

Spatial distribution of life-history traits and their response to environmental gradients across multiple marine taxa

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Abstract. Trait-based approaches enable comparison of community composition across multiple organism groups. Yet, little is known about the degree to which empirical trait responses found for one taxonomic group can be generalized across organisms. In this study, we investigated the spatial variability of marine community-weighted mean traits and compared their environmental responses across multiple taxa and habitats, including pelagic zooplankton (copepods), demersal fish, and benthic infaunal invertebrates. We used extensive, spatially explicit datasets collected from scientific surveys in the North Sea and examined community composition of these groups using a trait-based approach. In order to cover the key biological characteristics of an organism, we considered three life-history traits (adult size, offspring size, and fecundity) and taxon-specific feeding traits. While many of the traits co-varied in space and notably demonstrated a south–north gradient, none of the traits showed a consistent spatial distribution across all groups. However, traits are often correlated as a result of trade-offs. When studying spatial patterns of multiple traits variability in fish and copepods, we showed a high spatial correlation. This also applied to a lesser extent to fish and benthic infauna, whereas no correlation was found between benthic infauna and copepods. The result suggested a decoupling in the community traits between strictly benthic and strictly pelagic species. The strongest drivers of spatial variability for many community traits are the gradients in temperature seasonality, primary productivity, fishing effort, and depth. Spatial variability in benthic traits also co-varied with descriptors of the seabed habitat. Overall, results showed that trait responses to environmental gradients cannot be generalized across organism groups, pointing toward potential complex responses of multi-taxa communities to environmental changes and highlighting the need for cross-habitat multi-trait analyses to foresee how environmental change will affect community structure and biodiversity at large.

Key words: community composition; copepod; environment; fish; habitat; infauna; multi-taxa; North Sea; trait.

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INTRODUCTION

Characterizing species by their key traits (e.g., body size) allows understanding the mechanisms behind community assembly and the processes influencing species presence in communities (Kraft et al. 2008, Weiher et al. 2011, Pecuchet et al. 2016). Community traits composition and spatial patterns of community mean traits, as well as their relationship with the environment, are generally assessed in the empirical literature on individual taxonomic groups separately. Yet, by using life-history traits common to every organism, trait-based approaches also enable comparison of community composition across multiple organism groups and facilitate the search for common drivers of community composition (Van der Plas et al. 2012).

Life-history traits are often related through trade-offs that define the life-history strategy of a given organism (Winemiller et al. 2015). Such life-history strategies are used to shed light on the evolution of organisms, as well as the environment in which the species occur (Charnov et al. 2013). Two well-known examples of life-history theories or models to explain life-history strategies are *r*- vs. *K*-selected species (Pianka 1970) and the competition–stress–disturbance vegetation classification (Grime 1974), while more recently for fish communities, Winemiller and Rose (1992) developed the equilibrium–periodic–opportunistic model which links three strategies through trade-offs between fecundity, juvenile survival, and generation time. Some traits and trade-offs are unique for a particular group of organisms, while others, termed life-history invariants, can be used to compare across taxa (Charnov 1993).

Despite a large theoretical framework and recent advances within trait-based ecology, surprisingly little is known about the degree to which empirical trait responses to environmental gradients can be generalized between different taxonomic groups and trophic levels. On a global scale, there are indications that some traits follow similar spatial patterns between different taxa. For instance, body size tends to increase with latitude for many groups such as birds (Ashton 2002), phytoplankton (Barton et al. 2013), and zooplankton (Brun et al. 2016a). On a smaller spatial scale, the response of community traits to

external pressures might be less generalizable across taxonomic groups due to the influence of local processes, such as differences in micro-habitat structure (Lamouroux et al. 2004). Indeed, the response of traits to the same environmental gradient might vary between and within taxonomic groups, as different traits might be associated with different ecophysiological strategies adopted by the organisms to cope with the environment (Ackerly et al. 2002). For example, along a gradient of disturbance, communities of carabids, spiders, and plants did not express a generalized trait–environment relationship, but their trait variation along the gradients could be consistently interpreted in terms of dispersal ability (Pedley and Dolman 2014). Investigating spatial variability of trait patterns across different taxonomic groups might clarify whether the response of traits to the environment can be generalized between taxonomic groups or whether each group responds to it independently.

Marine food webs are often characterized by complex trophic interactions and habitat strategies that regulate pelagic and benthonic pathways of energy (Rooney et al. 2006, Lindegren et al. 2012, van Denderen et al. 2018). Phytoplankton, which is at the basis of the pelagic food web, encompasses micro-algae that are grazed upon by zooplankton, a group of primary consumers that in the size range of 0.2–20 mm is mainly dominated by crustacean copepods (Kiorboe 2008), which represent up to 70% of mesozooplankton biomass in the North Sea (Clark et al. 2001). Benthic invertebrates are a major component of the benthonic compartment and belong to numerous taxonomic entities that live inside (infauna) or on the seabed surface (epifauna). This heterogeneous group encompasses species with various feeding strategies and body sizes, ranging from micrometers (microfauna and meiofauna) to tens of centimeters (macrofauna). Both zooplankton and benthos are preyed upon by fish (Fig. 1). Hence, the three groups, fish, benthos, and zooplankton, are composed of organisms living in different vertical habitats, characterized by different mobility, body size, and lifespan, but which are linked through trophic interactions. Despite these interactions, it is unclear how these groups overlap in communities' trait composition, spatial distribution, and environmental sensitivity.

In this study, we analyze the spatial variability and co-variability in key life-history traits of demersal fish, copepods, and benthic infauna and analyze whether community mean traits respond to similar environmental variables across groups. More specifically, we aim to answer the following research questions: (1) Is there a consistent spatial pattern in key traits across groups? (2) What are the abiotic drivers regulating spatial patterns of these traits? (3) Do these drivers differ between groups? We focus on life-history traits that are common between these diverse organism groups in order to be able to compare their spatial patterns: adult body size, fecundity, and offspring size. Body size is often defined as a master trait as it is correlated with many other key traits, for example, growth rates and generation time, and can bring information on the capabilities and limitations of organisms (Andersen et al. 2016). Fecundity, that is, the number of offspring produced per female, and offspring size, that is, the size of released offspring in the water, are useful descriptors to characterize reproductive strategies, which can be regrouped in two main types: organisms releasing numerous small offspring and organisms releasing a few large offspring (Neuheimer

et al. 2015). In addition to these three traits, we included the feeding types or diet of the taxa to provide insight into potential prey–predator relationships and trophic interactions between the three groups considered. These traits were selected to cover key biological performances of an organism (such as feeding, growth, and reproduction) and because they are expected to respond to environmental gradients (Brun et al. 2016a, Beauchard et al. 2017, Pecuchet et al. 2017). We study the spatial patterns using community data in the North Sea from the end of the 1980s as a case study. Although reflecting historical conditions, this community dataset comprises the most detailed and spatially resolved data available for the three organism groups and therefore suits the aims of this study.

