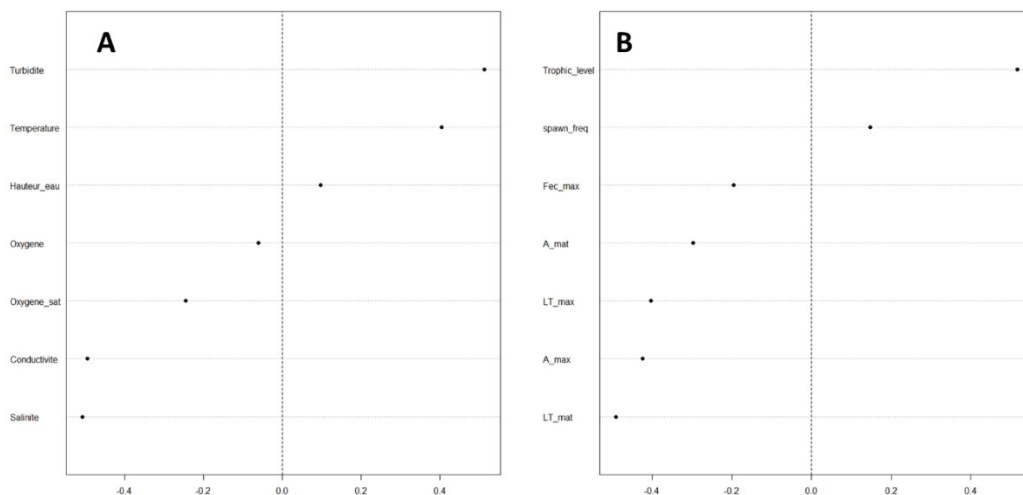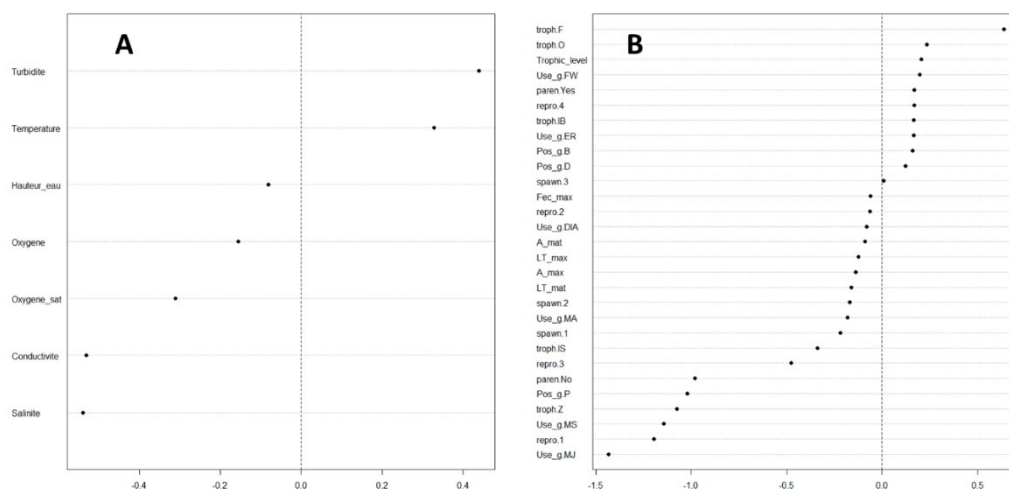

Figure 24 Loadings of traits (A) and environmental variables (B) on the first axis of the RLQ implemented on only quantitative traits. Positive and negative values show the associated scores.

Highest positive scores (> 0.3) on RLQ for environmental variables are associated with high turbidity and temperature while highest negative scores (<-0.4) are associated with low salinity and conductivity (that are highly correlated by nature) (Figure 24A). Furthermore, our results show positive scores for traits associated to slow life history (high trophic level, high spawning frequency) while highest negative scores (<-0.4) are mainly associated with smaller species (low total length and max life span) with rather fast life history (low size-at-maturity) (Figure 24B. This mainly confirm previous results based on the CWM analysis. In a second step, in order to account for both

quantitative and qualitative traits, we implemented a Hill and Smith multivariate analysis on the species-traits matrix instead of a classical principal component analysis. This allows to further consider the different modalities of qualitative traits as a set of quantitative scores. The total amount of co-inertia explained by this second RLQ analysis was much higher and amounted to 0.49 with the first dimension (i.e., RLQ axis) contributing to 93.5% of the total explained covariance. Here again, we will only present the scores of the first axis (Figure 25). By construction, the results for environment is the same as in the previous analysis. Concerning traits, the only high positive score (>0.5) is associated with piscivorous fishes followed by omnivorous ones and highest trophic level. Opposite of the graph, we found the highest negative scores (<-0.5) associated with Marine fish (MJ and MS), oviparous species with pelagic eggs, zooplanktivorous species, pelagic species with no parental care comportment.

Figure 25 Loadings of traits (A) and environmental variables (B) on the first axis of the RLQ implemented on both quantitative and qualitative traits. Positive and negative values show the associated scores.

3.3.5.   Summary of the main findings

- Our results demonstrate a general pattern that could be related to the spatial dynamics of estuarine fish assemblages along the estuarine salinity gradient.
- Indeed, in our dataset, freshwater and diadromous fish, which are more abundant in upstream stations (low salinity, high turbidity), are mainly characterised by higher TL, LT_mat, LT_max, whereas the most abundant marine species associated with downstream sites (highest salinities) are mainly pelagic, zooplanktivorous and are rather associated with fast life history traits.
- However, the estuarine environment is undergoing drastic changes mainly characterised by a 'marinisation of the environment' (mean salinity becomes higher with decreasing river flows). Thus, our results highlighted we can expect that fish assemblages would be more and more characterised by species with fast life history traits (fast growing and short-lived opportunistic marine pelagic species). This could lead to less resilient fish community or, at least, more fluctuating fish assemblages and thus very unstable estuarine food webs.

3.4.   *Macrobenthic communities on Karpathos (SL27)*

3.4.1.   Study organism and area

The Northern Karpathos and Saria MPA is located in the Dodecanese islands (Greece), Eastern Mediterranean Sea, and covers an area of about 154 km^2 (Figure 26) (Nikolopoulou et al., 2021).

Saria is a small island separated from Karpathos by a narrow sea strait less than 100 m wide. The MPA is included in the list of Natura2000 sites (GR4210003) and hosts a rich biodiversity and many endemic species (flora and fauna, including birds). Populations of several charismatic marine species such as the Mediterranean monk seal (*Monachus monachus*) (MOm, 2009), the dolphin *Tursiops truncatus* and the marine turtles *Caretta caretta* and *Chelonia mydas* are present in the MPA. Tristomo Bay is an enclosed highly productive fishing area in the MPA with extensive *Posidonia oceanica* and *Cymodocea nodosa* meadows surrounded by hard substrate. Tristomo gulf is protected by sea waves and is characterised by very limited anthropogenic activity, thus it may act as a climate refugium and a hotspot for preservation and conservation of several marine species, from schools of fish to the critically endangered noble pen shell (*Pinna nobilis*) and the Noah's Ark shell (*Arca noae*). *P. oceanica* is spread around the coasts of Karpathos and Saria. The meadows are healthy, existing for about a decade and they are hosting rich populations of invertebrates. The region is close to the Suez Canal, which is the main point of entrance for invasive alien species (IAS) in the Mediterranean. Thus, the islands of Karpathos and Saria are characterized by the high prevalence of marine IAS, which form dense populations. Examples of such IAS are the seaweed *Halophila stipulacea*, the lionfish (*Pterois miles*) and the invasive long-spined sea urchin (*Diademasetosum*). Although the number of non-native species, such as *Caulerpa taxifolia* and *Halophila stipulacea*, are increasing in the area, *P. oceanica* has been proven so far, a good competitor maintaining the ecosystem balance. These habitats provide a range of services, such as: a) provisioning services (i.e., dead leaves can be used in industry and agriculture); b) regulation and maintaining services (i.e. seawater is purified by filtration, the leaves reduce water turbidity, offer shelter and nursing habitat, protect the seabed from erosion and support nutrient cycling and oxygenation; and c) cultural services (preservation of the underwater cultural heritage, diving tourism, marine environmental education).
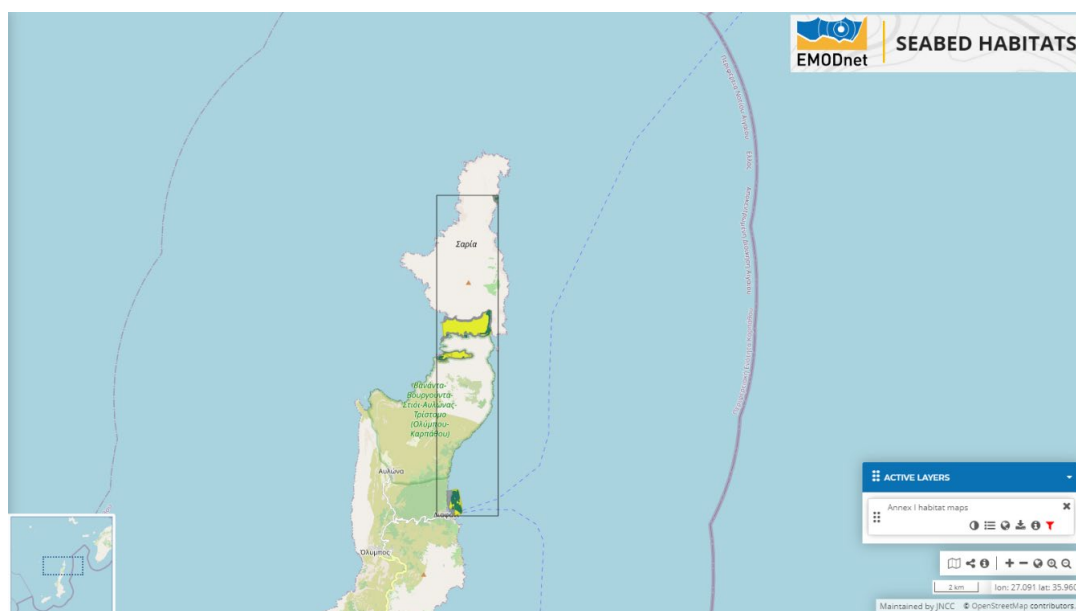
Figure 26 Map of the northern Karpathos and Saria MPA (Greece).

The area has a significant archaeological value due to the 7th-10th century AC settlements that are present, while the Ephorate of Underwater Antiquities performs field research as there are remains which are yet to be studied. The Management Agency of Dodecanese Protected Areas (formerly Management Agency of Karpathos-Saria) was established in 2002, and its primary objective is the management, protection and conservation of the species and habitats of the MPA. Since 2022 the Management Agency of Dodecanese Protected Areas operates under the central management of the

Natural Environment and Climate Change Agency (N.E.C.C.A). The aim of this study is to identify the key response traits of macrobenthic communities in the Storyline area of Northern Karpathos and Saria MPA (#27) allowing them to occupy their respective habitats and areas and investigate their links to potential environmental characteristics, illustrating the trait-environment relationships.

3.4.2. Data description

We compiled available data on soft- and hard bottom macrobenthic communities, collected in 2017-2020. Data on hard bottom macrobenthic communities were based both on samples (5 replicates) scraped from the rock surfaces, as well as on the presence of species confirmed by underwater photography and visual census. Data on soft bottom macrobenthic communities were derived from sediment samples collected using cylindrical corers (3 replicates). Sampling was conducted in July of 2018. Abundances of the retrieved taxa were averaged between the replicate samples. Two matrices were created, one containing abundance data for molluscs and polychaetes (161 taxa) and one containing presence absence data for molluscs, polychaetes, crustaceans, algae, ascidians, bryozoans, cephalopods, echinoderms, fish, hexacorallians, hydrozoans, phanerogams and sponges (308 taxa). The taxonomy of the reported taxa was verified and whenever needed updated according to the World Register of Marine Species ([WoRMS](#)).

To represent the general ecology and life history of the species the following 6 traits and sub-traits (modalities) were selected: Mobility (sessile/semi-mobile, mobile), Feeding type (photoautotroph, deposit feeder, grazer/herbivore, predator, parasite, scavenger, suspension feeder), Reproduction (gonochoristic, hermaphrodite, asexual), Ecosystem engineering (bioturbator, structural engineer, light engineer, chemical engineer, none), Maximum body size and Fecundity. Fecundity data were scarce, and we were not able to retrieve them for all species (with the exception of fish species) and also, they were not uniform in units, thus we decided to exclude Fecundity from further analyses.

To characterize the environmental conditions, data for the following variables for both the water column and sediments were collected on the basis of *in-situ* sampling:

- temperature
- salinity
- oxygen (water column only)
- Chlorophyll a concentrations
- Phaeopigments
- chloroplastic pigment equivalents (CPE)
- particulate organic carbon (POC)
- phosphate concentration
- nitrate concentration
- ammonium concentration
- silicate concentration
- redox potential (sediment only)

3.4.3. Trait-environment relationships using RLQ

The RLQ analysis was performed in four successive steps: 1) a correspondence analysis (COA) on the **abundance** matrix (**L**) of the 161 taxa of molluscs and polychaetes; 2) a multivariate analysis on the **trait** matrix (**Q**) using column weights from step 1, which can be either a) a Principal Component Analysis (PCA) on the numeric trait matrix; b) a Multiple Correspondence Analysis (MCA) on the categorical trait matrix; c) a Hill and Smith analysis on the mixed trait matrix; 3) a multivariate

analysis (PCA) on the **environmental** matrix (**R**) using row weights from step 1; 4) the RLQ analysis comparing the co-variance of the three previous steps with co-inertia analysis.

Since our numeric trait matrix contained only one trait, we focused on the categorical and the mixed trait matrix. The RLQ analysis with the maximum value of the total amount of co-inertia was the one performed with the mixed trait matrix; co-inertia amounted to 4.249 with the first dimension (i.e., RLQ axis) contributing to 86.93% of the explained covariance. The RLQ analysis performed with the categorical trait matrix resulted in total amount of co-inertia 1.039 and project inertia on the first axis contributing to 88.32% of the explained covariance. The second axis in both cases explained less than 10% of the covariance. Hence, we only present the scores of the first axis and using the RLQ on the mixed trait matrix. In terms of traits, RLQ1 demonstrates positive scores for traits associated to ecosystem engineering and mobility and negative score for traits associated to feeding type and reproduction (Figure 27). Interestingly, the top taxa with positive scores are molluscs, whereas the top taxa with negative scores are polychaetes (Table 2).
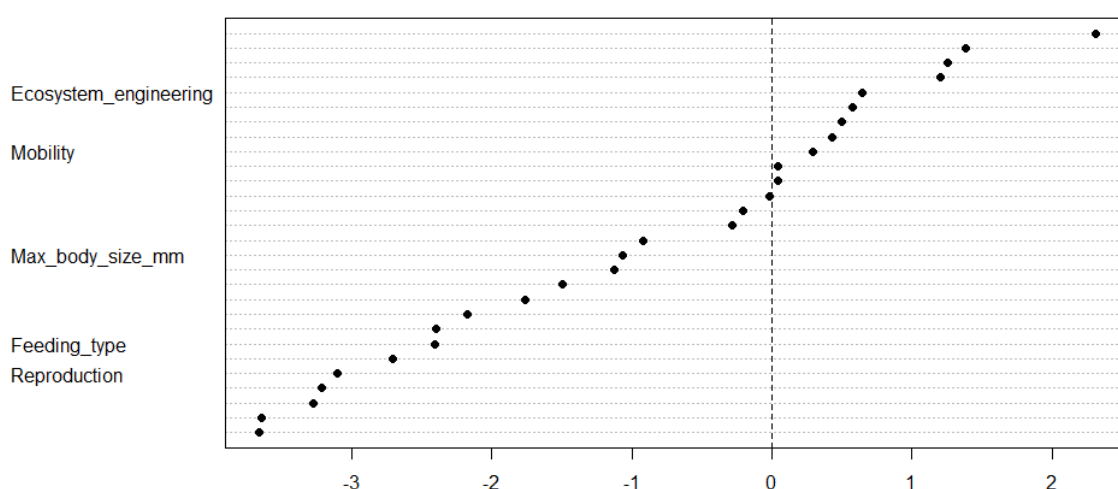
Figure 27 Loadings of traits on RLQ1. Positive and negative values show the associated scores.

Table 2 Taxa with top positive and top negative scores RLQ1.

Taxa with positive scores	Taxa with negative scores
Aplysia depilans	Maldanidae
Limidae	*Cirratulus cirratus*
Williamia gussoni	Spionidae
Leptochiton scabridus	*Capitella capitata*
Scissurella costata	*Capitella giardi*
Smaragdia viridis	*Prionospio perkinsi*
Cerithium scabridum	*Prionospio steenstrupi*
Steromphala albida	*Aonides oxycephala*
Eulimella ventricosa	*Caulleriella alata*
Cylichna alba	*Cirriformia tentaculata*

In terms of environmental variables, RLQ1 shows a gradient between warmer, higher nutrient waters and colder, lower nutrient waters (Figure 28). Interestingly, all the sampling sites with positive scores are located in the eastern part of the Karpathos island, whereas sampling sites with negative scores are located in the western part of the island (Table 3).
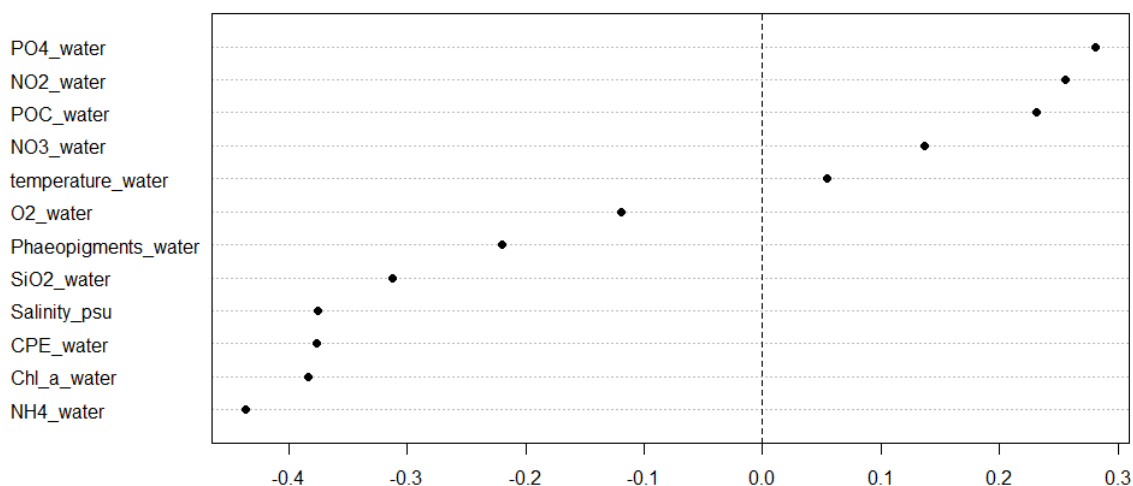
Figure 28 Loadings of environmental variables on RLQ1. Positive and negative values show the associated scores.

Table 3 Sites with positive and negative scores RLQ1.

Sites with positive scores	Sites with negative scores
Diafani (Hard substrate)	Tristomo Middle (Soft substrate)
Diafani (Soft substrate)	Tristomo Outside (Hard substrate)
Saria (Soft substrate)	Tristomo Outside (Soft substrate)
	Astakidopoulo(Hard substrate)
	Steno (Soft substrate)

3.4.4. Trait-environment relationships using HMSC

This section presents results of joint species distribution model runs using HMSC aiming to investigate species response to the environment conditioned on their traits. The model requires the same basic input as in the RLQ analysis (i.e., the three matrices of species abundances (or occurrences), traits and environmental variables per grid cell), but also use a matrix of pair-wise species relatedness (here derived based on taxonomy, rather than phylogeny), as well as spatial random effects (here grid cells). The model was setup, fitted and cross-validated using taxa presence-absence as input, using a probit link function (308 taxa from all the investigated taxonomic groups).

