

# From traits to life-history strategies: Deconstructing fish community composition across European seas

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## Abstract

**Aim:** The life history of a species is determined by trade-offs between growth, survival and reproduction to maximize fitness in a given environment. Following a theoretical model, we investigate whether the composition of marine fish communities can be understood in terms of a set of life-history strategies and whether the prevalence of the strategies follows specific spatial patterns that can be related to the environment.

**Location:** European seas.

**Time period:** 1980-2014.

**Major taxa studied:** Fish.

**Methods:** An extensive set of scientific bottom trawl surveys was collected to obtain the species composition of fish communities across European seas. We complemented these data with species-specific information regarding six life-history traits, reflecting reproductive, growth and feeding modes. We then calculated the optimal number of strategies needed to summarize the information contained in the traits by using archetypal analysis. The proportion of each obtained strategy in the communities and their spatial patterns were explained as a function of the environment and their temporal changes were investigated.

**Results:** The species could be decomposed into a continuum of three life-history strategies—opportunistic, periodic and equilibrium—resulting from trade-offs between traits. The marked spatial patterns of these strategies could be explained by depth, temperature and its seasonality, chlorophyll and fishing effort. In recent years, opportunistic and equilibrium strategies significantly increased, probably due to an increase in temperature and decrease in fishing effort.

**Main conclusions:** Our empirical analysis supports a theoretical framework outlining three life-history strategies of fish. The strategies vary predictably in space and time in response to the environment. This highlights the underlying process whereby fitness is optimized through trade-offs between growth, feeding and reproduction under different environmental conditions. Due to their response to the environment, life-history strategies provide a suitable tool for monitoring and understanding community changes in response to natural and anthropogenic stressors, including fishing and climate change.

## KEYWORDS

archetypal analysis, community composition, depth, fecundity, life-history strategies, marine fish, offspring survival, size, temperature, trade-off, trait

## 1 | INTRODUCTION

The trait-based study of biodiversity is a field that has been an expanding in recent decades (Cadotte, Albert, & Walker, 2013; Petchey & Gaston, 2002; Schleuter et al., 2010). Traits are often referred to as any characteristics of an individual organism, or group of organisms, which encompass morphological, demographic or physiological attributes (Violle et al., 2007). The use of traits instead of taxonomic information has several advantages for the study of biodiversity because they provide a more fundamental and mechanistic approach to understanding community composition (McGill, Enquist, Weiher, & Westoby, 2006; Pecuchet, Törnroos, & Lindegren, 2016; Shipley, Vile, & Garnier, 2006). Trait-based approaches also permit a reduction of the complexity of community diversity by focusing on the factors that best characterize an organism's fitness (Litchman, Ohman, & Kiorboe, 2013) and they have also been successfully related to ecosystem functions and services in the terrestrial (Diaz & Cabido, 2001; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011) and marine (Bellwood, Hoey, & Choat, 2003) realms.

The selection of a relevant set of key traits to characterize species, and ultimately communities, can, however, be difficult (Petchey & Gaston, 2006), especially when the aim is to explain ecosystem functions (Lavorel & Garnier, 2002; McIntyre, Lavorel, Landsberg, & Forbes, 1999). In particular, the decision on how many traits to include is controversial, because the use of too many traits increases complexity and may introduce redundancy due to correlation among closely related traits. Trait information can instead be reduced to combinations of particular trait values, so-called functional groups. Functional groups are defined as a unit of species sharing similar trait attributes, for example body size and trophic guild (e.g., Halpern & Floeter, 2008). However, adding new traits to this analysis can substantially increase the number of functional groups.

In contrast to functional groups, life-history strategies are defined as a combination of trait attributes and are the result of inter-relationships and trades-offs among key traits (Winemiller, Fitzgerald, Bower, & Pianka, 2015). They are often based on a theoretical framework and are used to shed light on the evolution of the life history of organisms, as well as the environment in which the species occur (Charnov, Gislason, & Pope, 2013). Some well-known examples of life-history theories or models are *r*- and *K*-selection (Pianka, 1970) or the fast-slow life-history continuum (Franco & Silvertown, 1996). Due to their simplicity, these linear models of life-history strategies have been used in numerous studies, ranging from population dynamics (e.g., Oli, 2004) to community spatial patterns (e.g., Wiedmann, Primicerio, Dolgov, Ottesen, & Aschan, 2014). However, this approach has also been criticized for oversimplifying reality (Bielby et al., 2007; Nichols, Conley, Batt, & Tipton, 1976).