MATERIALS AND METHODS

Study area

The North Sea is a shelf sea characterized by strong south–north environmental gradients from the shallow, productive, and highly seasonal southern area to the deeper and less variable northern part. This south–north gradient has been shown to influence the distribution of

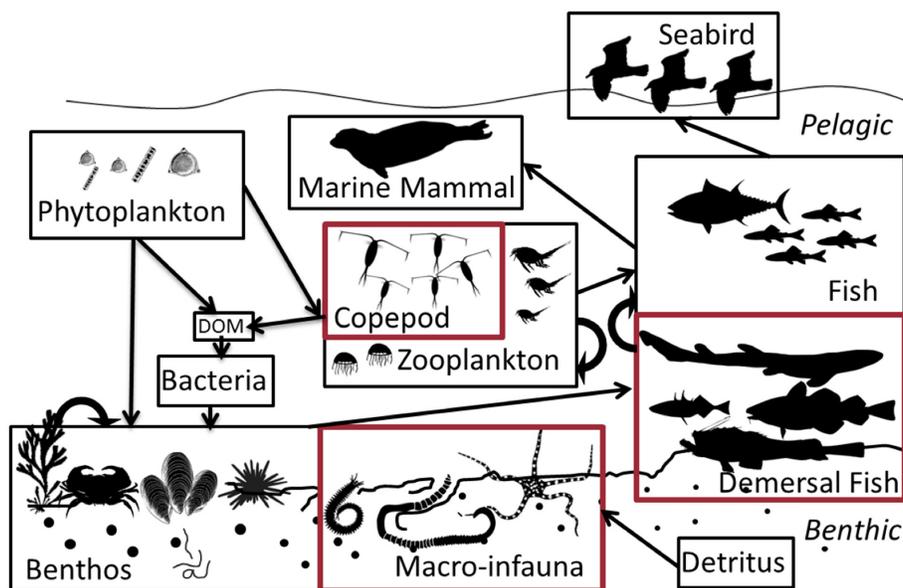


Fig. 1. A schematic food web of the North Sea partly adapted from Christensen (1995). Black arrows indicate a feeding link from one compartment to the other, while half-circle arrows represent intra-guild predation. The boxes highlighted in red represent the part of the community that was analyzed in this study.

species and influence the composition and dynamics of different pelagic and benthic communities (Beaugrand et al. 2001, Reiss et al. 2010, Frelat et al. 2017). The North Sea is also characterized by strong anthropogenic impacts arising from multiple activities such as run-off from agriculture, oil extraction, shipping, and fishing. Fishing in particular has been historically very intense in the North Sea and has impacted the fish and benthos communities through overfishing and perturbation of seabed habitats (van Denderen et al. 2015, Neumann et al. 2016). In addition, recent changes in climate have impacted the distribution of multiple organisms in the North Sea (Beaugrand 2004, Hiddink et al. 2015), as well as the trait composition of their communities (Engelhard et al. 2015). These increasing anthropogenic pressures and environmental changes on the biological communities show the need to understand the sensitivity of multiple taxa community traits to these external pressures.

Community data collection

Species composition and abundance data for fish, copepods, and benthic infauna were extracted from three different scientific surveys that covered the entire North Sea. The analysis was restricted to the late 1980s due to the availability of only one regional sampling event for benthic infauna in 1986. To characterize the community composition of the three groups in the late 1980s, the survey data were thus centered around the year 1986, including one and two years prior to and after 1986 whenever possible, to achieve a robust spatial coverage. We thus compared datasets in the following periods: fish (1985–1987), copepod (1984–1988), and benthic infauna (1986).

Records for the infauna communities were gathered from the North Sea Benthos Survey (Rees et al. 2007). A total of 235 stations spread throughout the North Sea were done in this survey between January and May 1986 (Appendix S1: Fig. S1). This survey sampled benthic communities with either a 0.1-m² van Veen grab or a 0.068-m² box corer, with on average three samples taken per station. Both sampling gears are designed to quantitatively sample infaunal benthic organisms and small epifauna. At each station, all the individuals were sorted and identified to the lowest

possible taxonomic level and their abundance recorded as number of individuals per m². This study focused on the macrofauna; thus, species belonging to the meiofauna (<1 mm in adult body size) that were too small to be adequately retained on the sieve were excluded from the analysis.

Data on fish assemblages were obtained from the North Sea bottom trawl survey (ICES 2012, www.datras.ices.dk) for the years 1985–1987, corresponding to a total of 990 hauls (Appendix S1: Fig. S1). In this scientific survey, which is performed every year between January and March, each haul lasts approximately 30 min and covers three nautical miles. At each station, fish specimens are taxonomically sorted and their abundance recorded as number of individuals caught per hour. Only data on demersal fish species were kept in this study, as these are the species targeted by the bottom trawl gear.

Plankton (copepod) data were obtained from the Continuous Plankton Recorder (CPR) Survey (Richardson et al. 2006, SAHFOS 2016a), a long-term plankton monitoring program relying on a network of transects sampled monthly by ships of opportunity along their standard routes. The CPR is equipped with a filtering mesh of 270 µm that, towed at high speed (~5–9 m/s), adequately samples subsurface mesozooplankton, in particular copepod species, at a standard depth of ~7 m (Richardson et al. 2006). Each CPR sample corresponds on average to 10 nautical miles and ~3 m² of sea water filtered. After each tow, samples are returned to the laboratory for the analysis. A categorical index that provides an estimate of phytoplankton biomass, the so-called Phytoplankton Colour Index (PCI), is determined based on the greenness of the silk (SAHFOS 2016b). Each PCI record is determined by comparison with a standard color chart associated with four defined greenness categories (i.e., 0, 1, 2, and 6.5) indicating increasing phytoplankton standing stock. In each sample, phyto- and zooplankton taxa are also taxonomically identified and counted. The abundance per sample of each taxon is based on a semi-quantitative count, with each number counted being converted to a categorical value, from 1 to 12, and then reported into a defined abundance value (Richardson et al. 2006). To ensure a consistent spatio-temporal coverage and comparability between the different datasets, we used a total of 624 CPR

samples collected during winter and spring months (January–May) from 1984 to 1988. Samples only collected during the day were selected in order to reduce biases due to zooplankton diurnal vertical migration.