The fitted model demonstrated a good performance (mean AUC = 0.96) with an average explained variance of observed species occurrences amounting to 63.6%. A variance partitioning analysis showed that almost all of the explained variance could be attributed to the set of environmental predictors, albeit with differences between individual species (Figure 29). The main environmental drivers were phosphate and nitrite.
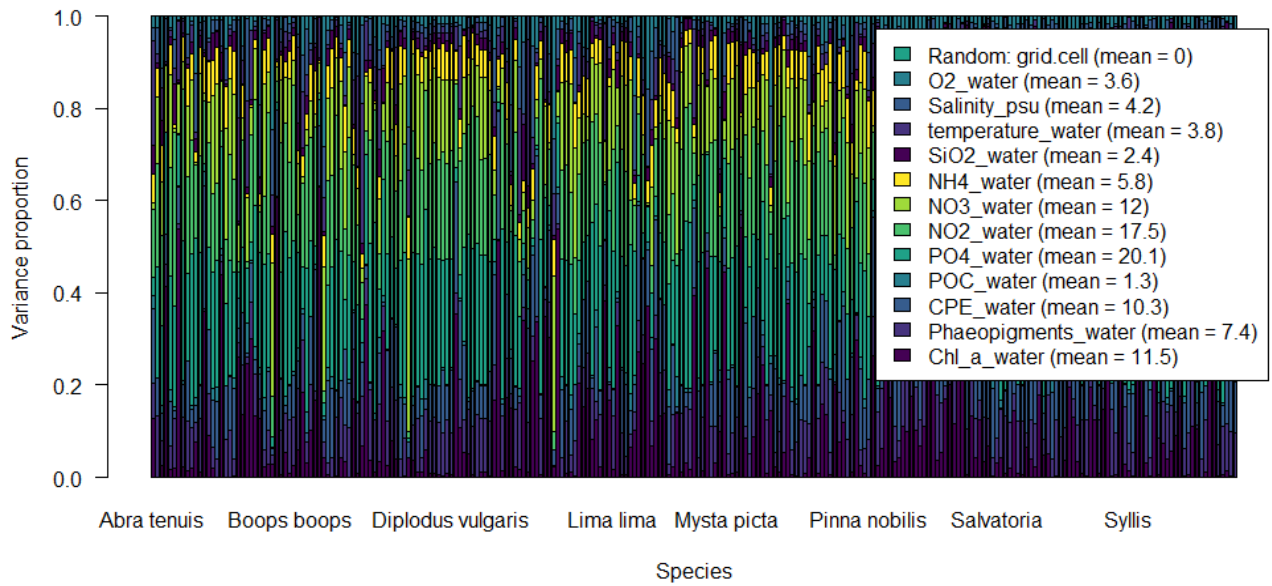
Figure 29 Variance partitioning of fixed and random effect on species occurrences, as well as the associated mean values across species for each predictor (see insert).

Interestingly, the traits contribute substantially to the variation in species occurrences. This is reflected by several pair-wise relationships between traits and environmental variables with high statistical support, such as between nitrate and ammonium with maximum body size (Figure 30).
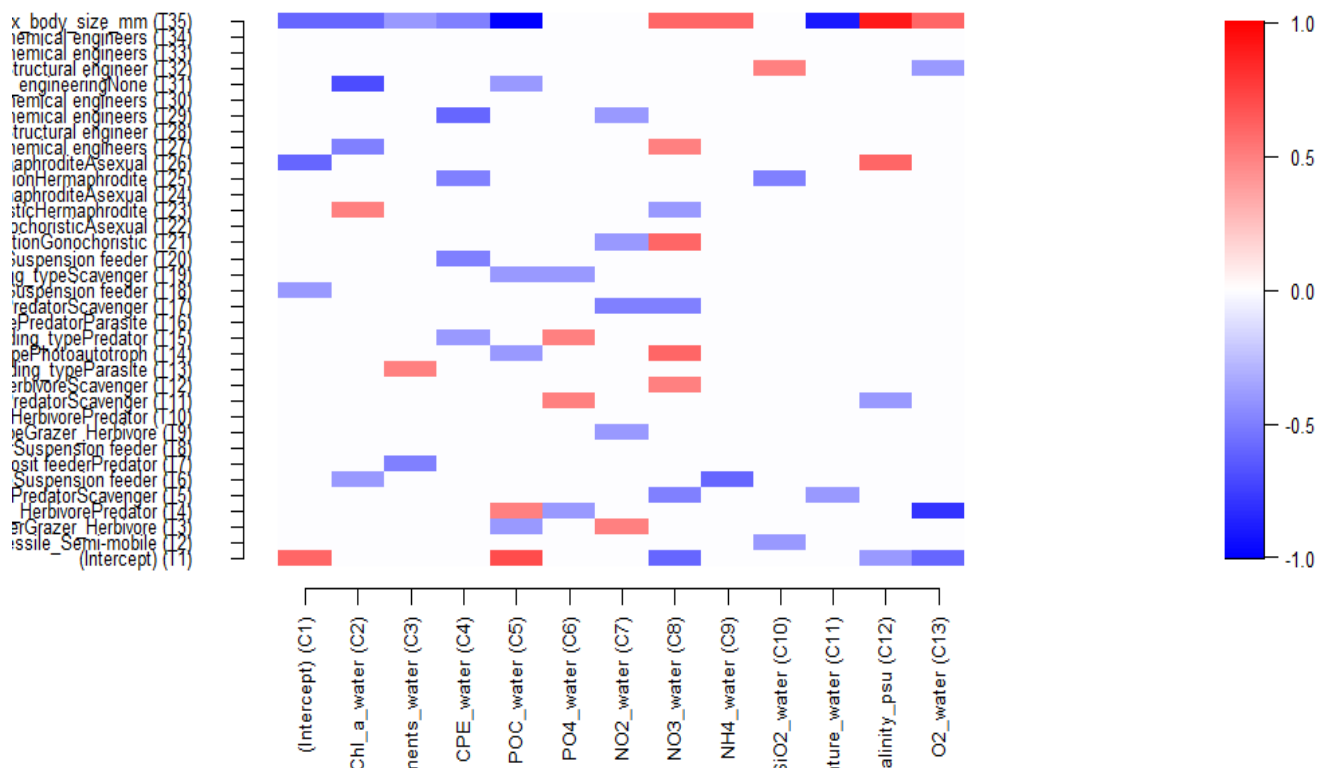
Figure 30 Pair-wise relationship between traits and environmental variables, illustrated by the mean posterior estimates of the gamma parameters with a support level p>0.7. Red and blue colours indicate positive and negative parameter values, respectively.

Overall, the traits explain 14.7% of variation in species occurrences. Also, the traits explain most out of the variation in species responses to all the environmental variables, with ~22% for POC in the water column, ~20% for phosphate, ~16% for chlorophyll a in the water column and ~12% for nitrite.

The realized trait-environment responses show similar relationships as observed using RLQ, such as a negative relationship between maximum body size with water temperature (Figure 31).
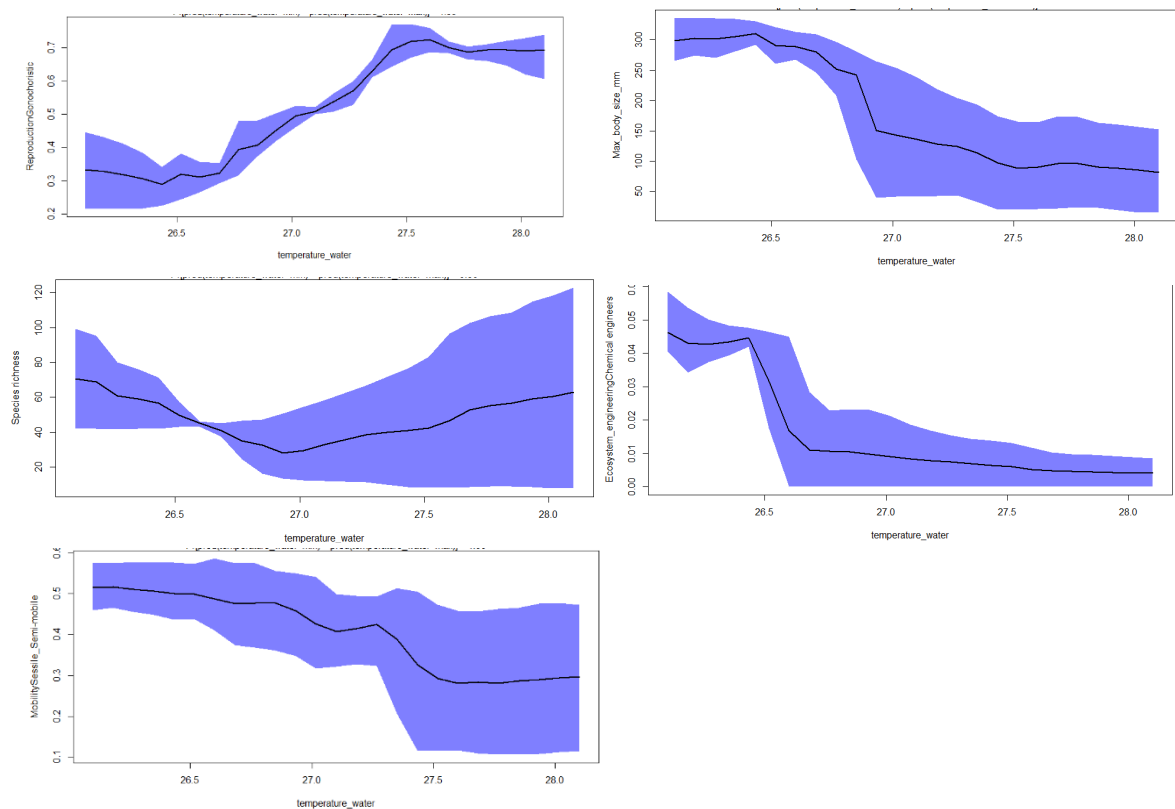
Figure 31 Predicted community trait values across the entire range of observed environmental conditions using water temperature as an example. Black lines and blue shaded areas show means and 95% confidence intervals of model predictions, respectively

3.4.5.   Summary of main findings

● The investigation of trait-environment relationship for macrobenthic communities in the Northern Karpathos and Saria MPA show broadly consistent results across the two methods, indicating that patterns and findings seem robust to model choice.
● The primary traits explaining the spatial occurrence and/or abundance patterns of species are mainly associated with ecosystem engineering and mobility, indicating that these are the primary "response" traits of macrobenthic communities, and more specifically of molluscs and polychaetes.
● The key environmental variables explaining the distribution of species are primarily associated with nutrients (POC, phosphate, chlorophyll a and nitrite) and water temperature.

3.5.   Benthic communities in the Tuscan Archipelago (SL28)

3.5.1. Study organism and area

The study was done in the Tuscan Archipelago (TA), along the coast of the Island of Capraia, (43.048 N, 9.828 E), about 40 miles off the west coast of Italy (north-west Mediterranean). Low shore assemblages (0.4 –0.4 m above/below mean low water level) are composed by the canopy-forming fucoid *Ericaria amentacea* (previous name *Cystoseira amentacea Bory var. stricta Montagne*) (Figure 32) which alternate with patches occupied by algal turfs, encrusting coralline algae or bare rock varying in size between tens and hundreds of cm^2 (Bulleri et al., 2002; Tamburello et al., 2013).

Figure 32 Intertidal forests formed by Ericaria amentacea along the coast of Capraia Island.

3.5.2. Sampling and data description

Assemblages were sampled annually in summer, from 2007 to 2016, in 64 contiguous quadrats, 50 x 50 cm in size, that were marked permanently using epoxy putty on two randomly chosen shores that were 73 and 85.5 m in length (Tamburello et al., 2013). There was a total of 128 plots. The abundance of sessile macroalgae and invertebrates was assessed visually in 20 x 20 cm quadrats that were placed in the middle of each 50 x 50 cm quadrat along each transect. Sampling was carried out using a plastic frame divided into 25 sub-quadrats and giving each taxon a score of 0 (absent), 1 (occupation of 1/4 of the sub-quadrat), 2 (occupation of 1/2 of the sub-quadrat), 3 (occupation of 3/4 of the sub-quadrat) or 4 (occupation of the entire sub-quadrat) to each sub-quadrat. The final percentage covers were calculated by summing over the 25 sub-quadrats (Dethier et al., 1993). Our dataset included 61 taxa.

In order to describe the general ecology and life history of the species, in terms of their feeding, dispersal, body size and shape, we took into account the following life-traits:

- Feeding habit
- Body size
- Flexibility
- Adult potential dispersal
- Life-span
- Body complexity

For most of the taxa, information on traits was not readily available from one single database and it had to be obtained from different sources, including scientific publications and dedicated websites, details of which are provided in (see Table S1 in Appendix 1). In the case in which no information could be retrieved, we proceeded to the scoring of traits using expert judgement. In order to determine trait-environment relationships, we selected the following ten environmental variables:

- Wave-exposure
- Maximum wave-exposure
- Mean Chl concentration
- Maximum Chl concentration
- Minimum Chl concentration
- Standard deviation of Chl concentration
- Mean seawater temperature
- Maximum seawater temperature
- Minimum seawater temperature
- Standard deviation of seawater temperature

Temperature and chlorophyll concentration data for the period of interest were extracted from NCEP Global Ocean Data Assimilation System (GODAS 1980-2020) at a spatial resolution of 0.05° (about 4 x 4 km). Wave exposure was extracted from a wind wave numerical model that was developed at the scale of the whole Mediterranean (Bulleri et al., 2018).
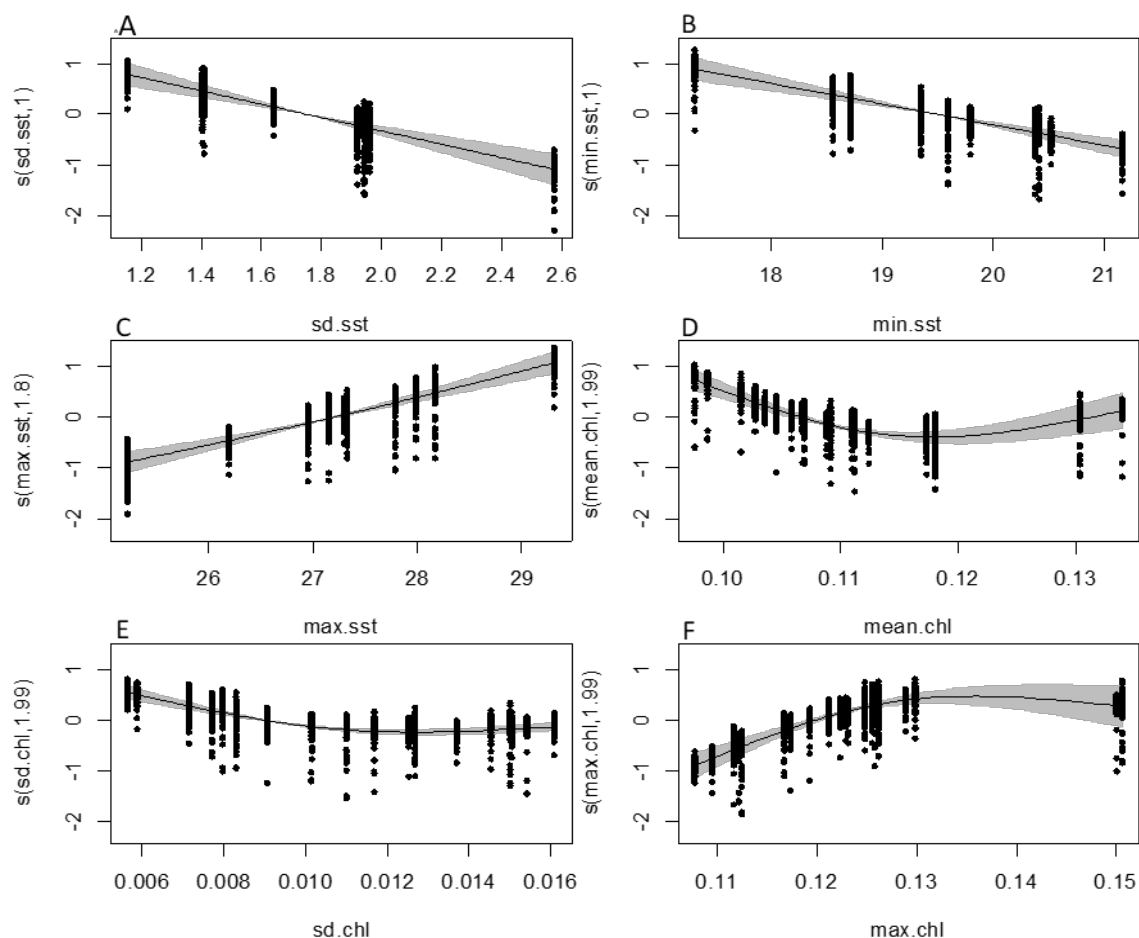
Figure 33 GAM partial smooth demonstrating the statistical relationships between CWM life span and water temperature ((A) standard deviation, (B) minimum and (C) max) and Chlorophyll concentration ((D) mean, (E) standard deviation and (F) maximum). Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

3.5.3. Patterns and drivers of CWM traits

The Community Weighed Mean (CWM) represent the average of the values of traits across taxa in a community, weighted by the relative abundance of each taxon. Given that our dataset was limited to two shores only 100s of m apart, we did not assess spatial variations in CWM, but only variation through time. Trait-environment relationships were modelled at the community level (CWM) using GAMs. Maximum wave exposure was fitted as a fixed term as it was characterized by two levels, while the other environmental variables were included as smoothers. Models for life span and body size explained 19% and 16% of total variation, respectively, while those for other traits explained little variation. The best fitting GAM for lifespan, as indicated by the lowest AIC value, retained minimum, maximum and standard deviation of SST and mean, maximum and standard deviation of chlorophyll concentration (Figure 33). In particular, it showed a significant increasing linear relationship between CWM and maximum SST and decreasing negative relationships with both minimum and standard deviations of SST. Relationships with Chlorophyll content, either mean, maximum and standard deviation were non-linear.
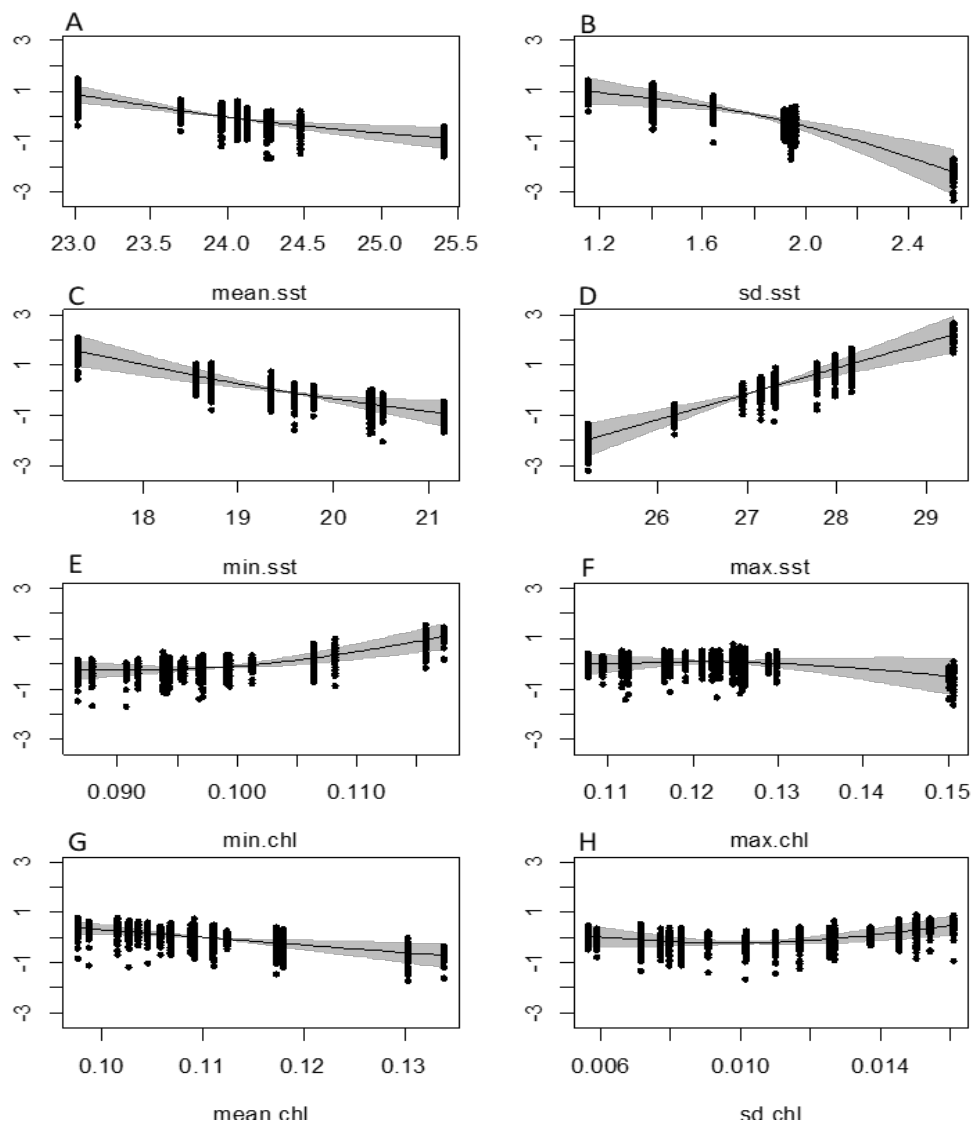
Figure 34 GAM partial smooth demonstrating the statistical relationships between CWM body size and A) mean, B) standard deviation, C) minimum and D) max temperature and E) minimum, F) maximum, G) mean and I) standard deviation of chlorophyll concentration. Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

The best fitting GAM for body size was the one that retained all the environmental variables. The CWM of body size increased with wave-exposure and there were significant decreasing relationships between CWM and minimum, mean and standard deviation of SST and a positive relationship between CWM and maximum temperature (Figure 34). There were also non-linear relationships between CWM and minimum, maximum, mean and standard deviation of chlorophyll concentration.

3.5.4. Trait-environment relationships using RLQ

The total amount of co-inertia explained by the RLQ was 0.124, with the first dimension (i.e., RLQ axis) contributing to 90.4 % of the explained covariance. The RLQ1 show a positive score only for the feeding habit, that is with traits and species associated with suspension feeders, grazers and predators and negative score for body complexity and life span, that is with trait and species characterized by crustose, flat tubular or filamentous forms and short lived (Figure 35.A). Scores for other traits, such as body size, flexibility and adult dispersal, although negative, have very low values. In terms of environmental variables, the RLQ1 shows positive scores for wave exposure and maximum wave-exposure, indicating that our study site is swept by waves (Figure 35.B). All other environmental variables have yield scores close to zero.
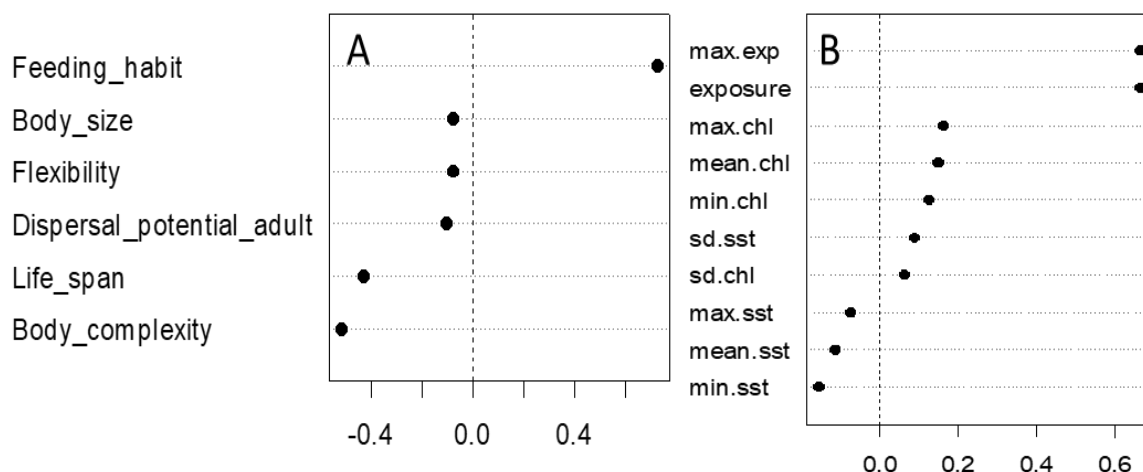
Figure 35 Loadings of traits (A) and environmental variables (B) on RLQ1. Positive and negative values show the associated scores.

3.5.5. Trait-environment relationships using HMSC

The HMSC model on fitted abundances showed an average explained variance of observed taxa abundances of about 6 %. However, the habitat-forming species (i.e., *E. amentacea*) explained 30.2 % of variance. A variance partitioning analysis show that a large amount of variance (72.8 %) in species abundance was explained by random factors, both describing spatial (i.e., the Plot and the Shore) and temporal (i.e., the Year) sources of variation. The remaining part of variation was mostly explained by two environmental predictors, namely maximum exposure and mean SST, although with differences between individual taxa (Figure 36).
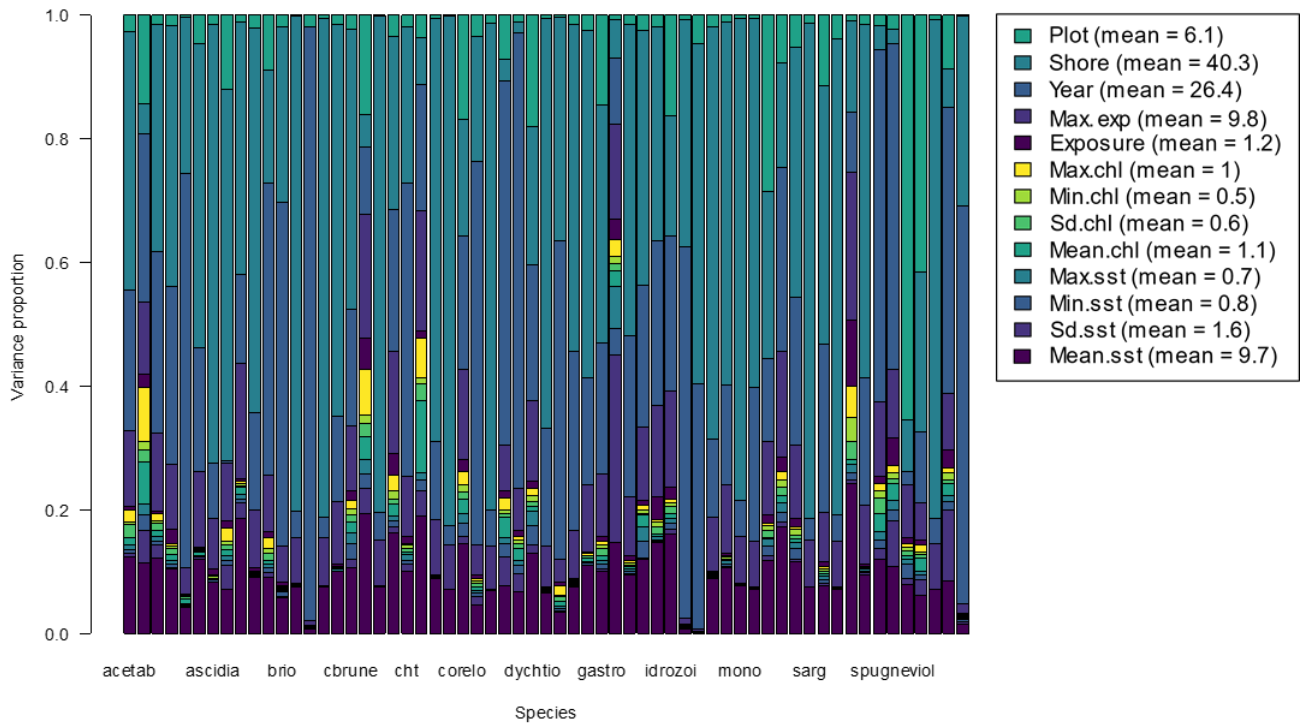
Figure 36 Variance partitioning for a sample of species. The legend shows the percentage of explained variation across species for each predictor (fixed and random).
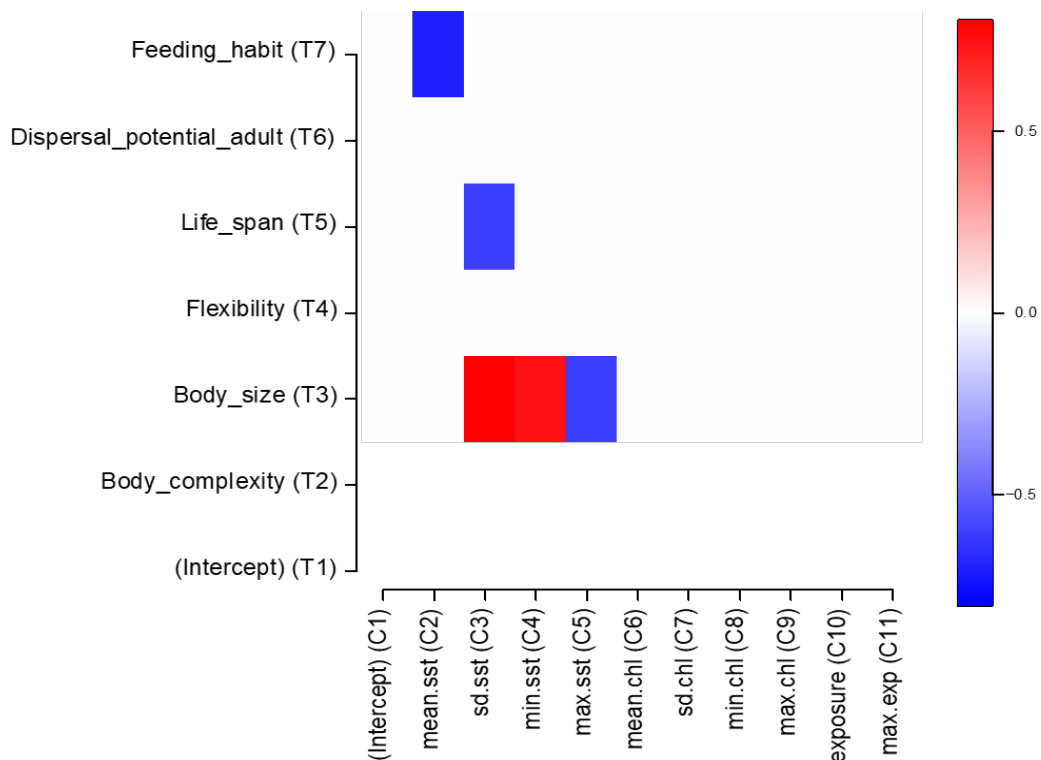
Figure 37 Pair-wise relationship between traits and environmental variables, illustrated by the mean posterior estimates of the gamma parameters with a support level p>0.9. Red and blue colours indicate positive and negative parameter values, respectively.

Traits regulate the variation in species abundances, as shown by statistically supported relationships between traits and environmental factors (Figure 37). For instance, a positive correlation between body size and the minimum and standard deviation of SST and a negative with maximum SST indicates that larger bodied species are more frequent at lower seawater temperatures. Likewise, primary producers and suspension feeders are more frequent at higher values of mean SST, while grazers and predators at high values of mean SST. Finally, large variability in SST appears to reduce the abundance of taxa characterized by short lifespan.

3.5.6. Summary of key findings

- The primary traits explaining the spatial occurrence and/or abundance patterns of taxa are mainly associated with feeding habit, lifespan, body size and complexity and fecundity, indicating that these are the primary "response" traits in intertidal benthic assemblages dominated by the canopy-forming species *Ericaria amentacea*.
- The key environmental variables explaining the distribution of taxa are primarily associated with wave exposure and seawater thermal regime (i.e. mean, minimum and maximum SST) and chlorophyll content. Other environmental factors not identified by our study could be, however, important drivers of species life-traits. This suggests that temperature is not the overarching factor regulating traits distribution in these assemblages.
- Our results indicate that life-traits are important drivers of the response of low-shore communities of rocky shores to changes in environmental conditions

3.6.   Marine Forests in the Northern Iberian Peninsula (SL 21,23)

3.6.1.   Study organism and area

The study area encompasses intertidal macroalgae communities inhabiting the northern Portuguese coast within a maximum 100km distance between shallow rocky shores (Fig. 38). Even though the area covers a short latitudinal gradient, differences in environmental variables are present, in part, as a consequence of the upwelling processes observed on this coast. The Iberian upwelling provides cold and nutrient-enriched oceanic waters during the summer season. This influences the diversity and composition of the seaweed communities spatially, with several boreal species, such as *Laminaria hyperborea, Saccharina latissima, Ascophyllum nodosum* or *Fucus serratus* having their southern distributional limits at these northern Portuguese regions. These species are collectively known as marine forests and are widely recognized by their several ecosystem services (Piñeiro-Corbeira et al. 2022), including climate change mitigation owing to its blue carbon potential (Duarte et al. 2022). Nevertheless, the fragmentation of populations has been reported (Casado-Amezúa et al. 2019), mostly linked to recent climate change (Franco et al. 2018). This study aims to identify key traits of macroalgae species, including marine forest ones, that allow them to occupy respective habitats and areas and investigate their links to potential environmental characteristics illustrated by the trait-environment relationships, considering spatial and temporal changes as a whole.
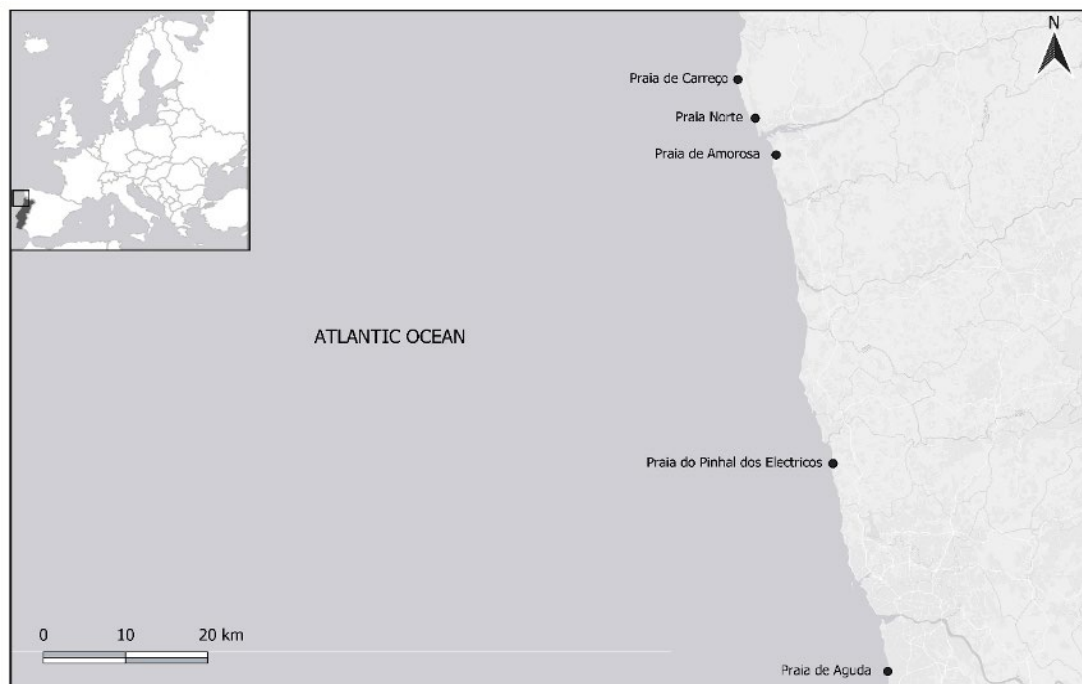
Figure 38 Study area and sampling locations within the Northern Portugal coast.

3.6.2.   Data description

We collected data from five rocky intertidal macroalgal communities on the northern coast of Portugal in two sampling time periods, one from 2006 to 2008 and a more recent one from 2019 to 2022 (6 annual campaigns in total). Data were collected in the late winter (March/April) to ensure standardization across time periods and always during low tide. We identified the species to the lowest taxonomic level possible *in situ* and accessed their cover percentage within 50x50 cm quadrats (0.25 m2). Fifteen quadrats were haphazardly selected per beach/rocky shore per year.

Table 4 List of seaweed traits and respective categories for the nominal traits.

Traits	Categories
Vertical space occupied	Canopy Subcanopy Turf Encrusting
Presence of pneumatocysts	1 (yes); 0 (no)
Type of holdfast	Rhizoids Bulbous Disc
Body complexity	Crustose Erect Foliose Filamentous Globose Shrublike
Life span	Annual Perennial
Life cycle	Diplontic Haplodiplontic
Capacity of asexual reproduction	1 (yes); 0 (no)
Fertilization	Water column Female gametophyte
Maximum Depth	<10m 10-20m 20-30m >30m
Environmental position possibilities (within Epilithic, Epiphytic, Epiflora or Epizoic, and unattached)	1 (Epilithic or Epiphytic) 2 (2 positions within Epilithic, Epiphytic, Epiflora or Epizoic) 3 (3 positions within Epilithic, Epiphytic, Epiflora or Epizoic) 4 (possibility of Epilithic, Epiphytic, Epiflora or Epizoic positions) Possibility of Unattached position
$CaCO_3$ content presence	1 (yes); 0 (no)

We selected eight categorical nominal traits and three binary (0 or 1, Table 4) that represent the species' general ecology and life history considering their morphology, life cycle and growth,

reproduction, dispersal and colonization, interactions with the environment and matter and energy flow. The trait information was obtained from multiple online databases, including the World Register of Marine Species (WORMS), scientific bibliography and complemented by expert judgement. For an overview of definition of each trait category please see Vranken et al. (2022).

We collected data from the *FutureMARES* WP2 models to characterize the environmental conditions, considering the average of the 12 months prior to the sampling and 5m depth. From the available dataset, the following variables were considered as potentially affecting the distribution of macroalgae species:

- SST: sea surface temperature in °C
- Chl *a*: Chlorophyll *a* concentration (in *mg.m*−3)
- pH: pH values
- O2: dissolved oxygen

3.6.3. Patterns and drivers of CWM traits

This section investigates the patterns and underlying environmental drivers of macroalgae CWM traits, i.e., characterizing the mean trait value of each community weighted by the relative abundances of species. We selected the Subcanopy category from the Vertical space trait and Asexual reproduction possibilities as examples since these were among the dominant categories across space/years, together with the Turf category for the Vertical space trait and Unviability of asexual reproduction. As several of the marine forest species present in the Northern Iberian communities, with their southern distributional limit, are canopy ones, we also include information on this CWM, despite not being within the dominant ones for our datasets.

These traits have different ecological relevance, as vertical space is related to body size and growth, while the possibility of asexual reproduction relates to reproduction and dispersion (Martini et al., 2020), but also reflect contrasting strategies. Both Canopy and Subcanopy species denote higher structural complexity and investment in biomass growth. In comparison, a possibility of asexual reproduction is a sign of lower reproduction complexity that could, however, be advantageous under stressful conditions and foment dispersion. First, we will provide an overview of the spatial and temporal changes in the selected CWMs considering time periods (2006-2008 and 2019-2022), then their relationships with the environmental drivers based on models. The spatial patterns of the CWM for the selected traits showed higher spatial variability than temporal throughout the study (Fig. 39 and Fig. 40).