Traits data

To be able to compare trait patterns across taxa, we selected key life-history traits common to all: adult size, fecundity, and offspring size. In addition to these three traits, we included the feeding types or diet of the taxa.

For the benthic infauna, adult size (mm), fecundity (estimated number of eggs produced per female per year), offspring size (egg size, μm), and feeding types were gathered from published databases (available in Garcia 2010, Törnroos et al. 2014) and sourced from published papers, books, and websites (www.marlin.ac.uk/biotic). Four feeding type categories were considered, that is, suspension feeder, deposit feeder, scavenger, and predator (Pearson 2001). Since species may feed in different categories, we used a fuzzy-coding approach to assign a score between 0 and 3 to each category describing the affinity of the species to that category (Chevenet et al. 1994), with 0 being no affinity, 1 and 2 being intermediate affinity, and 3 being total and exclusive affinity. Afterward, these scores were converted to proportion with the sum of the proportions adding to one.

Fish adult size (cm) corresponds to the maximum total length ever reported for the species, while fish diet was characterized into three feeding groups: benthivorous, planktivorous, or piscivorous. Size and diet traits were extracted from FishBase (Froese and Pauly 2018). Fish fecundity is the average total number of offspring produced per mature female per year, usually calculated as the number of oocytes in the ovary. Offspring size corresponds to the average size of the offspring released in the water, that is, eggs for oviparous or larvae/juveniles for ovoviviparous. These two traits were collected primarily from the literature (available in Pecuchet et al. 2017).

Copepod size (female size in mm), offspring size (egg diameter in μm), and feeding modes were obtained from Brun et al. (2016b). For the feeding mode, the species were categorized as either passive, active, or mixed feeders (Brun

et al. 2016b), while fecundity, calculated as the number of eggs produced per female per day, was obtained from Hirst and Kiørboe (2002).

Several biological records were registered at the genus or family taxonomic level instead of at the species level. For these records, we assigned the average traits of all informed species of the same genus or family in the North Sea. For simplicity in the rest of the manuscript, we will refer to these different entities, both species and higher taxonomic grouping, as species. For each species, only one value per trait was assigned, and we thus did not take into account intra-specific variability.

Interpolating survey data into a regular grid

Due to different distributions in the sampling sites between the three surveys and the heterogeneity of the sampling sites locations, the abundance of each species was interpolated in a regular grid of 0.1° latitude \times 0.1° longitude from 52° N to 61.5° N and from 3.5° E to 8.5° W covering the whole North Sea area (Fig. 2) to allow a comparison of trait distributions across taxa. Records collected over a few years were pooled together prior to interpolation, to maximize the spatial coverage. The interpolation was obtained using an isotropic kriging algorithm from the *gstat* package in R (Pebesma 2004). First, we calculated a regional variogram for each species. The variogram characterizes the variance in the species abundance between sampled points at different distances; that is, it is based on the assumptions that samples within a close range will be more similar than samples taken far apart (Legendre and Legendre 1998). A mathematical model was then fitted to the variogram data to describe the spatial dependence of the data. We tested four types of fit (Gaussian, exponential, spherical, and Matern), and we applied the best fitting model based on visual assessment of the fit. In most of the cases, a spherical model was fitted to the variogram and to a lesser extent a Gaussian model. Finally, the fitted model was used to interpolate the abundance of the species on the selected regular grid covering the entire area. The species abundances were log-transformed as the kriging procedure works best when the distribution is close to normal (Isaaks and Srivastava 1989). Isotropic kriging assumes homoscedasticity of the data (i.e., homogeneity

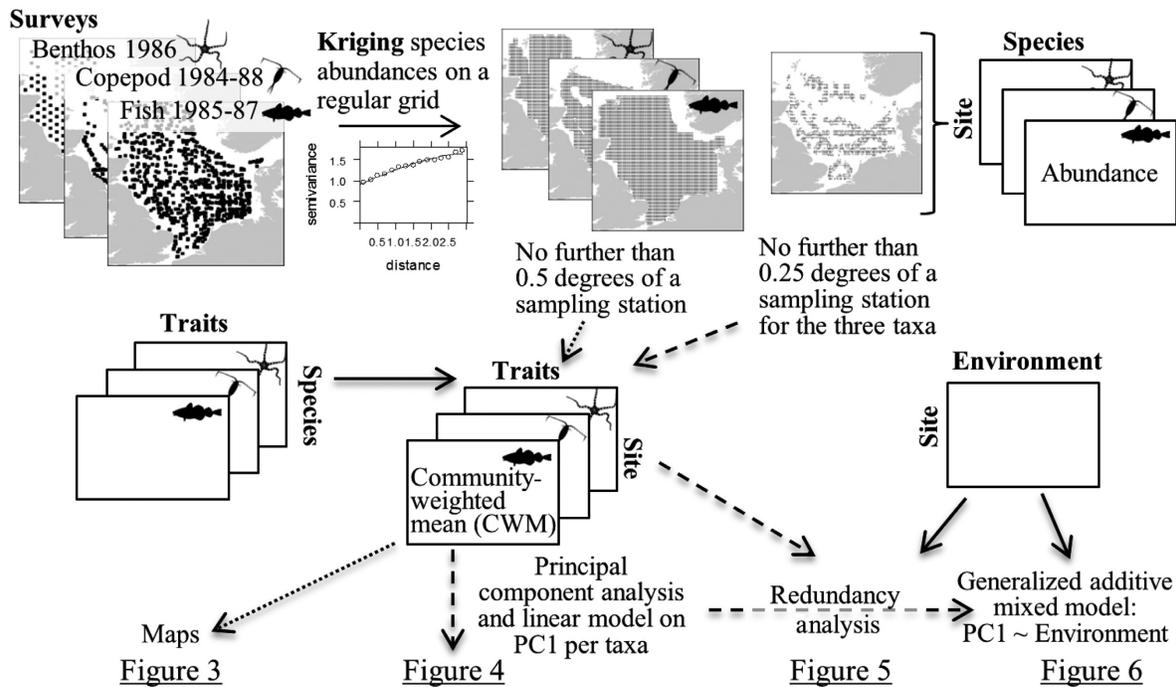


Fig. 2. A schematic representation of the data pre-handling, the different datasets used, and analyses performed in this study.

of variance), which is not always appropriate for copepod data for which other interpolation method such as the inverse square distance can be preferred (Beaugrand et al. 2010). Nevertheless, we chose to use the same kriging method for the three taxonomic communities to avoid biases due to different methods but instead restricted the statistical analyses on the interpolated data to the areas that were near a sampled station (Fig. 2). Species which were occurring in few samples (typically less than eight samples) were excluded from the analysis as their abundance could not be adequately interpolated.