For the Subcanopy, there was an increasing trend from the north to south rocky shores, which increased over time for one of the rocky shores at the south. Canopy was never a dominant category in the communities (Fig. 39). Its trends remained within similar values over space and time (Fig. 39 and Fig. 40), with a slight decrease over time (Fig. 39). For the Asexual reproduction possibility, we found an opposite spatial trend when comparing both time-periods, as this trait increased over time for the rocky shores at the north and decreased for the ones at the south. Still, overall, asexual possibilities are more present in northern locations.
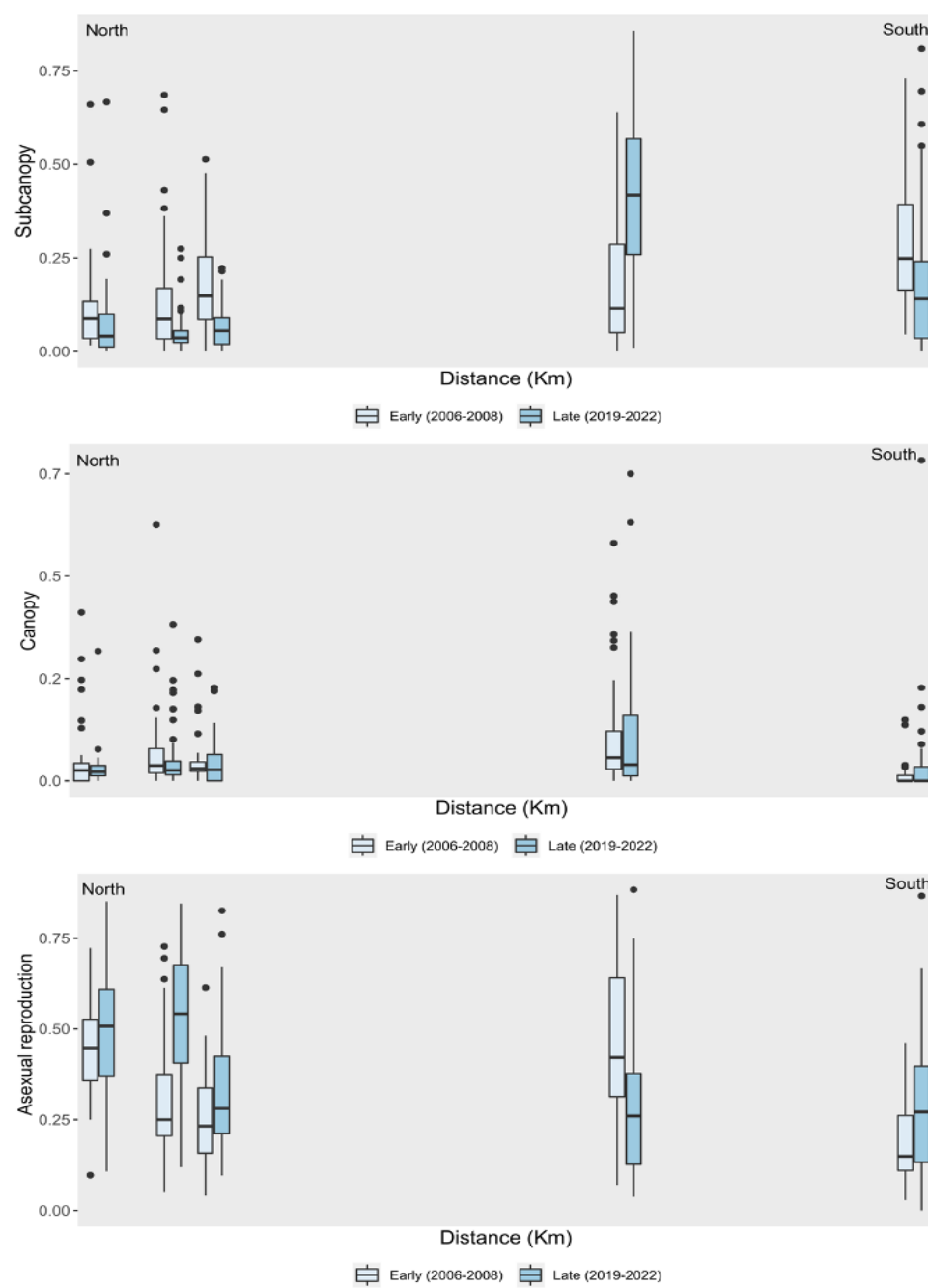
Figure 39 CWM trait values for Canopy and Subcanopy trait categories and for Asexual reproduction trait possibility of seaweed intertidal communities across the study area and two time periods, from 2006 to 2008 and from 2019 to 2022. (For the trends per year, please see Fig. 40).

The CWM results show that spatial differences between communities are present even though our spatial scale is small (± 100km). Furthermore, although temporal differences are minor (Fig. 40), they are also present, suggesting changes in the community and functional structure along a temporal scale.
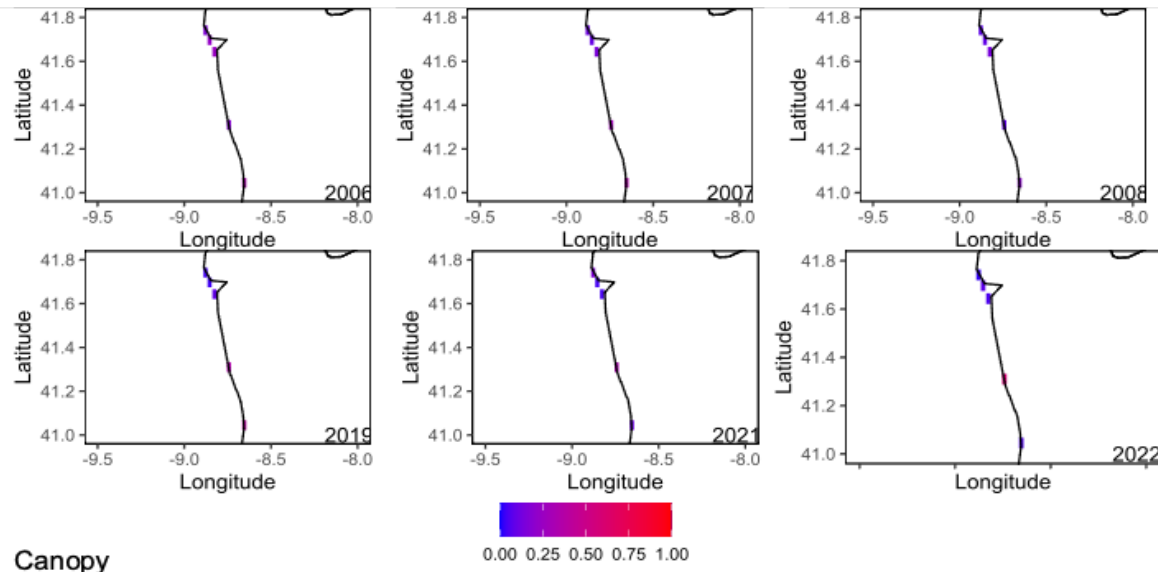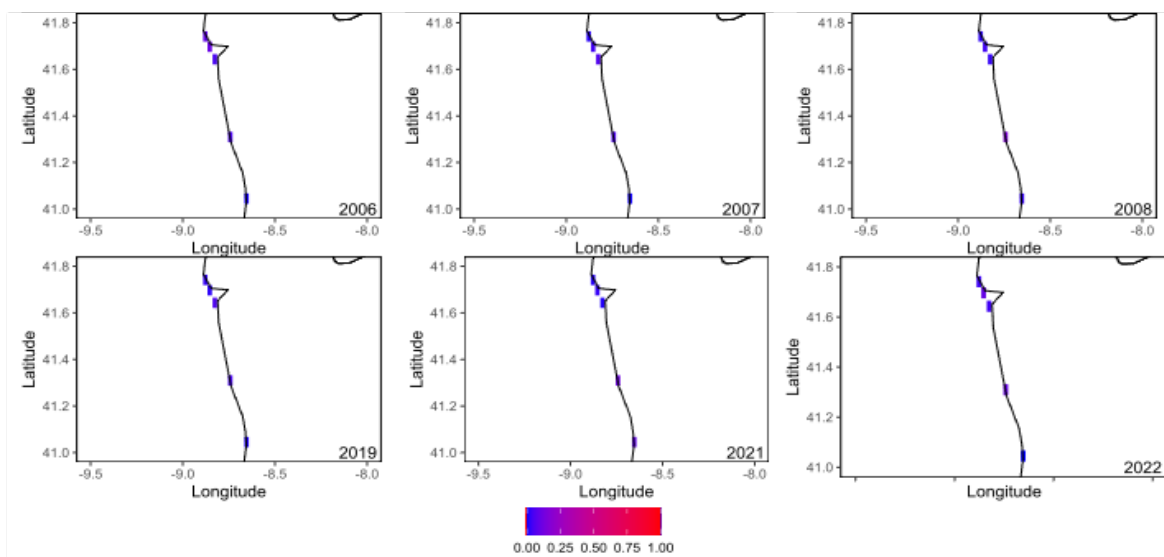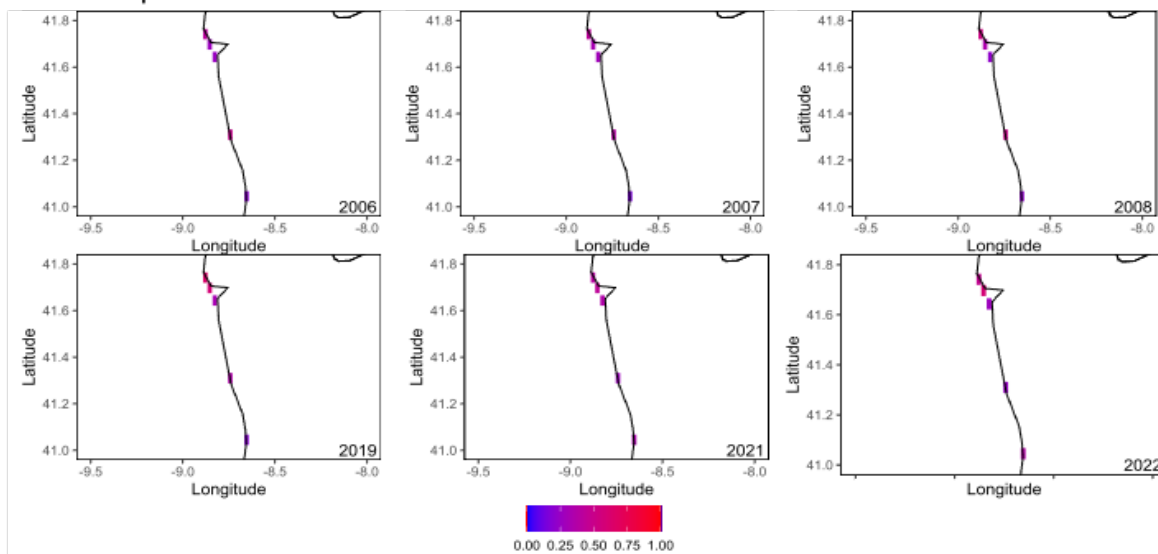
Figure 40 Maps of CWM Subcanopy and Canopy trait categories and for the Asexual reproduction possibility within the seaweed intertidal communities across the study area, through time.

Since methods in the following sections are capable of jointly investigating and illustrating multiple trait-environment relationships, this section will report on individual response of CWM traits (here using the selection above) to the environmental predictors using both GAM or GLM's and Random Forests. The GLM's were applied whenever the distribution of the response variables (CWM as percentage data) was highly skewed, and considered a quasibinomial distribution due to overdispersion.
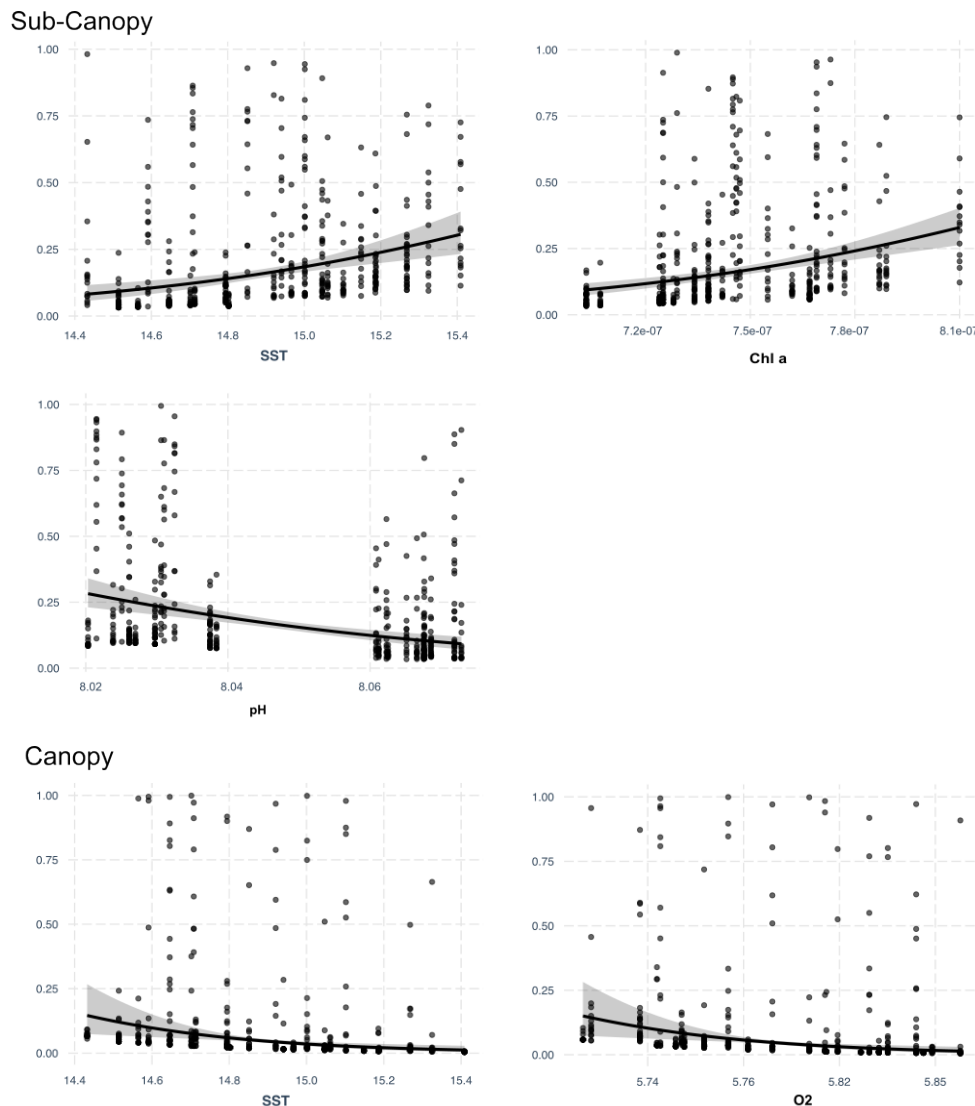
Figure 41 Partial plots demonstrating the statistical relationships between the trait categories Sub-Canopy and Canopy and their significant predictors, based on the GLM models. Black lines show the fitted line by the models and grey shaded polygons the 95% confidence interval.

After a formal model selection routine, the final GLM for Subcanopy patterns identified temperature (SST), Chlorophyll *a* and pH as significant predictors. However, the model explained only 14.5% of the deviance. Positive increasing relationships were identified for SST and Chlorophyll *a*, while negative for increasing pH (Fig. 41). For Canopy, only two predictors were significant, SST and O2, which had a negative relationship (Fig. 41). This model, however, explained an extremely low variability – 4%.
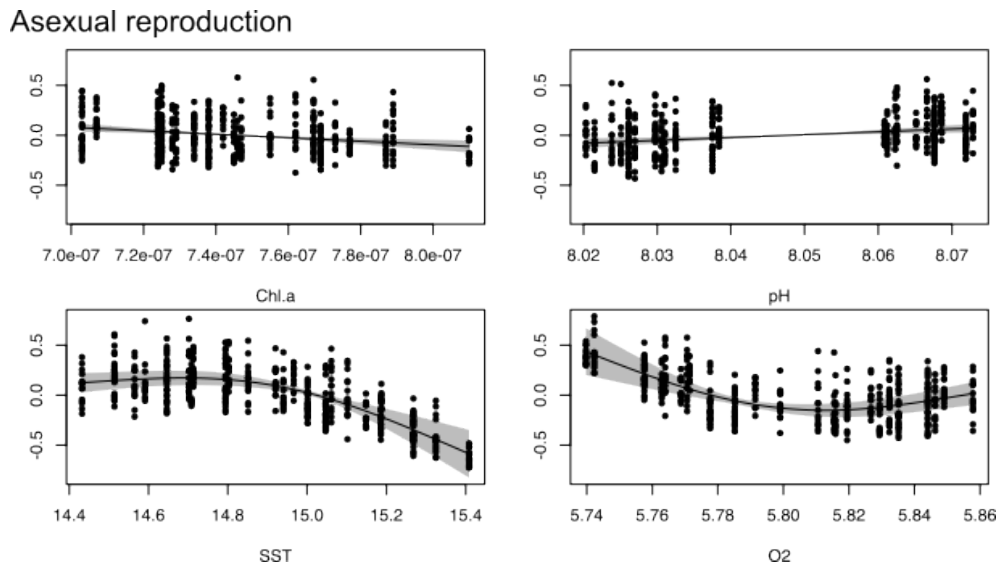
Figure 42 Partial smooth based on the final GAM demonstrating the statistical relationships between Asexual reproduction possibility and the significant predictors. Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

For the asexual reproduction possibility, GAM was a better model for the data. After a formal model selection routine comparing all combinations of predictors, the final GAM (demonstrating the lowest AIC) identified all variables as the main predictors contributing to the patterns in asexual reproduction possibility. Again, the model explained a rather low degree of the total variability - 17.6%. Negative relationships were observed between the asexual reproduction possibility and all their predictors, reflecting the trait-environment relationships (Figure 42). The complementary analysis using Random Forest (RF) confirmed these results (Figure 43, 44). Yet, with all predictors included for the three response variables – Subcanopy, Canopy and asexual reproduction, and slightly higher variability explained. The RF model explained 43% of the variance for the CWM Sub-Canopy and 23.6% for CWM Asexual reproduction. However, note that no exclusion of predictors was undertaken, as it could result in ~45% increase in prediction errors (Fig. 43).
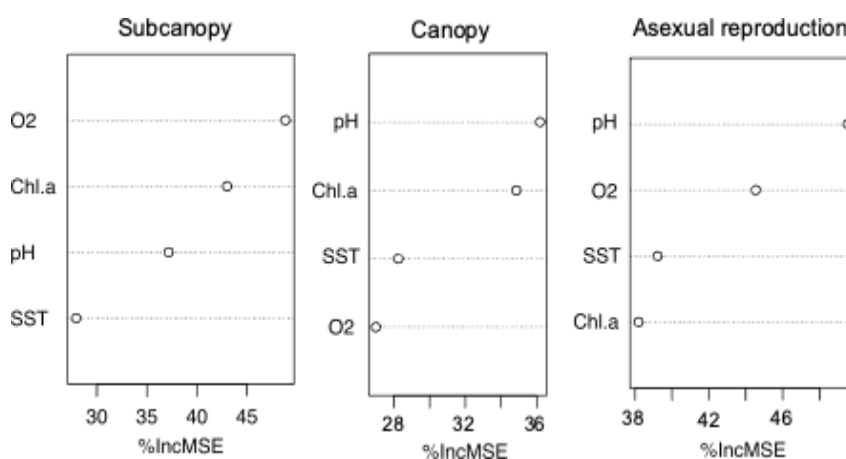
Figure 43 Variable importance of all predictors in RF illustrated by the increase in mean squared errors (MSE) of model predictions (if a given predictor is left out of the model).
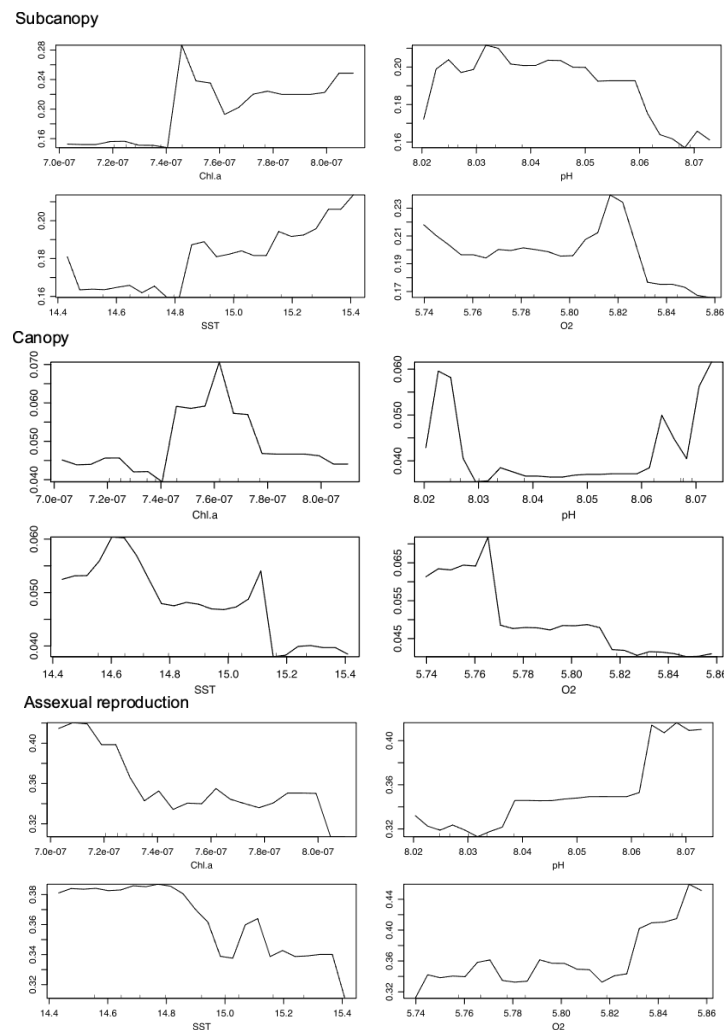
Figure 44 Partial dependence plots based on the RF demonstrating the predicted responses of CWM for the subcanopy and for the Asexual reproduction to changes in each of the predictors, while maintaining all other predictors at their mean levels.