Overall, 172 out of 715 recorded benthic infaunal species, 12 out of 23 recorded copepod species, and 56 out of 68 demersal fish species were used in the analysis. The species were excluded due to either missing traits information or low occurrence (Appendix S1: Tables S1–S3). Nevertheless, the species which were kept in the analysis were the most abundant in the communities. On average, the percentage of individuals modeled in this study represented 78%, 94%, and 99%, of the individuals in the survey of infauna, fish, and copepod, respectively. Consequently,

the large majority of the community composition was included and analyzed.

Community-weighted mean traits

For each group (copepods, benthic infauna, and fish), we calculated the community-weighted mean (CWM) reproductive, feeding, and size traits at each grid point (Fig. 2). This was done by averaging the trait values of the species present in each grid cell, weighted by their relative abundances. Community-weighted mean values were then mapped for the three different groups. To avoid over-extrapolation, we mapped only the CWM on grid cells that were located at a maximum distance of 0.5 degrees from a sampled station.

As traits are often correlated, we performed a principal component analysis (PCA) on each group to explore patterns of co-variability between CWM traits and assess spatial congruence across groups. The resulting first principal component (PC1), corresponding to the loading of each grid cell (site) on the first axis, represents the strongest pattern of multi-traits spatial variability. We compared PC1 across the different taxa to assess whether the dominant patterns of

spatial variability in the CWM traits are similar across groups. We used a generalized least square (gls) model with a Gaussian spatial autocorrelation structure to estimate the significance and slope of the spatial correlation between taxa PC1s. The PC1s were standardized (zero unit and one variance) beforehand to allow the slope comparison across groups. A significant correlation between two taxa PC1s means that the spatial variability of multiple traits of these two taxa communities is co-varying spatially, whereas a non-significant correlation points toward differentiated spatial turnover in community traits. We also looked at cross-taxa correlations using the second principal component (PC2), whenever this represented an important percentage of the total variance. For this analysis, only the grid cells that were no further than 0.25 degrees from a sampled station in the joint three taxa surveys were retained in the analysis ($n = 1789$).

Environmental data and anthropogenic pressures

In order to quantify the effect of the environmental gradient and anthropogenic pressure on the distribution of the CWM traits, the following variables describing the hydrography, habitats characteristics, and anthropogenic pressure were gathered for the analysis: mean depth per grid cell (m), mixed layer depth (m), and annual mean and seasonality of sea surface temperature ($^{\circ}\text{C}$), annual mean and yearly variability of the PCI, tidal bed stress (Pa), sediment occurrence (sand to mud, mud to sand, and coarse), sea surface salinity, beam trawling, otter trawling, and the combined bottom trawling effort (number of hours fished).

Temperature, salinity, and mixed layer depth for the years 1985–1988 were obtained from an oceanographic analysis product (AHOI; Núñez-Riboni and Akimova 2015). Annual averages were calculated for sea surface temperature and salinity, while temperature seasonality was measured as the difference between summer (June–August) and winter (December–February) temperatures.

Mixed surface layer depth was defined as the depth where temperature has decreased by 0.5°C from the temperature measured at 10 m depth and was calculated as an annual mean. Seabed depth was obtained from the General Bathymetric Chart of the Oceans (GEBCO, www.gebco.net). The seabed sediment type was extracted from

the European Marine Observation Data Network (EMODnet) Seabed Habitats project on a very fine scale (1:250 000; www.emodnet-seabedhabitats.eu), classified into three main categories: sand to muddy, mud to sandy, and coarse, the later containing all sediments classified as rock, mixed, or coarse. For each grid cell, the sediment categories were assessed as a coverage proportion, with the proportion of all categories in a grid cell summing up to one. The semi-quantitative PCI was used as a proxy of primary productivity. Mean annual PCI was calculated as the average of 12 monthly PCIs, while PCI variability was calculated as the standard deviation of the monthly means. Tidal bed shear stress, the force created at the seabed by tidal currents, was obtained from Hiddink et al. (2006). Fishing effort, calculated as the average number of hours fished by beam trawlers or otter trawlers per year and per 1° longitude \times 0.5° latitude grid, was obtained for the years 1991–1995 (Jennings et al. 1999). Since standardized and spatially resolved fishing effort data prior to the 1990s are unavailable, we made the assumption that the spatial patterns of the early 1990s were similar to the late 1980s. This assumption is supported by an overall consistency in the spatial distribution of beam trawl effort between the early 1990s and the mid-2000s (Engelhard et al. 2015), despite a reduction in the overall fishing effort caused by a fleet reduction scheme initiated by the European Commission in the late 1990s (Villasante 2010).

Redundancy analysis on CWM traits (CWM-RDA)

Community-weighted mean-redundancy analysis (CWM-RDA) is a community-based analysis which permits the response of biological traits to environmental variables to be assessed. It is based on redundancy analysis (RDA), but instead of using species abundance as input, we used CWM traits value (Kleyer et al. 2012). This method has been shown to be adequate to study the response of CWM mean traits to environmental gradients (Kleyer et al. 2012). This method allows analysis of the relationship (expressed as covariance) between two matrices, a matrix of observed variables (CWM traits) and a matrix of explanatory variables (environment; Fig. 2). The RDA combines ordination methods and multi-linear regression in order to represent the CWM traits as linear functions of the environment. The CWM-RDA

results are represented in a triplot, which consists of two biplots on top of each other. The CWM-RDA axes are not only linear combinations of the CWM traits but also of the environmental variables, and only the information in the CWM traits that can be linearly related to the environment is displayed on the triplot (Zuur 2007).