The derived response curves showed positive non-linear relationships between Sub-Canopy CMW and Chlorophyll *a* and Sea Surface Temperature (SST), and negative with pH (Figure 44). For oxygen, trends were less clear except for its decline with the highest measured values. Also note that variability in Chlorophyll *a* is extremely low. For the Asexual reproduction CWM, we found the opposite trend, with negative non-linear relationships with SST and Chlorophyll *a,* and positive for the remaining predictors. For the Canopy, we found a non-linear negative relationship with SST and Oxygen.

Taken together, the derived trait-environment relationships suggest a higher dominance of subcanopy in warmer waters and higher Chlorophyll a, within the measured range. It is worth mentioning that these higher warmers, contrarily to the expected, were registered at the 2006-2008 period, when subcanopy species abundance were higher at the rocky shores most at North. However, for the canopy species the negative trend with increasing SST was observed, concomitant with previous research (Franco et al., 2018; CasadoAmezúa et al., 2019; Smale et al., 2020), despite the low variance explained by the model.

3.6.4. Trait-environment relationships using RLQ

This section presents the results of the RLQ analysis aiming to investigate the trait-environment relationships using the three matrices R (the environment), L (the species abundances), and Q (the species traits) as input. We used the whole dataset to identify the trait-environment relationships.

The total amount of co-inertia explained by the RLQ amounted to 0.33, with the first dimension (i.e., RLQ axis) contributing to 80.2% of the explained covariance. Hence, we will only present the scores of the first axis (but similar visualization could be carried out for the subsequent axis). In terms of traits (Figure 45A), RLQ1 demonstrate positive scores for traits' categories and species associated with higher complexity regarding the vertical space occupied (e.g., sub-canopy species with erect and shrub-like body forms) with an annual life cycle, different possibilities of relating to a substrate (either rock, animal, other flora) and also with higher investment in reproduction (e.g., female gametophyte fertilization). On the negative scores, we found more opportunistic traits, such as the possibility of asexual reproduction and fertilization in the water column, as well as a free-living (unattachment) environmental position. We also found structural forms with lower complexity, such as filamentous and crustose, and dominance for a horizontal substrate space occupation expressed through the encrusting and turf species.
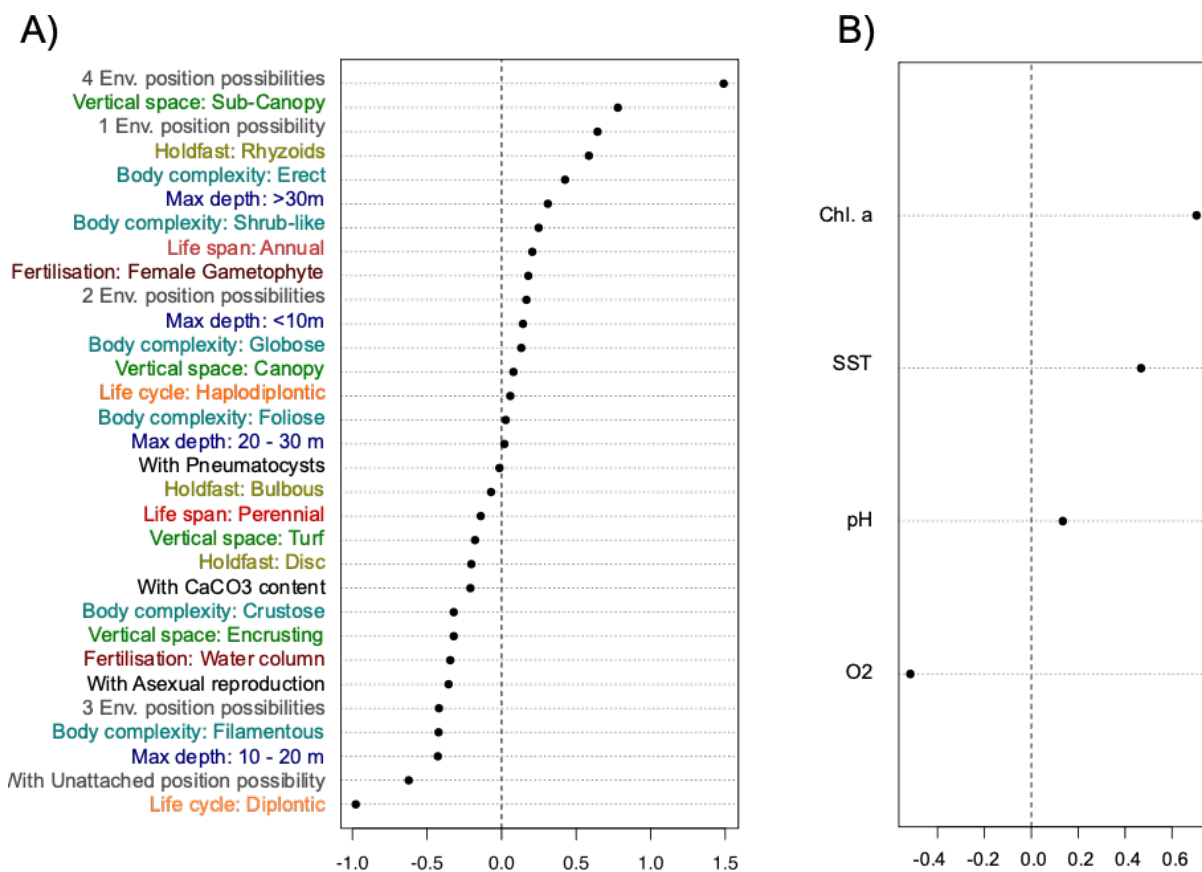
Figure 45 Loadings of traits (categories and binary traits) (A) and environmental variables (B) on RLQ1. Positive and negative values show the associated scores. Similar colours represent the categories within the categorical traits, while binary (0,1) traits are represented in black.

Regarding environmental variables, RLQ1 shows positive scores for environments characterized by higher Chlorophyll a (as a proxy of higher productivity in the water column), temperature and oxygen (Figure 45B). Conversely, sites with negative scores have lower oxygen levels. It is worth mentioning that specifically regarding temperature, comparing both sampling periods, there was a decrease in the

latest period (2019-2022), contrary to the expected. These values, however, reflect the sea surface temperature measured at 5m depth, which does not truly reflect intertidal conditions and the local upwelling events known to maintain several cold-water species in the Northern Portuguese region, as discussed in Vale et al. (2021).

3.6.5. Summary of main findings

- Although with a short latitudinal gradient and distance within surveyed rocky shores, spatial variability in the traits' identity and dominance was more evident than the temporal one.
- The primary traits explaining this spatial differentiation and abundance were mainly associated with vertical space occupied by the species (also a proxy of body size and structural complexity), body form complexity, environmental position possibilities and life cycle, suggesting that these might be primary "response" traits for the seaweeds.
- Overall, the investigation of the trait-environment relationship for intertidal seaweeds in Northern Portugal shows broadly consistent results across the three methods, indicating that findings seem robust to model choice. However, the variance explained by these relationships varied between 4 to 43%, depending on method, suggesting low representativeness of the selected environmental predictors for the habitat intertidal conditions.
- Trait distribution patterns seemed to have some association primarily with chlorophyll *a* and temperature. However, their relationship with increasing temperature did not reflect local upwelling, which is fundamental to maintaining some of the most structurally complex traits in the region.
- The marine forest species which fall in the canopy trait had an antagonistic relationship with temperature.
- Our results showed signs of a continuum within species with more opportunist traits (simple body forms with dispersal potential due to unattached position and asexual reproduction possibilities) to those with higher structural complexity in their body forms and vertical space and slow life histories.

3.7. Macroalgae communities along the Atlantic coast (SL36)

3.7.1. Study organism and area

The study area encompass 20 exposed to moderately exposed rocky shores along the European Atlantic coast from SouthWest Scotland to South Spain with a span of approximately 20 degrees of Latitude (Figure 46). Throughout the study area climatic and oceanographic conditions vary greatly. In particular, there is a marked north to south cline in sea temperature during Winter, and an alternation between warm and cold coastal pockets in Summer. For example, in Summer and early Autumn, the oceanographic conditions in the Bay of Biscay are in general characterised by weak upwelling, low mixing, and high stratification (Borja et al., 2008), while in the NorthWestern Iberia coastal temperatures are under the effect of strong upwelling phenomena which promotes mixing and brings about cold water to the surface (Peliz et al., 2002; Lemos & Pires, 2004) (Figure 47) These patterns in temperature have long been associated with regional dominance of either cold- or warm-water adapted faunas and floras (Breeman, 1988; Van den Hoek & Donze, 1967). However, the extent to which these biogeography patterns are also associated with species traits is not known. This study aims at identifying key traits of macroalgae species which may be associated with particular environmental conditions and quantifying those trait-environment relationships at large spatial scales (Atlantic coast of Europe).
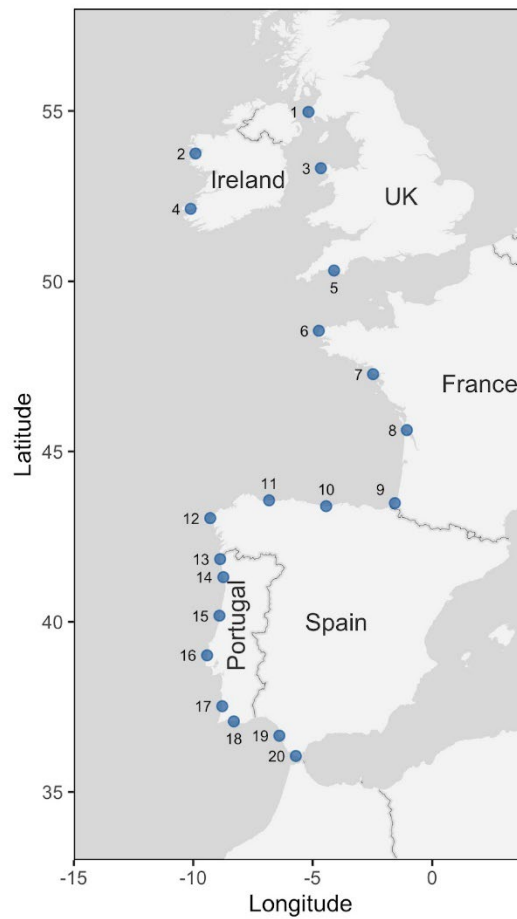
Figure 46 Study area and sampling locations along the Atlantic coast of Europe: 1 - South Cairn, 2 - Emlagh, 3 - Holyhead, 4 - Minard Castle, 5 - Wembury, 6 - Landunvez, 7 - Le Croisic, 8 - Royan, 9 - Biarritz, 10 - San Vincente de la Barquera, 11 - Pormenande, 12 - Cabo Touriñan, 13 - Moledo, 14 - Mindelo, 15 - Buarcos, 16 - São Lourenço, 17 - Alteirinhos, 18 - Evaristo, 19 - Peginas, and 20 - Paloma.
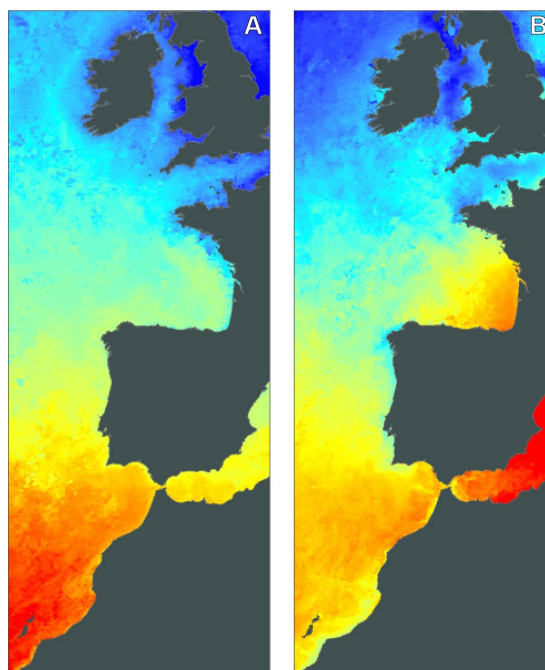
Figure 47 Typical sea surface temperature (SST) patterns along the Atlantic coast of Europe. A - SST during Winter, with a cline from cold water in the north (~5 ºC) to warm water in the south (~25 ºC). B - SST in Summer, with an alternation between cold and warm-water pockets (~12 ºC to ~28ºC).

3.7.2. Data description

We collected data from twenty rocky intertidal macroalgal communities on the European coastline from March to July 2022. At each location and during low tide, we surveyed conspicuous intertidal seaweed, totalizing 157 species. We identified them in situ to the lowest possible taxonomic level and assessed their abundance via a semi-quantitative estimation of abundance. We used a modified version of the scale established by Crisp and Southward (1958) — SACFOR, where abundances were encoded from 6 to 0 (6 means Superabundant; 5, Abundant; 4, Common; 3, Frequent; 2, Occasional; 1, Rare; and 0, not found). This scale was then converted to percentage abundance for this analysis following the approach by Strong and Johnson (2020). We used the same traits as in section 3.6 (please see table 3.6.1 for details), except for the depth and fertilization, and the same four environmental parameters from the *FutureMARES* WP2 models, considering the average of the 12 months prior to the sampling and 5m depth.

3.7.3. Patterns and drivers of CWM traits

This section investigates the spatial patterns and underlying environmental drivers of macroalgae community weighted trait means (CWM). We selected two categories from the vertical space trait that reflect contrasting ecological strategies (Martini et al. 2020), namely (i) turf and (ii) canopy. Turf was the dominant category within the trait and whole spatial dataset (always >50%, Figure 48). In this particular case, we did not consider the sub-canopy category as previously done in section 3.6, as this category had an extremely low CWM percentage. We focused on the "canopy" category, as it reflects higher structural complexity and investment in biomass growth, providing habitat for several associated species and blue carbon potential (Mauffrey et al., 2020). In comparison, "turf" species have a much more restricted three-dimensional structure due to their limited vertical height (Vranken et al., 2022). A community change from canopy-dominated to turf-dominated forms indicates a general shift between species that are structurally complex to species that have less structure and which grow fast and in an opportunistic way (Mauffrey et al., 2020). We also focused on a reproductive trait, namely the ability to perform "asexual reproduction". This is also a trait associated with lower complexity

which is considered advantageous under stressful conditions and which has the potential to promote rapid dispersion. First, we will provide an overview of the spatial changes in the selected CWMs, and then on their relationships with environmental conditions.
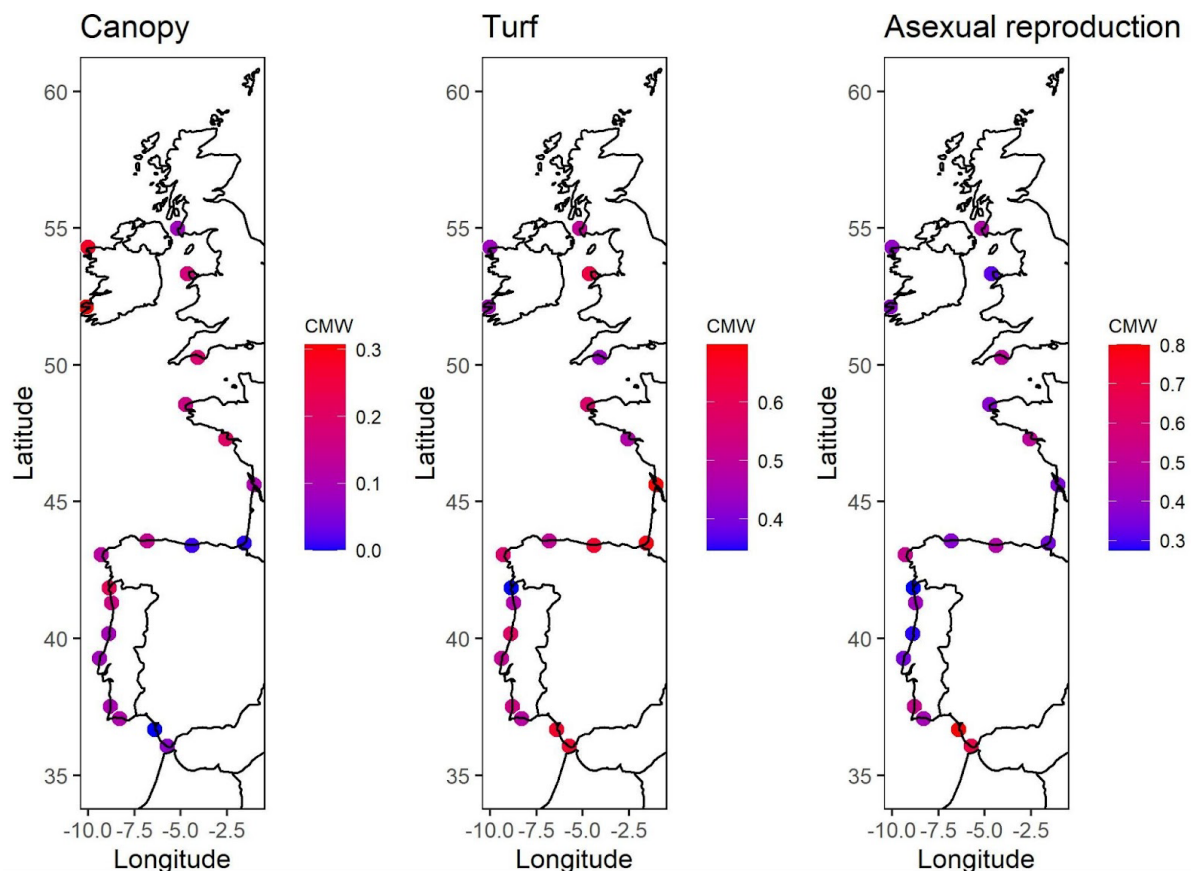
Figure 48 Maps of community weighted trait means (CWM) for "canopy", "turf" and "asexual reproduction" categories across the study area.

Spatial patterns on the CWM showed different trends along the European coast, depending on the trait (Fig. 48). Canopy CWM was higher at higher latitudes and in Northern Portugal (in line with section 6.3), and decreased in the Bay of Biscay and further south along the Portuguese coast. This agrees with the abovementioned temperature trends in the area: due to the effects of Summer upwelling in NW Iberia, seawater temperature in the area is almost as cold as that at higher latitudes. Conversely, oceanic weather is much more "continental" in the Bay of Biscay, where summer temperatures reach much higher values (Seabra et al., 2015). Thus, canopy-forming species, such as those that dominate in kelp forests, are more abundant and generate higher biomass in colder waters (Smale, 2019). On the other hand, turf species are typical of warm-temperate and tropical areas probably due to competition release from kelps in those regions. This work shows that turf is highly dominant along the European coast, particularly in areas where canopy dominance is weaker. The capacity for asexual showed a less clear pattern. Still, it was more prevalent at the southernmost locations, and in some particular locations at higher latitudes (e.g., NW Iberia, S Brittany, SW England and S Scotland, Fig. 3.7.3).

This section reports on some of the individual responses of CWM traits (using the same trait selection as above) to the environmental predictors using both GAM and Random Forests. Prior to these analyses, we analysed collinearity among environmental parameters and removed dissolved oxygen as it was highly correlated (correlation > 0.99) with sea surface temperature (SST). After a formal model selection routine comparing all combinations of predictors, the final GAM (i.e., that with the lowest

AIC) identified SST as the main predictor contributing to "canopy" and "asexual reproduction" patterns. For the "turf", however, none of the predictors was significant. For "canopy", the model explained 44.9% of the variance, while for asexual reproduction, it explained 48.4%. A linear and negative relationship was observed between "canopy" and SST. As for the "asexual reproduction", it generally increased non-linearly with temperature (Fig. 49).
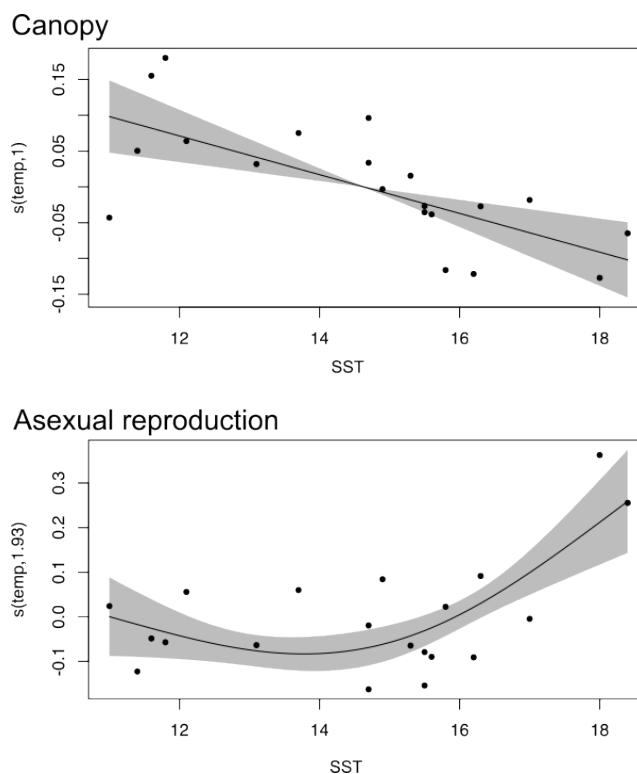
Figure 49 Statistical relationships from GAM between the traits "canopy" and "asexual reproduction" and the significant predictor (SST). Black lines show the fitted line, dots the partial residuals and grey shaded polygons the 95% confidence interval.

The complementary analysis using Random Forest (RF) confirmed the GAM results (Figure 50, 51) but included other predictors for the "canopy" and a model for "turf". The RF model explained 47.2% of the variance for the "canopy" CWM with two predictors (Figure 50), as chlorophyll-a did not affect the outcome. On the contrary, excluding temperature or pH could increase the prediction errors by up to ~35%. Canopy abundance decreased with increasing SST and increased with the increasing pH, yet within pH varied within small variation range (Figure 51). The model on the "turf" CWM only explained 4% of the variability, also with two predictors (Figure 50). An increase in the "turf" trait was associated with increasing SST and decreasing chlorophyll-a (Figure 51). This agrees with recent literature suggesting that heat stress has been driving the extirpation of canopy-dominated forests, which are being replaced by turf-dominated communities (Filbee-Dexter & Wenrberg, 2018). For the "asexual reproduction" trait, SST was enough for the model, with an overall importance of about 25% (Figure 3.7.5).
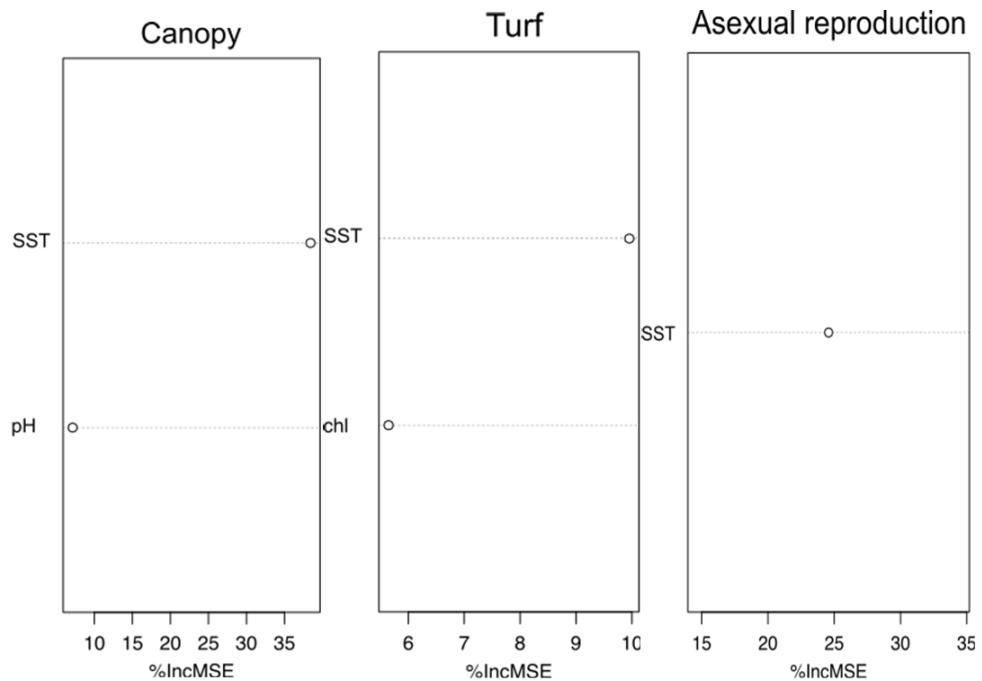
Figure 50 Variable importance for the predictors used in RF measured by the increase in the overall error (mean squared error, MSE) when predictors are, in turn, excluded from models.

Overall, SST was the most determinant parameter for the trait-environment relationships from both models. The models suggest that communities should be dominated by canopy-forming species in cold waters, with their influence declining from 16 ºC upwards (Figure 48, 50). This relationship, however, was not ascertained for turf species due their extremely low variability in the RF model. In other words, turf species were highly dominant across all sampling areas (Figure 46), which indubitably degraded the ability to detect subtle environmental effects. Yet, results still suggest that these species should increase in warmer waters. For asexual reproduction, we also found an increase with increasing SST for temperatures higher than 16 ºC (Figure 51).
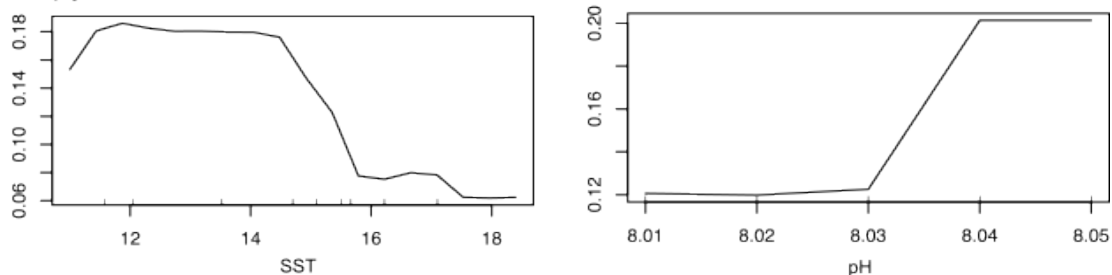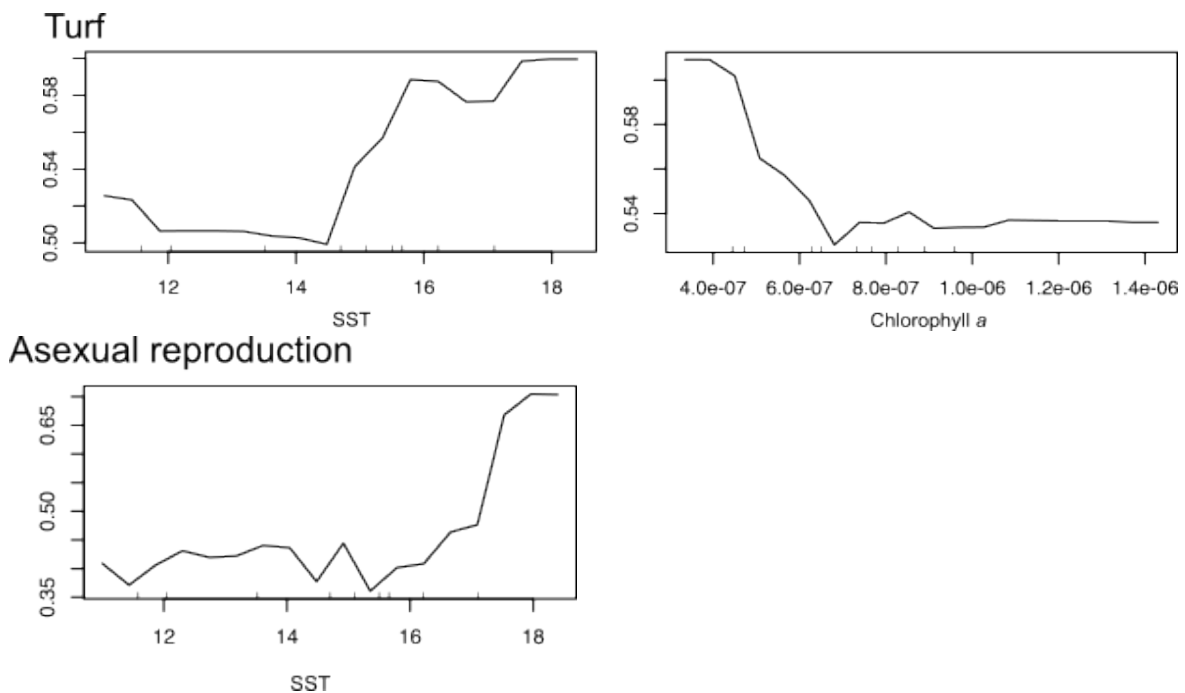
Figure 51 Partial dependence plots based on the RF demonstrating the predicted responses of CWM for the "canopy", "turf" and "asexual reproduction" trait categories to changes in their predictors.

3.7.4. Trait-environment relationships using RLQ

The total amount of co-inertia explained by the RLQ amounted to 0.23, with the first dimension (i.e., RLQ axis) contributing to 91.5% of the explained covariance. Hence, we only show the scores of the first axis (but a similar visualisation could be done for the subsequent axis). In terms of traits, RLQ1 demonstrate positive scores for more opportunistic traits, such as the possibility of asexual reproduction, free-living (unattachment) environmental position and holdfast, with encrusting species that privilege horizontal growth (in opposition to those that growth mostly vertically,, see Figure 52 A). These traits categories were associated with increasing SST, which was associated with the positive score (Figure 52 B). On the negative scores, the analysis highlighted categories of traits associated with higher complexity regarding the vertical space occupied and potential habitat provided (such as canopy and sub-canopy species with bulbous holdfast). These categories were associated with lower temperature scores. RLQ analyses also confirmed the patterns described above, stressing the importance of SST as a determinant parameter for the trait-environmental relationships. Overall, traits associated with higher complexity were linked to lower temperatures, while traits characteristic of opportunistic life cycles were linked to higher temperatures.
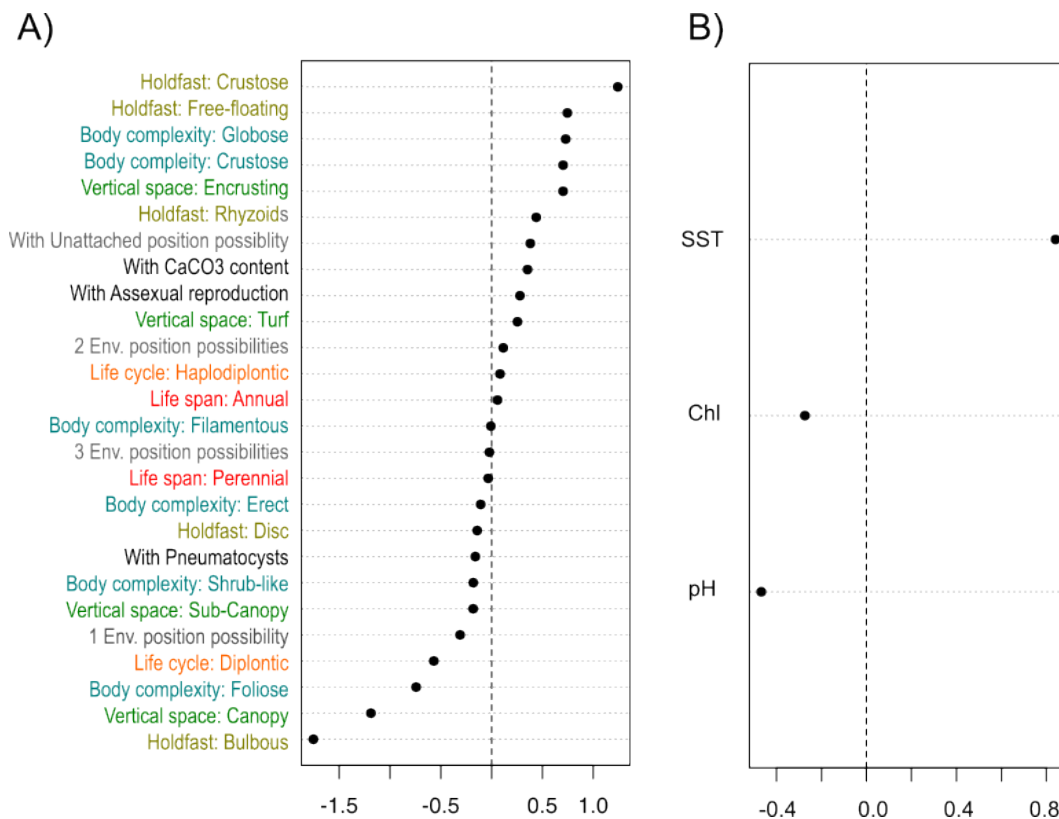
Figure 52 Loadings of traits (categories and binary traits) (A) and environmental variables (B) on RLQ1. Positive and negative values show the associated scores. Similar colours represent the categories within the categorical traits, while binary (0,1) traits are represented in black.

3.7.5. Summary of main findings

- The primary traits explaining the observed spatial differentiation and abundance were mainly associated with vertical space occupied by the species (also a proxy of body size and structural complexity), holdfast and body form complexity, suggesting that these might be primary "response" traits for seaweeds at the spatial scale here considered.

- Overall, the investigation of the trait-environment relationship for intertidal seaweeds across the European rocky shores shows broadly consistent results across the three methods, indicating that findings are robust.

- The most important environmental variable explaining the distribution of the traits was temperature. Still, the variability explained by temperature was always below 50 %, suggesting that other environmental parameters may also play an important role driving species traits.

- Our results suggest that there is a continuous pattern from species with more opportunist traits associated to higher temperature (simple body forms with dispersal potential due to unattached position and asexual reproduction possibilities), to species with higher structural complexity across their body forms, holdfast and vertical space. These relationships with temperature seem to hold true at lower temperature values and higher chlorophyll.

- The relation between the dominance of canopy species and temperature were consistent with literature, showing a clear decline of this trait at higher temperatures.

4. Cross system synthesis

The statistical analysis of trait-environment relationships featured within this deliverable report (see section 3) represent a broad range of marine organisms and ecosystems, ranging from fish, benthos and macroalgae communities samples across coastal-, estuarine- and shelf seas throughout Europe. Consequently, the organisms and areas considered are exposed to very different local environmental conditions, both in terms of climate and hydrography, but also with regards to the type and level of human activities and their associated pressures. Furthermore, the Storylines differ in terms of the spatio-temporal extent and scale of the analysis, as well as the amount and resolution of monitoring data on species abundances and their associated trait information for the organism group in question. However, despite these differences, the results and outputs generated from our trait-based approach allows us to identify common and generally applicable outcomes in terms of the key traits, environmental conditions and trait-environment relationships of marine organisms in general.

Table 5 Summary of key results across Storylines representing individual analysis carried out on selected organisms groups and regions.

Summary of key results across Storylines representing individual analysis carried out on selected organisms groups and regions.

Regional seas / area	Organism group	Storyline number	Spatio-temporal scale	Nr of species, traits and predictors	Methods tested	Key traits identified	Key environments identified
European Shelf seas	Demersal fish	8 (also fitting other SL)	Individual hauls aggregated at 1x1° and across years	>150 taxa, 7 traits, 7 env. variables	GAM, RF, RLQ, HMSC	Age at maturity, Lifespan, Body size, Fecundity	Depth, Temperature, Salinity, Seasonality,
Mediterranean / Aegean- and Ionian Sea	Reef - associated fish	26	158 sampling stations, aggregated over time	64 (56 native, 8 invasive), 8 traits, 9 env. var	GAM, RF, RLQ	Lifespan, Growth	Temp min, Temp. seasonality
Atlantic coast / Gironde estuary	Estuarine fish	16, 17	4 transects sampled >40 years.	40 species, 13 traits, 7 env.var	GAM, RF, RLQ	Length at maturity, Trophic level, Length max	Turbidity, Salinity, Temperature
E. Med. /Karpathos	Macrobenthos	27	Individual samples 2017-2020	161 taxa; 6 traits (+modalities); 12 env. variables	RLQ, HMSC	Ecosystem engineering, Mobility, Body size	Nutrients (e.g., PO4; NO2, POC), Chla, temperature
N-W Med / Tuscan Archipelago	Invertebrates and macroalgae	28	Samples in 128 plots from 2007-2016	61 taxa; 6 traits; 10 env. variables	GAM, RF, RLQ, HMSC	Feeding habit, Life span, Body size - complexity	Wave exposure, Temperature (min,max), Chl a
Atlantic coast / Portugal	Macroalgae	21, 23	5 sites sampled 2006-2008 and 2019-2022	11 traits; 4 env. variables	GLM/GAM, RF, RLQ	Vertical space, Body size and complexity, Life cycle (diplontic)	Temperature, Chl a

Atlantic coast (Scotland to Spain)	Macroalgae	36	20 sites sampled March-July 2022	157 taxa; 11 traits; 4 env. variables	GAM, RF, RLQ	Vertical space, Body size and complexity	Temperature

In terms of traits, a majority of studies present a pronounced structuring in space and time for characteristics and adaptations relating to lifespan (or longevity), age (or size) at maturation, growth and body size (Table 5). This was particularly evident for fish- and benthic communities across a range of habitats (i.e., reefs, estuaries, coasts and continental shelves) and at different geographical scales (i.e., local, regional, or European wide). Consequently, such life-history traits should be regarded as key response traits for these groups and marine organisms in general. Similarly, the studies on seaweeds and macroalgae communities also demonstrate a pronounced structuring of body size and complexity, whether studied at a more local, or European scale. To that end, traits mainly associated with the vertical space and physical structure of species might be considered as primary response traits for seaweeds across the spatial scales and areas considered here. With regards to the set of environmental conditions included in our analysis, most Storylines identified temperature, or the degree of temperature seasonality as key determinants explaining the observed trait distributions. However, more local conditions specific to a Storyline were also identified as important determinants. Notable examples include turbidity and salinity determining changes in fish community traits in the Gironde estuary, the magnitude of wave exposure affecting trait composition of macroalgae and invertebrates in the intertidal zone of the Tuscan Archipelago, as well as local nutrient conditions affecting macrobenthos traits on Karpathos. Hence, it is evident that a combination of both large-scale climatic drivers, notably temperature, but also more local and regional pressures may jointly determine the trait composition and responses of marine organisms to change. However, it is important to note that other variables and pressures not included, or sufficiently accounted for may also impact the trait distribution of marine organisms. A notable example is commercial fishing, where the analysis on demersal fish communities across European shelf seas identified a positive interaction between a global proxy for fishing effort and offspring size/fecundity, but a negative interaction with growth. Rather than a direct fishing effect this rather counterintuitive relationship likely reflects a co-occurrence and spatial allocation of fishing effort in areas with commercially targeted species characterized by relatively high fecundity, but slow growth (such as gadoids). However, since fishing is known to affect fish community dynamics and traits (e.g., Bianchi et al., 2000; Greenstreet & Rogers, 2006), especially by targeting large-sized species that are particularly vulnerable to fishing (Jennings et al., 1998), further work should be undertaken to include better estimates of fishing effort into trait-environment analysis, preferably including a temporal dimension as well.

In summary, our results suggest that there is a general and continuous gradient from species with more opportunist traits being associated with environments characterized by higher temperature, degree of seasonality and other forms of exposure, compared to species inhabiting colder, deeper, less seasonal and/or exposed environments. This is notable for fish communities demonstrating species with generally faster growth, smaller size and lower lifespan in warmer and seasonal environments, compared to species with larger size, slow growth and long lifespan inhabiting more stable and therefore predictable environments. Likewise, the studies on seaweeds and macroalgae show a similar gradient from opportunistic species, here characterized by more simple body forms, high dispersal potential (due to unattached position) and asexual reproduction, compared to species with higher structural complexity in terms of their body forms and vertical space. Taken together, our results are consistent with the "fast-slow" continuum of species life histories (Stearns 1983; Reich 2014) and supports "environmental filtering" as a primary assembly process determining community composition and diversity at large (Keddy, 1992; Pecuchet et al., 2016).

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Abrego, N., Norberg, A., Ovaskainen, O. (2017) Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. Journal of Ecology, 105, 1070– 1081.