Finally, we analyzed the PC1 obtained from the PCA on taxa CWM traits by the environmental variables using a generalized additive mixed model, allowing for potential nonlinearities between the response and explanatory variables and correcting for spatial autocorrelation. We also analyzed the relationship between the

second principal component (PC2) and the environment to assess whether PC2 also contains important spatial patterns. The smoothing spline function (s) was constrained to three degrees of freedom ($k = 3$), which allows for second-order relationships, but restricts flexibility during model fitting. Spatial autocorrelation was modeled by a Gaussian structure.

RESULTS

Trait spatial patterns

Most of the CWM traits demonstrate a south–north gradient (Fig. 3). Notably, fecundity displays

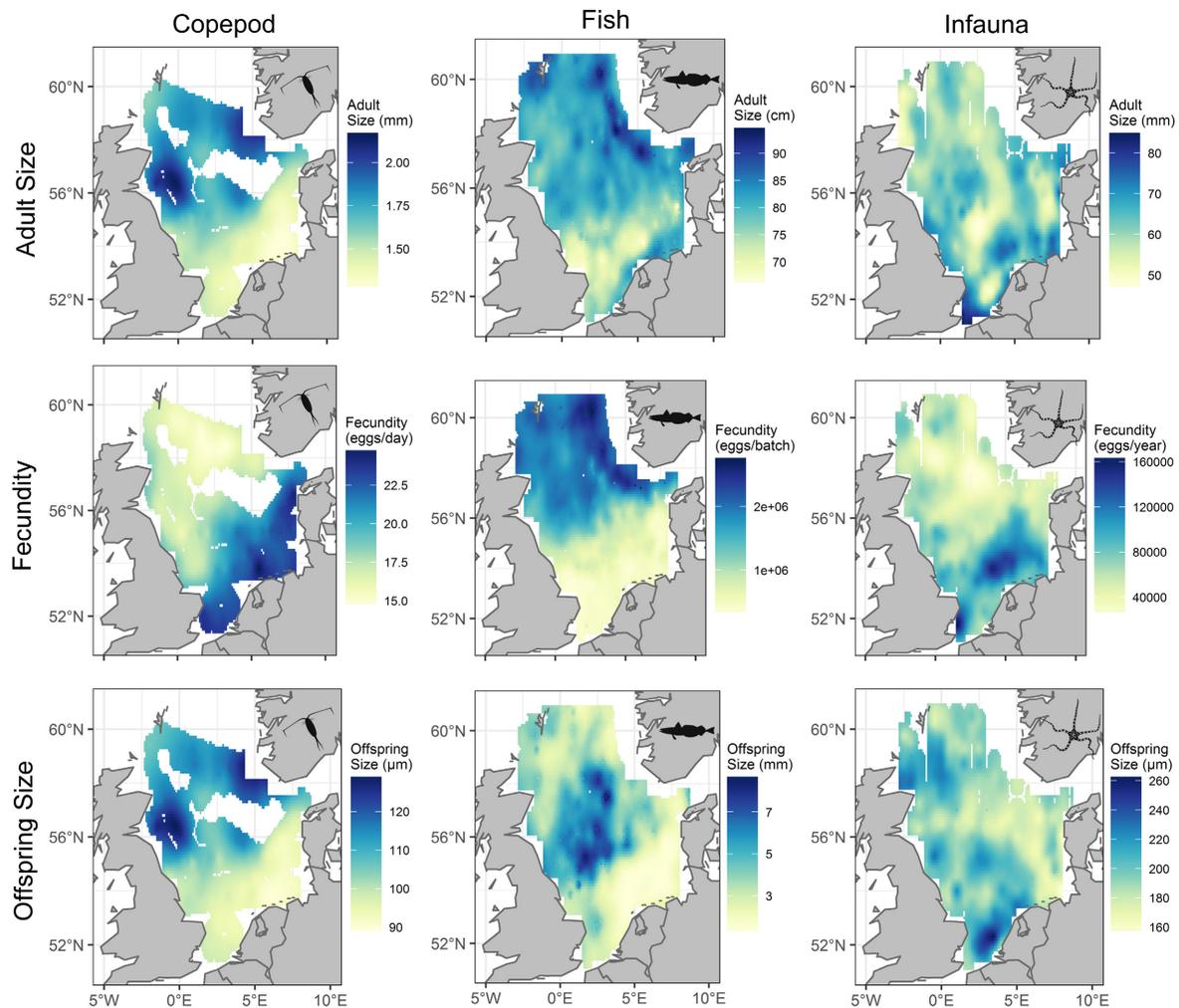


Fig. 3. Spatial patterns of community-weighted mean traits of copepods (left column), fish (middle column), and benthic infauna (right column), including adult size (top panel), female fecundity (middle panel), and offspring size (lower panel).

a pronounced north–south gradient for all three groups but with opposite direction for copepod and benthic infauna compared to fish that on average show higher fecundity in the northern part. Offspring size displays different patterns across the groups; it is higher in the central North Sea for fish, while it is higher in the north for copepods and in the western region for the benthic infauna. The benthic infauna adult size is rather patchily distributed and shows high values primarily along the coasts, while for both copepod and fish community, mean size appears to follow a south–north gradient. Overall, none of the life-history traits have a consistent spatial pattern across the three different groups. The spatial patterns observed for copepod and fish CWM traits in the late 1980s remain largely similar through time, as shown by recent maps calculated for the years 2005–2010 (Appendix S1: Fig. S3).

The first principal component (PC1) explained a high percentage of the CWM traits spatial variability for copepods and fish, 71% and 76%, respectively, and 42% of the benthic infauna variability (Fig. 4). This means that several traits are spatially co-varying, particularly for copepods and fish, and that the PC1 largely captures the main multi-trait spatial pattern while PC2 explains a low percentage of trait variability. Zooplankton communities characterized by large adult copepods are mainly associated with large offspring size and low fecundity. Fish communities with a high proportion of benthivorous species have low fecundity and relatively small adult size. Fish communities with large offspring size appear to vary independently of fecundity and adult size. The benthic infauna associated with PC1 mainly reflects the variability in feeding strategies (deposit feeding, suspension feeding, and predator) and to a lesser extent fecundity and offspring size. While adult size and fecundity of benthic infauna seem to co-vary, they appear independent of offspring size. PC1s of copepods and fish are correlated (Fig. 4; slope of 0.85 and $P < 0.001$) demonstrating a similar spatial structure of community key traits spatial variability for these two groups, that is, a similar spatial gradient in community traits turnover. Infauna and fish PC1s are also correlated but to a lesser extent (slope of 0.19 and $P < 0.001$), while copepod and infauna are not significantly correlated. PC2 relationships across taxa were

relatively weak with the higher one being between fish PC1 and copepod PC2 with a slope of 0.26 (Appendix S1: Fig. S4).