Ackerly, D.D., Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within-and among-community components. Ecology Letters, 10, 135-145.

Alpert, P. (2005) The limits and frontiers of desiccation-tolerant life. Integrative and Comparative Biology, 45, 685-695.

Badalamenti, F., Ramos, A. A., Voultsiadou, E., Sánchez Lizaso, J. L., D'Anna, G., Pipitone, C., Mas, J., Fernandez, J. A. R., Whitmarsh, D., Riggio, S. (2000) Cultural and socio-economic impacts of Mediterranean marine protected areas. Environmental Conservation, 27(2), 110–125.

Barton, A.D., Pershing, A.J., Litchman, E., et al. (2013) The biogeography of marine plankton traits. Ecology letters, 16, 522–34.

Barton, K. (2016) MuMIn: Multi-Model Inference. R package version 1.40.4.

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D., Marshall, T.C. (2014) Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. Global Change Biology, 20, 1023– 1031.

Beukhof, E., Dencker, T.S., Pecuchet, L., Lindegren, M. (2019a) Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series, 610, 205–222.

Beukhof, R., Dencker, T.S., Palomares, M.L.D., Maureaud, A. (2019b) Trait collection of marine fsh species from North Atlantic and Northeast Pacific continental shelf seas. PANGAEA https://doi.org/10.1594/PANGAEA.900866

Borja, Á., Fontán, A., Sáenz, J. O. N., & Valencia, V. (2008) Climate, oceanography, and recruitment: the case of the Bay of Biscay anchovy (*Engraulis encrasicolus*). Fisheries Oceanography, 17(6), 477-493.

Bianchi, G. et al. (2000) Impact of fishing on size composition and diversity of demersal fish communities. ICES J. Mar. Sci. 57, 558–571.

Bolam, S.G. (2013) Relationships between macroinvertebrate biological traits and sea bed functioning in European waters. FP7 BENTHIS Task, 1.

Breeman, A.M. (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. Helgoländer Meeresuntersuchungen, 42(2), 199-241.

Breiman, L. (2001) Random Forests, Machine Learning 45, 5-32.

Bremner, J. (2008) Species' traits and ecological functioning in marine conservation and management. Journal of Experimental Marine Biology and Ecology, 366, 37–47.

Brun, P., Payne, M.R., Kiørboe, T. (2016) Trait biogeography of marine copepods – an analysis across scales. Ecology Letters, 19, 1403–1413.

Brun, P., Stamieszkin, K., Visser, A.W., Licandro, P., Payne, M.R., Kiørboe, T. (2019) Climate change has altered zooplankton-fuelled carbon export in the North Atlantic. Nature Ecology & Evolution 3, 416–423.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F., Hawkins, S.J. (2002) The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. Journal of Experimental Marine Biology and Ecology 267, 89-106.

Bulleri, F., Cucco, A., Dal Bello, M., Maggi, E., Ravaglioli, C., Benedetti-Cecchi, L. (2018) The role of wave-exposure and human impacts in regulating the distribution of alternative habitats on NW Mediterranean rocky reefs. Estuarine Coastal and Shelf Science 201, 114-122.

Casado-Amezúa, P., Araújo, R., Bárbara, I., Bermejo ,.R, Borja, Díez I., Fernández, C., Gorostiaga, J.M., Guinda, X., Hernández, I, Juanes, J.A., Peña,. ,V, Peteiro C., Puente, A., Quintana, I., Tuya, F, Viejo, R.M., Altamirano, M., Gallardo, T., Martínez, B. (2019) Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. Biodiversity and Conservation 28, 1151–1172.

Chevillot, X., Drouineau, H., Lambert, P., Carassou, L., Sautour, B., Lobry, J. (2017) Toward a phenological mismatch in estuarine pelagic food web? PLoS One 12, e0173752.

Chevillot, X., Tecchio, S., Chaalali, A., Lassalle, G., Selleslagh, J., Castelnaud, G., David, V., Bachelet, G., Niquil, N., Sautour, B., Lobry, J. (2019) Global Changes Jeopardize the Trophic Carrying Capacity and Functioning of Estuarine Ecosystems. Ecosystems 22, 473–495.

Clark, J.S., Gelfand, A.E., Woodall, C.W., Zhu K. (2014) More than the sum of the parts: Forest climate response from joint species distribution models. Ecology 24, 990–999.

Costello, M.J., Claus, S., Dekeyzer, S., Vandepitte, L., Tuama, É.Ó., Lear, D. and Tyler-Walters, H., (2015) Biological and ecological traits of marine species. PeerJ, 3, p.e1201.

Dencker, T.S., Pecuchet, L., Beukhof, E., Richardson, K., Payne, M.R., Lindegren, M. (2017) Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: Causes and consequences. PLoS ONE 12(12): e0189731. https://doi.org/10.1371/journal.pone.0189731

Denelle, P., Violle, C., Munoz, F. (2019) Distinguishing the signatures of local environmental filtering and regional trait range limits in the study of trait–environment relationships. Oikos, 128(7), 960-971.

Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M. (1993) Visual versus random-point percent cover estimations: ''objective'' is not always better. Marine Ecology Progress Series 110, 9-18.

Díaz, S., Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution, 16, 646–655.

Dolédec, S., Chessel, D., ter Braak, C. J. F. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. Environmental Ecological Statistics 3, 143–166.

Dray, S., Dufour, A. (2007) The ade4 Package: Implementing the Duality Diagram for Ecologists. Journal of Statistical Software, 22, 1–20.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., Ter Braak, C.J.F. (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95, 1421.

Duarte CM, Gattuso JP, Hancke K, Gundersen H, Filbee-Dexter K, Pedersen MF, Middelburg JJ, Burrows MT, Krumhansl KA, Wernberg T, Moore P, Pessarrodona A, Ørberg SB, Pinto IS, Assis J, Queirós AM, Smale DA, Bekkby T, Serrão EA, Krause-Jensen D (2022) Global estimates of the extent and production of macroalgal forests. Glob Ecology and Biogeography 31, 1422–1439.

Filbee-Dexter, K., & Wernberg, T. (2018) Rise of turfs: a new battlefront for globally declining kelp forests. Bioscience, 68(2), 64-76.

Fisher JAD, Frank KT, Leggett WC (2010a) Breaking Bergmann's rule: truncation of Northwest Atlantic marine fish body sizes. Ecology, 91, 2499–2505.

Fisher JAD, Frank KT, Leggett WC (2010b) Global variation in marine fish body size and its role in biodiversity-ecosystem functioning. Marine Ecology Progress Series, 405, 1–13.

Frainer A, Primicerio R, Kortsch S, Aune M, Dolgov A V, Fossheim M, Aschan MM (2017) Climate-driven changes in functional biogeography of Arctic marine fish communities. Proceedings of the National Academy of Sciences of the United States of America, 144, 12202–12207.

Franco JN, Tuya F, Bertocci I, Rodríguez L, Martínez B, Sousa-Pinto I, Arenas F (2018) The 'golden kelp' Laminaria ochroleuca under global change: Integrating multiple eco-physiological responses with species distribution models. Journal of Ecology 106:47–58.

Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018) Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography, 27, 1268–1276.

Gardarin A, Garnier É, Carrère P et al. (2014) Plant trait-digestibility relationships across management and climate gradients in permanent grasslands. Journal of Applied Ecology, 51, 1207–1217.

Garnier, E., Navas, M.L., Grigulis, K. (2016) Plant functional diversity: organism traits, community structure, and ecosystem properties. Oxford University Press.

Garnier E, Cortez A, Billès G et al. (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology, 85, 2630–2637.

Girardin, M., Castelnaud, G., Beaulaton, L. (2006) Surveillance halieutique de l'estuaire de la Gironde : suivi des captures 2004 - Etude de la faune circulante 2005. Bordeaux.

Green, S.J., Brookson, C.B., Hardy, N.A., Crowder, L.B. (2022) Trait-based approaches to global change ecology: moving from description to prediction. Proceedings of the Royal Society B, 289(1971), p.20220071.

Greenstreet SPR, Fraser HM, Rogers SI, Trenkel VM, Simpson SD, Pinnegar JK (2012) Redundancy in metrics describing the composition, structure, and functioning of the North Sea demersal fish community. ICES Journal of Marine Science, 69, 8–22.

Greenstreet, S. & Rogers, S. (2006) Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. . ICES Journal of Marine Science, 63, 573–593.

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology, 86, 902–910.

Guidetti, P. (2011) The destructive date-mussel fishery and the persistence of barrens in Mediterranean rocky reefs. Marine Pollution Bulletin, 62(4), 691–695.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., … Walbridge, S. (2015) Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6, 1–7.

Harris, D.J. (2015) Generating realistic assemblages with a joint species distribution model. Methods in Ecology and Evolution, 6, 465–473.

Heip, C. (2003) What structures marine biodiversity and why does it vary? In: Wefer, G., Lamy, F., Mantoura, F. (Eds); Marine Science Frontiers for Europe. Springer-Vergal Berlin Heidelberg New York Tokyo, pp/ 251-264.

Henriques, S., Guilhaumon, F., Villéger, S. et al. (2017). Biogeographical region and environmental conditions drive functional traits of estuarine fish assemblages worldwide. Fish and Fisheries 18, 752–771.

Holmlund, C. M., & Hammer, M. (1999) Ecosystem services generated by fish populations. Ecological Economics, 29(2), 253–268. https://doi.org/10.1016/S0921-8009(99)00015-4

IPCC (2019): IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, 755 pp. https://doi.org/10.1017/9781009157964.

Jax, K. (2005). Function and "functioning" in ecology: what does it mean? Oikos, 111(3):641–648.

Jennings, S., Reynolds, J.D., Mills, S.C. (1998) Life history correlates of responses to Fisheries exploitation. Proceedings of the Royal Society of London B, 265, 333–339.

Jennings, S., Greenstreet, S.P.R., Reynolds, J.D. (1999a) Structural change in an exploited fish community: A consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology, 68, 617–627.

Jennings, S., Alvsvåg, J., Cotter, A. et al. (1999b) Fishing effects in northeast Atlantic shelf seas: Patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. Fisheries Research 40, 125–134.

Jiménez-Alfaro, B., Suárez-Seoane, S., Chytrý, M., Hennekens, S.M., Willner, W., Hájek, M., Agrillo, E., Álvarez-Martínez, J.M., Bergamini, A., Brisse, H., Brunet, J. (2018) Modelling the distribution and compositional variation of plant communities at the continental scale. Diversity and Distributions, 24(7), 978-990.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M. E., Oztürk, B., Grabowski, M., Golani, D., & Cardoso, A. C. (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. Aquatic Invasions, 9(4), 391–423.

Kavadas, S., Maina, I., Damalas, D., Dokos, I., Pantazi, M., & Vassilopoulou, V. (2015) Multi-Criteria Decision Analysis as a tool to extract fishing footprints and estimate fishing pressure: Application to small scale coastal fisheries and implications for management in the context of the Maritime Spatial Planning Directive. Mediterranean Marine Science, 16, 294. https://doi.org/10.12681/mms.1087

Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3: 157-164

Kiørboe, T., Visser, Andre´, and Andersen, K. H. (2018) A trait-based approach to ocean ecology. ICES Journal of Marine Science, 75, 1849–1863.

Koch, N.M., Matos, P., Branquinho, C., Pinho, P., Lucheta, F., de Azevedo Martins, S.M., Vargas, V.M.F. (2019) Selecting lichen functional traits as ecological indicators of the effects of urban environment. Science of the Total Environment, 654, 705-713.

Lam-Gordillo, O., Baring, R. and Dittmann, S., (2020) Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. Ecological Indicators, *115*, p.106379.

Last, P. R., White, W. T., Gledhill, D. C., Hobday, A. J., Brown, R., Edgar, G. J., & Pecl, G. (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: A response to climate change and fishing practices. Global Ecology and Biogeography, 20, 58–72.

Lavorel, S., Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556.

Lemos, R. T., & Pires, H. O. (2004) The upwelling regime off the west Portuguese coast, 1941–2000. International Journal of Climatology: A Journal of the Royal Meteorological Society 24(4), 511-524.

Liaw, A., Wiener, M. (2002) Classification and Regression by randomForest. R News 23: 18-22.

Litchman, E., Klausmeier, C.A. (2008). Trait-Based Community Ecology of Phytoplankton. Annual review of Ecology and Systematics 39, 615–639.

Litchman, E., Ohman, M.D., Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. Journal of Plankton Research 35, 473–484.

Lobry, J., Lepage, M., Rochard, E., (2006) From seasonal patterns to a reference situation in an estuarine environment: Example of the small fish and shrimp fauna of the Gironde estuary (SW France). Estuararine Coastasl and Shelf Science 70, 239–250.

Lobry, J., Mourand, L., Rochard, E., Elie, P., (2003). Structure of the Gironde estuarine fish assemblages: a comparison of European estuaries perspective. Aquatic Living Resources 16, 47–58.

Lykousis, V., Chronis, G., Tselepides, A., Price, N. B., Theocharis, A., Siokou-Frangou, I., Van Wambeke, F., Danovaro, R., Stavrakakis, S., Duineveld, G., Georgopoulos, D., Ignatiades, L., Souvermezoglou, A., & Voutsinou-Taliadouri, F. (2002). Major outputs of the recent multidisciplinary biogeochemical researches undertaken in the Aegean Sea. Journal of Marine Systems, 33–34, 313–334.

Martini, S., Larras, F., Boyé, A,. Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B.E., Bittner, L., Castella, E., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann, L., Thiébaut, E., Usseglio-Polatera, P., Vogt, M., Laviale, M., Ayata, S.D. (2021). Functional trait-based approaches as a common framework for aquatic ecologists. Limnology and Oceanography 66:965–994.

Mauffrey, A. R., Cappelatti, L., & Griffin, J. N. (2020) Seaweed functional diversity revisited: Confronting traditional groups with quantitative traits. Journal of Ecology, 108(6), 2390-2405.

Maureaud, A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M. L., Amador, K., Anderson, S. C., Arkhipkin, A., Auber, A., Barr, I., Bell, R., Belmaker, J., Beukhof, E. D., Lamine Camara, M., Guevara-Carrasco, R., Choi, J., Christensen, H. T., Conner, J., Cubillos, L. A. & 55 others. (2021) Are we

ready to track climate-driven shifts in marine species across international boundaries? - A global survey of scientific bottom trawl data. Global Change Biology. 27, 220-236

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M. (2006) Rebuilding community ecology from functional traits. Trends in Ecology and Evolution, 21, 178–185.

McLean, M., Mouillot, D., Auber, A. (2018a) Ecological and life history traits explain a climate-induced shift in a temperate marine fish community. Marine Ecology Progress Series, 606, 175–186.

McWilliam, M., Hoogenboom, M.O., Baird, A.H., Kuo, C.-Y., Madin, J.S., Hughes, T.P. (2018) Biogeographical disparity in the functional diversity and redundancy of corals. Proceedings of the National Academy of Sciences 115, 3084–3089.

Mermillod-Blondin, F., Rosenberg, R., François-Carcaillet, F., Norling, K., Mauclaire, L. (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquatic Microbial Ecology, 36, 271–284.

Millenium Ecosystem Assessment (2005) Ecosystems and Human Well-being: Current State and Trends, Volume 1 (eds Hassan R, Scholes R, Ash N). Island Press, Washington, 23 pp.

MOm (2009) Status Report of the Mediterranean Monk Seal *Monachus monachus* Population in Greece. URL: https://issuu.com/mom_greece/docs/namebca9f4

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013) A functional approach reveals community responses to disturbances. Trends in Ecology and Evolution, 28, 167–177.

Nikolopoulou, S., Berov, D., Klayn, S., Dimitrov, L.I., Velkovsky, K., Chatzinikolaou, E., Chatzigeorgiou, G., Karamfilov, V., Pavloudi, C. (2021) Benthic habitat mapping of Plazh Gradina – Zlatna ribka (Black Sea) and Karpathos and Saria Islands (Mediterranean Sea). Biodiversity Data Journal 9: e71972.

Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E. (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Marine Ecology Progress Series 332, 11–23.

Ovaskainen, O., Roy, D. B., Fox, R., Anderson, B. J. (2016) Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. Methods in Ecology and Evolution, 7, 428– 436.

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., … Abrego, N. (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters, 20, 561– 576.

Pecuchet, L., Törnroos, A., Lindegren, M. (2016) Patterns and drivers of fish community assembly in a large marine ecosystem. Marine Ecological Progress Series, 546, 239–248.

Peliz, Á., Rosa, T.L., Santos, A.M.P., Pissarra, J.L. (2002) Fronts, jets, and counter-flows in the Western Iberian upwelling system. Journal of marine systems, 35, 61-77.

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005) Climate change and distribution shifts in marine fishes. Science, 308, 1912–1915.

Piñeiro-Corbeira, C., Barrientos, S., Barreiro, R., de la Cruz-Modino, R. (2022). Assessing the importance of kelp forests for small-scale fisheries under a global change scenario. Frontiers in Marine Science, 9, 1–12.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine Taxa Track Local Climate Velocities. 341, 1239–1242.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., … Richardson, A. J. (2013) Global imprint of climate change on marine life. Nature Climate Change, 3, 919–925.

Pollock, L.J., Tingley, R., Morris, W.K. et al. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution, 5, 397–406.

Reich, P. B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology, 102, 275–301.

Ricotta, C., Moretti, M. (2011) CWM and Rao's quadratic diversity: A unified framework for functional ecology. Oecologia 167, 181–188.

Rilov, G. (2016). Multi-species collapses at the warm edge of a warming sea. Scientific Reports, 6(1), 36897.

Rijnsdorp, A.D., Bastardie, F., Bolam, S.G., Buhl-Mortensen, L., Eigaard, O.R., Hamon, K.G., Hiddink, J.G., Hintzen, N.T., Ivanović, A., Kenny, A., Laffargue, P. (2016) Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES Journal of Marine Science, 73(suppl_1), pp.i127-i138.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S., Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B. S., Hereu, B., Karamanlidis, A. A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., … Zabala, M. (2012) The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications. PLoS ONE, 7(2), e32742. https://doi.org/10.1371/journal.pone.0032742

Salomidi, M., Katsanevakis, S., Borja, A., Braeckman, U., Damalas, D., Galparsoro, I., Mifsud, R., Mirto, S., Pascual, M., Pipitone, C., Rabaut, M., Todorova, V., Vassilopoulou, V., & Vega Fernandez, T. (2012) Assessment of goods and services, vulnerability, and conservation status of European seabed biotopes: A stepping stone towards ecosystem-based marine spatial management. Mediterranean Marine Science, 13(1), 49

Seabra, R., Wethey, D. S., Santos, A. M., & Lima, F. P. (2015) Understanding complex biogeographic responses to climate change. Scientific reports, 5(1), 1-6.

Sini, M., Vatikiotis, K., Thanopoulou, Z., Katsoupis, C., Maina, I., Kavadas, S., Karachle, P. K., & Katsanevakis, S. (2019) Small-Scale Coastal Fishing Shapes the Structure of Shallow Rocky Reef Fish in the Aegean Sea. Frontiers in Marine Science, 6, 599.

Smale, D. A. (2020) Impacts of ocean warming on kelp forest ecosystems. New Phytologist, 225(4), 1447-1454.

Solan, M., R. J. Aspden, and D. M. Paterson (2012) Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration. OUP Oxford.

Sommer, B., Harrison, P.L., Beger, M., Pandolfi, J.M. (2014) Trait-mediated environmental filtering drives assembly at biogeographic transition zones. Ecology 95, 1000–1009.

Suding, K.N., Lavorel, S., Chapin, F.S. et al. (2008) Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14, 1125–1140.

Stearns, S.C. (1983) The infuence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41, 173–187.

Tamburello, L., Bulleri, F., Bertocci, I., Maggi, E., Benedetti-Cecchi, L. (2013) Reddened seascapes: experimentally induced shifts in 1/f spectra of spatial variability in rocky intertidal assemblages. Ecology 94, 1102-1111.

Teichert, N., Lepage, M., Chevillot, X., Lobry, J., (2018) Environmental drivers of taxonomic, functional and phylogenetic diversity (alpha, beta and gamma components) in estuarine fish communities. Journal of Biogeography, 45, 406–417.

Teichert, N, Lepage, M., Sagouis, A., Borja, A., Chust, G., Ferreira, M.T., Pasquaud, S., Schinegger, R., Segurado, P., Argillier, C. (2017) Functional redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems. Sci. Rep. 7.