Trait–environment relationships

Environmental variables explained 74% of the total variance of the CWM traits. The first two axes of the RDA explained 65.4% and 14.3% of this variance, corresponding in total to 48.4% (0.74×0.654) and 10.6% (0.74×0.143) of the total CWM traits variability, respectively (Fig. 5). The first environmental axis (RD1) depicts a gradient from high seasonality in temperature to high surface salinity and depth, and therefore reflects a gradient from the shallow southern North Sea to the deeper and saline northern parts. The second environmental axis (RD2) describes a gradient from high temperature, mud-to-sandy sediment, and primary productivity (PCI) variability to sand to muddy and high PCI.

The CWM traits of copepods and fish are mainly projected along RD1, while the CWM traits of infauna are mainly reflected along RD2. Several copepod and fish CWM traits appear to co-vary and follow the same environmental gradients; for example, the adult size and offspring size of copepods co-vary with depth and salinity gradient, as do fish adult size, piscivorous diet, and fecundity. On the other hand, most of the benthic infauna traits appear to follow different environmental gradients than fish and copepod, notably seabed sediment, seabed stress, and primary productivity. However, this is not true for benthic infauna fecundity, which co-varies with the gradient of temperature seasonality in a similar way as copepod fecundity. With the exception of offspring size, fish traits appear to follow the depth gradient whereas copepod traits co-vary with the mixed layer depth.

Temperature seasonality, beam trawling effort, and primary productivity (PCI) were the variables that explained most of spatial variability in multi-traits (PC1) across taxa (Fig. 6). Beam trawling was the descriptor explaining most of the variability in fish ($R^2 = 0.76$) and benthic infauna ($R^2 = 0.26$), while temperature seasonality was the main factor explaining copepods variability ($R^2 = 0.74$). This result appears to be robust through time as the same variables (temperature seasonality, PCI, beam trawl) are found

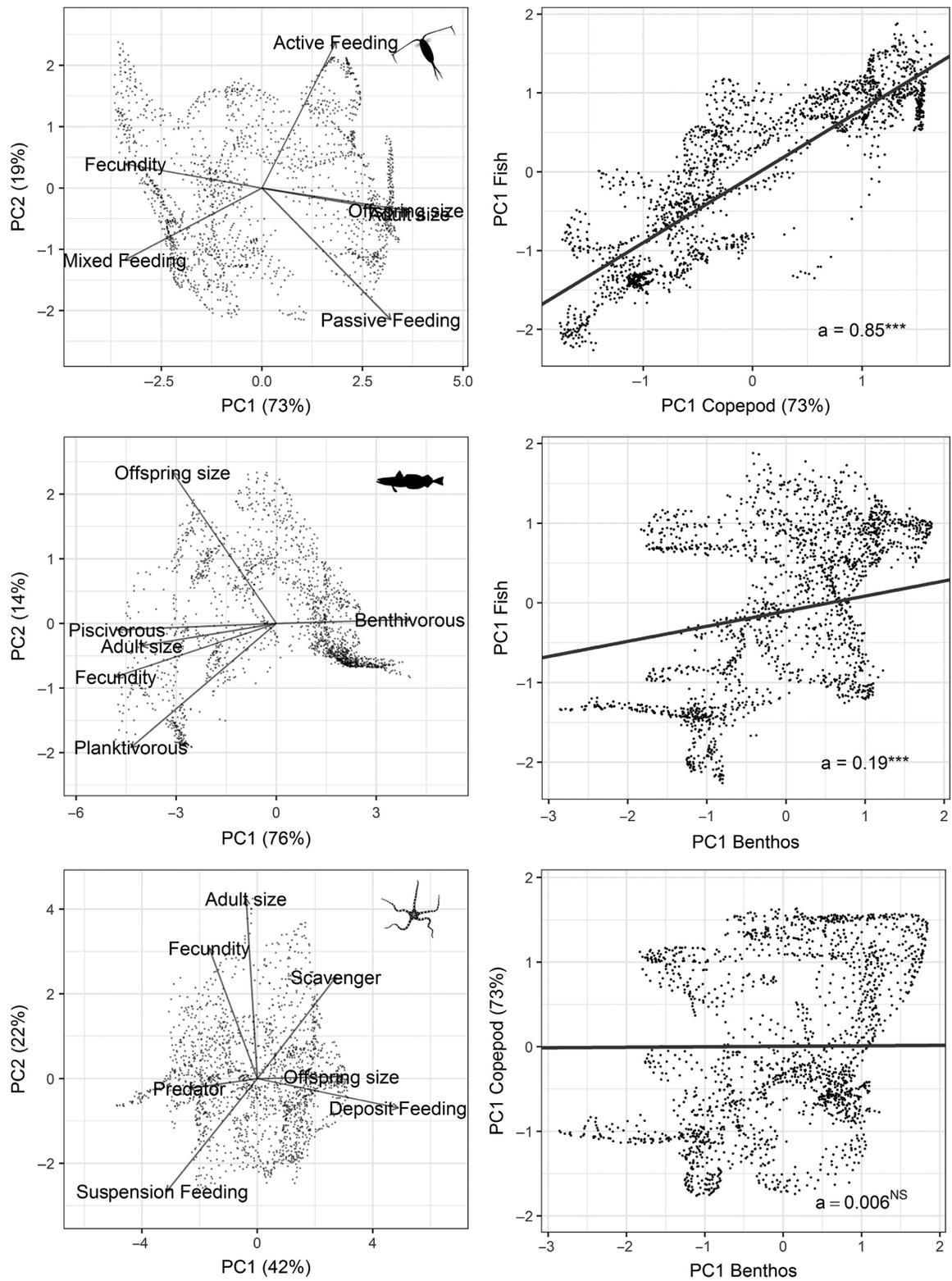


Fig. 4. Biplot of the principal component analysis of community-weighted mean traits of each group (left

(Fig. 4. *Continued*)

column) and the taxa pairwise relationships between the first principal components (PC1, right column). Each black dot represents a grid cell (site), the blue lines represent regression lines obtained from a generalized least square model with a Gaussian spatial autocorrelation structure, and “a” is the slope of the regression (** $P < 0.001$; NS: not significant).

to be most important for fish and copepod in more recent years (2005–2010; Appendix S1: Fig. S6). Relationships between PC2 and environmental factors were in general weaker ($R^2 < 0.2$) with beam fishing effort and bed stress being the variables explaining the most deviance for fish and benthic infauna, respectively (Appendix S1: Fig. S5).