Teichert, N., Pasquaud, S., Borja, A., Chust, G., Uriarte, A., Lepage, M. (2017) Living under stressful conditions: Fish life history strategies across environmental gradients in estuaries. Estuarine and Coastal Shelf Science, 188, 18–26.

Thomas, M.K., Kremer, C.T., Litchman, E. (2016). Environment and evolutionary history determine the global biogeography of phytoplankton temperature traits. Global Ecology and Biogeography 25, 75–86.

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A. (2006). Functional role of large organisms in intertidal communities: Community effects and ecosystem function. Ecosystems 9, 1029–1040.

Tikhonov, G., Opedal, Ø.H., Abrego, N., et al. (2020). Joint species distribution modelling with the R-package HMSC. Methods in Ecology and Evolution 11, 442–447

Tikhonov, G., Ovaskainen, O., Oksanen, J., de Jonge, M., Opedal, O., Dallas, T. (2019). Hierarchical Model of Species Communities. R package version 3.0-2.

Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series *318*, .31-45.

Tornero, V., Hanke, G. (2016). Chemical contaminants entering the marine environment from sea-based sources: A review with a focus on European seas. Marine Pollution Bulletin, 112(1–2), 17–38.

Tyler, E.H., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D., Webb, T.J. (2012). Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Global Ecology and Biogeography 21(9), pp.922-934.

Vale, C.G., Arenas, F., Barreiro, R., Piñeiro-Corbeira, C. (2021) Understanding the local drivers of beta-diversity patterns under climate change: The case of seaweed communities in Galicia, North West of the Iberian Peninsula. Diversity and Distributions, 27, 1696–1705.

Van den Hoek, C., & Donze, M. (1967) Algal phytogeography of the European Atlantic coasts. Blumea: Biodiversity, Evolution and Biogeography of Plants, 15(1), 63-89

Van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H., Marques, J.C. (2016). The performance of trait-based indices in an estuarine environment. Ecological Indicators, 61, 378–389.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E. (2007). Let the concept of trait be functional! Oikos, 116, 882–892.

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., Kattge, J. (2014). The emergence and promise of functional biogeography. Proceedings of the National Academy of Sciences 111, 13690–13696.

Violle, C., Choler, P., Borgy, B. et al. (2015). Vegetation ecology meets ecosystem science: Permanent grasslands as a functional biogeography case study. Science of the Total Environment 534, 43–51.

Vranken, S., Robuchon, M., Dekeyzer, S., Bárbara, I., Bartsch, I., Blanfuné, A., et al. (2022). AlgaeTraits: a trait database for (European) seaweeds. Earth System Science Data Discussions 1-57.

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015) So many variables: Joint modeling in community ecology. Trends in Ecology & Evolution, 30, 766– 779.

Westoby, M., Wright, I.J. (2006). Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution, 21, 261–268.

Wiedmann, M., Aschan, M., Certain, G., Dolgov, A., Greenacre, M., Johannesen, E., et al. (2014). Functional diversity of the Barents Sea fish community. Marine Ecological Progress Series 495, 205– 218.

Wood, S.N. (2017) Generalized Additive Models: An Introduction with R 2nd edition. Chapman and Hall/CRC.

Appendix 1

The online tutorial, including training data and example R code is available for online viewing and download following this link: https://rfrelat.github.io/TraitEnvironment.html

Appendix 2

Table A.2.1. Sources of information used to represent species life-traits for intertidal organisms reported under section 3.5.5. Details are reported in the associated References. EJ = Expert Judgement (Macroalgae: Prof. Fabio Rindi; Invertebrates: Dr. Joachim Langeneck and Dr. Jonathan Tempesti). References to the source listed in the table are provided below.

Taxon	Body complexity	Body size	Flexibility	Life span	Dispersal potential (adult)	Feeding habit
Fricaria amentacea	WORMS	WORMS	EJ	EJ	EJ	EJ
Cystoseira compressa	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Corallina officinalis	BIOTIC	EJ	EJ	EJ	BIOTIC; MarLIN	
Jania rubens	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	EJ
Amphiroa rigida	EJ	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	EJ	EJ
Liagora spp.	EJ	EJ	EJ	WORMS	EJ	EJ
Thin tubular thallus algae	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	EJ
Dictyota mediterranea	Bogaert et al. 2020	Bogaert et al. 2020	EJ	Baweja et al. 2016	EJ	EJ
Padina pavonica	Bevilacqua & Terlizzi 2019; MarLin	Bevilacqua & Terlizzi 2019; MarLin	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019; MarLIN	Bevilacqua & Terlizzi 2019	EJ
Rhodymenia sp.	WORMS	WORMS	EJ	EJ	EJ	EJ
Chondracanthus acicularis	Hommers and 1992	EJ	EJ	EJ	EJ	EJ
Flabellia petiolata	EJ	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Anadyomene stellata	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Halimeda tuna	Bevilacqua & Terlizzi 2019; Janes et al. 201	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019; Vroom et al. 2003	Bevilacqua & Terlizzi 2019	EJ
Acetabularia acetabulum	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Ulva sp.	BIOTIC	BIOTIC	BIOTIC	BIOTIC	EJ	EJ
Champia sp.	Titlyanov et al. 2017	WORMS	EJ	Bevilacqua & Terlizzi 2019	EJ	EJ
Cutleria multifida	EJ	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	EJ	EJ
Aglaozonia sp.	EJ	EJ	EJ	EJ	EJ	EJ
Chondria sp.	EJ	EJ	EJ	EJ	EJ	EJ
Gastroclonium sp.	EJ	EJ	EJ	EJ	EJ	EJ
Gelidium sp.	Janes et al 2017	EJ	EJ	EJ	EJ	EJ
Laurencia complex	EJ	EJ; Maggs & Hommers and 1993	Bevilacqua & Terlizzi 2019	EJ	EJ	EJ
Hypnea musciformis	Vázquez-Delfín et al. 2016	Vázquez-Delfín et al. 2016	EJ	EJ	EJ	EJ
Bryopsis sp.	EJ	EJ	EJ	EJ	EJ	EJ
Cladophora pellucida	EJ	EJ	EJ	EJ	EJ	EJ
Cladophora sp.	BIOTIC	EJ	EJ	EJ	EJ	EJ
Green filamentous algae	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	EJ	EJ
Filamentous algae	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	EJ
Falkenbergia sp.	EJ	EJ	EJ	EJ	EJ	EJ
Wrangelia sp.	WORMS	EJ	EJ	EJ	EJ	EJ
Valonia utricularis	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Botryocladia botryoides	EJ	EJ	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Codium sp.	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Palmophyllum sp.	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Caulerpa cylindracea	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	EJ
Stypocaulon scoparium	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ
Sargassum sp.	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	EJ
Peyssonnelia sp.	EJ	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi, 2020	EJ
Encrusting coralline algae	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	EJ	Bevilacqua & Terlizzi 2019	EJ
Encrusting brown algae	EJ	EJ	EJ	EJ	EJ	EJ
Dictostoma sp.	Krüger et al. 2018	EJ	EJ	Brunetti et al. 1988	BIOTIC	BIOTIC
Cliona sp.	Bevilacqua & Terlizzi 2019	WORMS	Bevilacqua & Terlizzi 2019	Piscitelli et al. 2011	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Aglaophenia sp.	BIOTIC	Gravili et al. 2015	BIOTIC	Faucci & Boero 2000	EJ	https://doris.ffessm.fr
Coryne muscoides	Bevilacqua & Terlizzi 2019	Angel & Cantero 2013	Bevilacqua & Terlizzi 2019	BIOTIC	Bevilacqua & Terlizzi 2019	BIOTIC
Actinia equina	BIOTIC (*Sagartia elegans*)	MarLIN	EJ	Briffa & Greenaway 2011	EJ	Chomsky et al. 2004
Cornularia cornucopiae	BIOTIC (*Sagartia elegans*)	Betti et al. 2011	EJ	Betti et al. 2011	Bevilacqua & Terlizzi 2019	Betti et al. 2011
Caricmella sp.	BIOTIC	BIOTIC	BIOTIC	BIOTIC	EJ	BIOTIC
Vermetus triquetrus	Bevilacqua & Terlizzi 2019	MarLIN	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Calvo & templado 2004
Pomatoceros triqueter	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi, 2019; BIOTIC	Bevilacqua & Terlizzi, 2019; BIOTIC	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Spirorbis sp.	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi, 2019; BIOTIC	Bevilacqua & Terlizzi, 2019; BIOTIC	EJ	Bevilacqua & Terlizzi 2019	Encyclopedia of Life
Patella aspera	BIOTIC	BIOTIC	BIOTIC	BIOTIC	BIOTIC	BIOTIC
Patella rustica	BIOTIC	Prusina et al. 2015	EJ	Prusina et al. 2015	BIOTIC	BIOTIC
Osilinus turbinatus	BIOTIC	EJ	EJ	BIOTIC	Crothers 2001	EJ
Fissurella sp.	EJ	EJ	EJ	EJ	EJ	EJ
Mytilus galloprovincialis	BIOTIC	WORMS	EJ	Ceccherelli & Rossi 1984	EJ	BIOTIC
Stramonita haemastoma	EJ	Pezy et al. 2019	BIOTIC	Rilov et al. 2001	EJ	WORMS
Balanus perforatus	BIOTIC	MarLIN	BIOTIC	BIOTIC	EJ	BIOTIC
Chthamalus stellatus	MarLIN	MarLIN	MarLIN	BIOTIC	BIOTIC	BIOTIC
Turbicellepora magnicostata	Alvarez 1990	WORMS	EJ	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Didemnidae	BIOTIC	Bevilacqua & Terlizzi, 2019; BIOTIC	BIOTIC	EJ	Bevilacqua & Terlizzi 2019	WORMS
Ascidians	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Rivularia sp.	EJ	EJ	EJ	EJ	EJ	Broady & Merican 2012
Chiton sp.	BIOTIC	Encyclopedia of Life	BIOTIC	Lord 2012	BIOTIC	BIOTIC
Spongia officinalis	Pansini et al 2011	Castritsi-Catharios et al. 2011	EJ	Pansini et al 2011	EJ	EJ
Sarcotragus spinulosus	Perez-Lopez et al 2017	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Perez-Lopez et al 2017	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Phorbas tenacior	De Caralt et al. 2018	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Pansini et al 2011	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Ircinia sp.	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Pansini et al 2011	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019
Spirastrella cunctatrix	Riesgo et al. 2014	Rützler 2002	EJ	Teixido et al. 2011	EJ	EJ
Crambe crambe	Galera et al. 2000	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019	Pansini et al 2011	Bevilacqua & Terlizzi 2019	Bevilacqua & Terlizzi 2019

Supporting references (See Table A2.1)

Alvarez, J.A. 1990. Notes on two species of the genus Turbicellepora Ryland, 1963 (Bryozoa, Cheilostomida) of the Atlanto-Mediterranean region: T. avicularis (Hincks, 1860) and T. magnicostata (Barroso, 1919). Cahiers de Biologie Marine 31, 473-483.

Angel, J.J.S, Cantero, A.L.P. 2013. Shallow-water benthic hydroids from the Maltese Islands (Central Mediterranean). Marine Ecology-an Evolutionary Perspective 34, 177-196.

Barton, A.D., Pershing, A.J., Litchman, E., Record, N.R., Edwards, K.F., Finkel, Z.V., Kiørboe, T., Ward, B.A. (2013) The iogeography of marine plankton traits. Ecology Letters, 16(4), pp.522-534.

Baweja, P., Kumar, S., Sahoo, D. & Levine, I. (2016). Biology of seaweeds. In Seaweed in Health and Disease Prevention (Fleurence, F. & Levine, I., editors), 41–106. Elsevier, Amsterdam.

Beauchard, O., Veríssimo, H., Queirós, A.M., Herman, P.M.J. (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecological Indicators, 76, pp.81-96.

Betti, F., Bo, M., Di Camillo, C.G., Bavestrello, G. 2012. Life history of Cornularia cornucopiae (Anthozoa: Octocorallia) on the Conero Promontory (North Adriatic Sea). Marine Ecology-an Evolutionary Perspective 33, 49-55.

BIOTIC - Biological Traits Information Catalogue. https://www.marlin.ac.uk/biotic/

Bolam, S.G., Coggan, R.C., Eggleton, J., Diesing, M., Stephens, D. (2014) Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. Journal of Sea Research, 85, 162-177.

Broady, P.A., Merican, F. 2012. Phylum cyanobacteria –blue-green bacteria, blue-green algae. In: Gordon DP ed. Volume 3: kingdoms bacteria, protozoa, chromista, plantae, fungi. New Zealand, Inventory of Biodiversity. Chirstchurch, Canterbury University Press. pp. 50–69.

Bogaert, K.A., Delva, S., De Clerck, O. 2020. Concise review of the genus Dictyota JV Lamouroux. Journal of Applied Phycology 32, 1521-1543.

Briffa, M., Greenaway, J. 2011. High In Situ Repeatability of Behaviour Indicates Animal Personality in the Beadlet Anemone Actinia equina (Cnidaria). PlosOne 6 : e21963. doi:10.1371/journal.pone.0021963

Brun, P., Kiørboe, T., Licandro, P., Payne, M.R. (2016.)The predictive skill of species distribution models for plankton in a changing climate. Global Change Biology, 22(9), 3170-3181.

Brunetti, R., Bressan, M., Marin, M., Libralato, M. 1988. On the ecology and biology of Diplosoma listerianum (Milne Edwards, 1841) (Ascidiacea, Didemnidae). Vie et Milieu: 123-131.

Calvo, M., Templado, J., 2004. Reproduction and development in a vermetid gastropod, Vermetus triquetrus. Invertebrate Biology 123, 289-303.

Castritsi-Catharios, J., Miliou, H., Kapiris, K., Kefalas, E., 2011. Recovery of the commercial sponges in the central and southeastern Aegean Sea (NE Mediterranean) after an outbreak of sponge disease. Mediterranean Marine Science 12, 5-20.

Ceccherelli, V.U., Rossi, R. 1984. Settlement, growth and reproduction of the mussel Mytilus galloprovincialis. Marine Ecology Progress Series 16, 173-184.

Chomsky, O., Kamenir, Y., Hyams, M., Dubinsky, Z., Chadwick-Furman, N.E. 2004. Effects of feeding regime on growth rate in the Mediterranean Sea anemone Actinia equina (Linnaeus). Journal of Experimental Marine Biology and Ecology 299, 217-229.

Costello, M.J., Claus, S., Dekeyzer, S., Vandepitte, L., Tuama, É.Ó., Lear, D., Tyler-Walters, H. (2015) Biological and ecological traits of marine species. PeerJ, 3, p.e1201.

Crothers, J.H., 2001. Common topshells: an introduction to the biology of Osilinus lineatus with notes on other species in the genus. Field Studies, 10, 115–160.

de Caralt, S., Gonzalez, J., Turon, X., Uriz, M.J. 2018. Reproductive strategies of two common sympatric Mediterranean sponges: Dysidea avara (Dictyoceratida) and Phorbas tenacior (Poecilosclerida). Peerj 6.

Díaz, S., Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution, 16(11), pp.646-655.

Dolédec, S., Chessel, D., Ter Braak, C.J., Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics, 3(2), pp.143-166.

DORIS - Données d'Observations pour la Reconnaissance et l'Identification de la faune et la flore Subaquatiques. https://doris.ffessm.fr/

Dray, S. and Legendre, P. (2008) Testing the species traits–environment relationships: the fourth-corner problem revisited. Ecology, 89(12), pp.3400-3412.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J. (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology, 95(1), pp.14-21.

Encyclopedia of Life. https://eol.org/pages/2971258 ; https://eol.org/pages/52351/data

Faucci, A., Boero, F. 2000. Structure of an epiphytic hydroid community on Cystoseira at two sites of different wave exposure. Scientia Marina 64, 255-264.

Galera, J., Turon, X., Uriz, M.J., Becerro, M. 2000. Microstructure variation in sponges sharing growth form: the encrusting demosponges Dysidea avara and Crambe crambe. Acta Zoologica 81, 93-107.

Gravili, C., De Vito, D., Di Camillo, C.G., Martell, L., Piraino, S., Boero, F. 2015. The non-Siphonophoran Hydrozoa (Cnidaria) of Salento, Italy with notes on their life-cycles: an illustrated guide. Zootaxa 3908, 1-+.

Green, S.J., Brookson, C.B., Hardy, N.A., Crowder, L.B. (2022) Trait-based approaches to global change ecology: moving from description to prediction. Proceedings of the Royal Society B, 289, p.20220071.

Greenslade, P.J. (1983) Adversity selection and the habitat templet. The American Naturalist, 122(3), pp.352-365.

Heip, C. (2003) What structures marine biodiversity and why does it vary? In: Marine Science Frontiers for Europe, pp. 251-264. Springer, Berlin, Heidelberg.

Hommersand, M., Fredericq, S., Cabioch, J. 1992. Developmental morphology of Gigartina pistillata (Gigartinaceae, Rhodophyta). Phycologia 31, 300-325.

Janes, H., Kotta, J., Parnoja, M., Crowe, T.P., Rindi, F., Orav-Kotta, H. 2017. Functional traits of marine macrophytes predict primary production. Functional Ecology 31, 975-986.

Kruger, I., Lenz, M., Thiel, M., 2018. The colonial ascidian Diplosoma listerianum enhances the occurrence of the hydrozoan Obelia sp. during early phases of succession. Helgoland Marine Research 72:4. https://doi.org/10.1186/s10152-018-0506-6.

Lam-Gordillo, O., Baring, R., Dittmann, S. (2020) Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. *E*cological Indicators, 115, p.106379.

Litchman, E., Edwards, K.F., Klausmeier, C.A., Thomas, M.K. (2012) Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. Marine Ecology Progress Series, 470, pp.235-248.

Litchman, E., Klausmeier, C.A. (2008) Trait-based community ecology of phytoplankton. Annual Review of Ecology, Evolution, and Systematics, pp.615-639.

Litchman, E., Ohman, M.D., Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. Journal of Plankton Research, 35(3), pp.473-484.

Lord, J.P. 2012. Longenvity and growth rates of the Gumboot chiton, Cryptochiton stelleri, and the black leather chiton, Katharina tunicata. Malacologia 55, 43-54.

Maggs, C.A., Hommersand, M.H. 1993. Seaweeds of the British Isles, Volume 1. Rhodophyta Part 3A Ceramiales. Natural History Museum, London.

Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F. (2015) Predictive ecology in a changing world. Journal of Applied Ecology, 52(5), pp.1293-1310.

Pansini, M., Manconi, R., Pronzato R. (Editors) 2011. Porifera I. Calcarea, Demospongiae (partim), Hexactinellida, Homoscleromorpha. Fauna d'Italia, Vol. 46. Bologna: Calderini-Il Sole 24 Ore. 554 pp. ISBN: 978–88–506–5395–9

Perez-Lopez, P., Ledda, F.D., Bisio, A., Feijoo, G., Perino, E., Pronzato, R., Manconi, R., Moreira, M.T. 2017. Life cycle assessment of in situ mariculture in the Mediterranean Sea for the production of bioactive compounds from the sponge Sarcotragus spinosulus. Journal of Cleaner Production 142, 4356-4368.

Pezy, J.P., Raoux, A., Kerckhof, F., Dauvin, J.C. 2019. First record of the gastropod Stramonita haemastoma (Linnaeus, 1767) in the English Channel. Bioinvasions Records 8, 266-272.

Piscitelli, M., Corriero, G., Gaino, E., Uriz, M.J. 2011. Reproductive cycles of the sympatric excavating sponges Cliona celata and Cliona viridis in the Mediterranean Sea. Invertebrate Biology 130, 1-10.

Queirós, A.M., Birchenough, S.N., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G. (2013) A bioturbation classification of E uropean marine infaunal invertebrates. Ecology and evolution, 3(11), pp.3958-3985.

Rützler, K. 2002. Family Spirastrellidae Ridley & Dendy, 1886. In: Hooper, J.N.A., Van Soest, R.W.M., Willenz, P. (eds) Systema Porifera. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-0747-5_23

Titlyanov, E.A., Titlyanova, T.V., Xiu-Bao, L., Huang H. 1997. Common Marine Algae of Hainan Island. In: Coral Reef Marine Plants of Hainan Island. pp.75-228.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E. (2007) Let the concept of trait be functional! Oikos, 116(5), pp.882-892.

World Register of Marine Species. https://www.marinespecies.org/index.php