DISCUSSION

We studied the spatial distribution in community traits of three different organism groups, fish, copepods, and benthic infauna, and investigated the influence of the environment and of fishing pressure on these patterns. There were no consistent spatial patterns between groups when

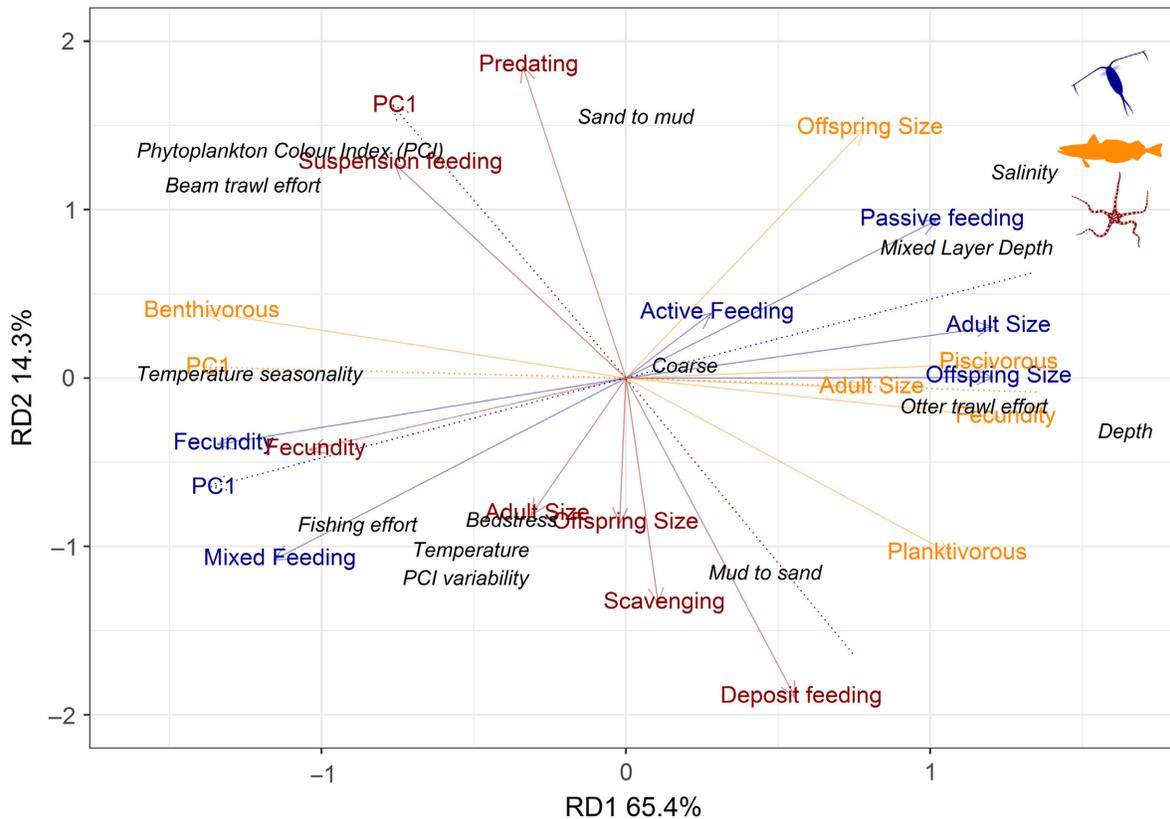


Fig. 5. Redundancy analysis showing the relationships among the community-weighted mean (CWM) traits (colors) and the set of environmental variables (black and italics). The length and orientation of the CWM traits (vectors and arrows) show the strength and direction of maximum correlation of the CWM traits of copepods (blue), fish (orange), and benthic infauna (red) on the first two principal components. Vectors that are close to each other are highly correlated and therefore follow similar spatial patterns and have similar response to the environment. Angles between the CWM traits and the environmental variables represent correlations: Small or straight angles (close to 0° or 180°) represent positive or negative linear relationship, respectively, while right angles (90°) express a lack of linear relations. PC1: first principal component from Fig. 4.

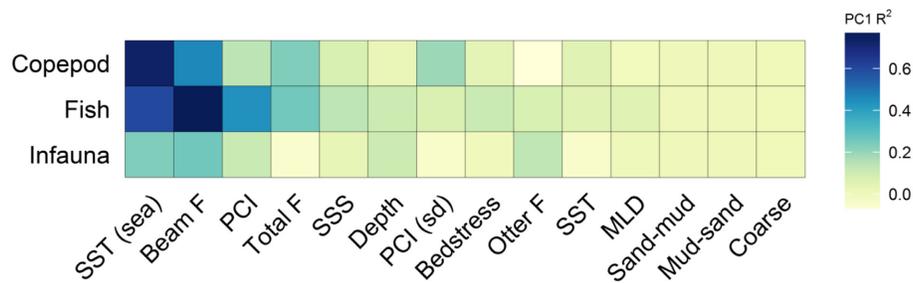


Fig. 6. Adjusted R -squared (R^2) obtained from a generalized additive mixed model with spatial autocorrelation structure between the first principal component (PC1) of copepod, fish, and infauna traits (from Fig. 4) and each environmental variable separately. The variables were ranked (left to right) from the variables with on average the largest R^2 to the ones with the lowest. SST (sea): sea surface temperature seasonality in $^{\circ}\text{C}$; Beam F, Otter F, Total F: fishing effort in number of hours of beam trawlers, that of otter trawlers, and total fishing effort by bottom trawlers, respectively; PCI and PCI (sd): Phytoplankton Colour Index annual mean and variability, respectively; SSS: sea surface salinity; Depth: depth in meters; Bedstress: tidal bed shear stress; SST: sea surface temperature in $^{\circ}\text{C}$; MLD: mixed layer depth in meters; Sand-mud, Mud-sand, Coarse: proportion of the sediment in the grid cell.

considering individual traits (fecundity, adult size, and offspring size) separately. However, we found that the overall spatial patterns of multiple CWM traits (illustrated by each group PC1) were correlated for copepods and fish and for fish and benthic infauna, while no significant relationship was found between copepods and infauna. The strongest driver of spatial variability for most of the CWM traits, notably for copepods and fish, appeared to be a pronounced south–north gradient in depth and seasonality, represented in the first axis of the RDA (Fig. 5). On the contrary, several benthic infauna CWM traits co-varied with other environmental variables, primarily related to seabed properties (sediment and bed stress) and primary productivity. Beam trawling effort and temperature seasonality appeared to be strong drivers of the overall trait variability (PC1; Fig. 6). We found that trait responses to environmental gradients cannot be generalized across organism groups, likely due to different life-history strategies and habitats (e.g., copepods are drifting in the water column, while benthic infauna is primarily sessile in the sediment).

As a result of this habitat decoupling, some spatial trait variability was explained by group-specific habitat conditions (Fig. 5). For example, benthic infauna adult size co-varied with tidal bed stress, which is a natural disturbance that influences the structure and composition of benthic communities (Hiddink et al. 2006). Bed

stress impacts the trait composition of the community by favoring species exhibiting opportunistic life-history strategies, such as short-lived polychaetes (Neumann et al. 2016). For demersal fish communities, many traits appear to be regulated by depth. Deep-water fish communities generally exhibit larger adult body size and offspring size as well as longer lifespan than inshore fish communities (Mindel et al. 2015).

Several fish and benthic infauna traits varied according to spatial gradients of fishing effort, notably beam trawling. While fishing has been shown to affect the traits of fish species, it is more likely here that it is the specific trait composition of the fish communities that drives high fishing effort rather than the inverse because beam trawlers target particular species with specific sets of traits. For example, high beam trawl effort is historically located in the southern North Sea, where abundant flatfishes (i.e., plaice and sole) are targeted. The high abundance of these species would strongly influence the CWM traits of the southern communities (high proportion of benthivorous, small size). Thus, the correlation observed between fish community traits and fishing effort might arise because fisheries have targeted these particular species. In addition, non-targeted fish species might be vulnerable to fishing due to their trait characteristics, for example, sharks and rays with large size, slow growth, and late maturation (Cheung et al. 2005). Beam trawl effort was also

the variable explaining most of the variance of benthic infauna multi-traits variability (Fig. 6). The trait composition of benthic communities is indeed known to be altered by fishing activities, with large, hard-bodied, and slow-growing species being more vulnerable to trawling (Callaway et al. 2007, van Denderen et al. 2015).

Seasonality of temperature and primary production variability both appear to affect reproductive and feeding strategies of the three groups. The gradient in temperature seasonality is marked in the North Sea where the southern part, due to permanent mixing and shallow depths, displays high seasonal patterns, as opposed to the northern part that experiences seasonal stratification and less variability. This spatial difference has been shown to impact the distribution of organisms and the communities they form (Künitzer et al. 1992, Dencker et al. 2017). Seasonality shapes annual cycles and food availability and by doing so impacts the composition of the communities by selecting for organisms with a particular set of life-history traits that enables them to grow, reproduce, and feed in these environments. This can, for example, be reflected in the prevalence of specific reproductive strategies in seasonal environments (Marshall and Burgess 2015).

The observed trait distributions in our study are likely a complex outcome of environment, anthropogenic impacts (e.g., fishing activity), biotic interactions (prey–predators) within and across the studied organism groups (Fig. 1), and evolutionary history. Here, we focused on trait relationships with the environment, yet life-history trait distributions cannot be dissociated from evolutionary history, as there might be trade-offs among traits and lineage-specific constraints on how traits can vary (Stearns 2000, Reich et al. 2003). Here, we found that several traits co-varied spatially and that when looking at combinations of traits, instead of a single trait, similar spatial structures were found between organisms (e.g., copepod and fish; Fig. 4). Life-history strategies emerge from evolution of suites of life-history traits in response to selection imposed by abiotic and biotic environmental forcing (Winemiller and Rose 1992) and as such are not randomly distributed through space (Pecuchet et al. 2017). As a result, multiple life-history traits have simultaneously evolved and are found in specific combinations, such as low

fecundity and large offspring size or high fecundity and small offspring size (Smith and Fretwell 1974). Despite obvious difference in strategies and habitats across our studied taxa, some of these typical life-history trait correlations, and how they are shaped by environmental constraints, could explain why we observed convergence in multiple taxa community trait responses (Ibañez et al. 2009, Winemiller et al. 2015).

The trait distributions presented in this study are limited to a time period in the late 1980s, due to the lack of a more recent survey for benthos. The aim of this study was to compare trait–environment relationships across organisms during the same period, whereas the age of the datasets was less important. In addition, we show that the historical patterns resemble more recent data for fish and zooplankton from the late 2000s (Appendix S1: Fig. S3). Given the similarity in trait distributions, as well as the consistency in the key environmental variables identified as drivers (Appendix S1: Fig. S6), the association between life-history traits and a given habitat remains robust for these two groups. Whether the same consistency in trait distributions and trait–environment relationships applies also to infauna, and whether the observed decoupling in the community traits between strictly benthic and strictly pelagic species remains constant, is unknown and merits further attention. In addition, intra-specific variability in trait values, which was unaccounted for in this study, due to lack of spatially resolved trait data, also deserves future attention, as it can provide further insights into the primary forces structuring communities (Violle et al. 2012).

The use of life-history traits that can be characterized in multiple taxa permits to compare different taxonomic groups and investigate environmental drivers of their communities' composition. In this study, we observed a decoupling in the community traits between the strictly pelagic and strictly benthic species, while the traits of demersal fish communities, living and feeding in both habitats, co-varied with both pelagic and benthic species' traits. We found that trait responses to environmental gradients cannot be generalized across organism groups, pointing toward potential complex responses of multi-taxa communities to environmental change. The functioning of an ecosystem depends on the

diversity and interactions of multiple taxonomic groups (Soliveres et al. 2016), and understanding the responses of these different groups to environmental pressures is a prerequisite to conserve and manage ecosystems.

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