For fish communities, Winemiller and Rose (1992) developed the equilibrium-periodic-opportunistic (EPO) model. This theoretical model links three strategies characterized by trade-offs between fecundity, juvenile survival and generation time to environmental stability and predictability: 'equilibrium species' with high juvenile survivorship;

'opportunistic species' with low generation time; and 'periodic species' with high fecundity. The equilibrium strategy is thought to prevail in stable and predictable environments, while the opportunistic strategy prevails in unstable and unpredictable environments. The periodic strategy is thought to occur in seasonal but periodically fluctuating environments. A number of studies have used the EPO model to investigate temporal changes in and spatial distribution of the composition of freshwater fish communities (Mims & Olden, 2012).

In this study we investigate whether marine fish species present in European seas can be categorized into similar life-history strategies based on their trait attributes. Furthermore, we investigate whether there are any consistent geographical and temporal patterns in the prevalence of life-history strategies within fish communities across Europe and whether the patterns and trends can be explained by external (environmental) factors. For this analysis, the shelf seas of the north-east Atlantic provide an excellent study area since they contain pronounced natural gradients in terms of temperature, productivity and biodiversity, for example, and are subjected to various anthropogenic pressures including fishing and eutrophication (Grizzetti, Bouraoui, & Aloe, 2012). Furthermore, these seas are also rich in data, and are therefore an ideal area for testing the life-history strategies hypothesis on fish communities using standardized datasets with a high taxonomic and spatial resolution.

## 2 | MATERIALS AND METHODS

### 2.1 | Bottom trawl surveys

Fifteen scientific bottom trawl surveys covering ecosystems from the Mediterranean Sea to Greenland and spanning on average 10 recent years (2002–12) were collated (see Appendix S1 in the Supporting Information). As our focus was on offshore fish communities, and due to different survey sampling schemes, hauls sampled at depths shallower than 20 m were excluded to avoid the inclusion of coastal fish species. The refined data set contained approximately 20,000 individual hauls (i.e., stations) that lasted on average 30 min and covered 3 nautical miles. Not all surveys used the same taxonomic recording, therefore species' scientific names were checked against the World Register of Marine Species and updated by the 'accepted' scientific name when appropriate. For some species that were difficult to identify, taxonomic recording was specified to the genus level. For each 0.5° latitude and longitude cell covered by the surveys, we derived the relative abundances of all the species present, calculated as the sum of its abundance in all the hauls performed in a grid cell divided by the total abundance of all the species in that grid cell. The species' abundances were log transformed prior to the calculation. A species was noted present in a grid cell if it was ever recorded in one of the hauls performed in that grid. In order to study temporal changes in the prevalence of life-history strategies, we calculated relative abundances and presence of species using the same method but for each year separately. Due to the limited time span of many surveys, we restricted the temporal analysis to the North Sea where time series are available from 1980 onwards.

## 2.2 | Trait information

Six traits were selected to cover the fundamental Darwinian objectives of an organism: to feed, survive and reproduce. These traits were also selected as they were previously used to describe the theoretical life-history strategies of fish species based on the EPO model (Mims, Olden, Shattuck, & Poff, 2010; Winemiller, 2005). These traits are: maximum length, life span, trophic level, fecundity, offspring size and parental care. The first three traits were extracted from FishBase (Froese & Pauly, 2012). Maximum length ( $L_{\max}$ ) represents the longest total length ever recorded for a given species. Life span is defined as the theoretical maximum expected age for a species and is estimated within FishBase using the growth ( $K$ ) and length at infinity ( $L_{\text{inf}}$ ) parameters from the Von Bertalanffy growth equation.  $L_{\text{inf}}$  is calculated from empirical growth data for the majority of the species but is inferred from  $L_{\max}$  for data-poor species, hence creating a dependency between these variables for some species in FishBase. Trophic level represents the position of a species in the food chain, ranging from a value of 2 when the diet is based on plants or detritus to 4.5 for top predators. Trophic level is primarily calculated from empirical diet studies or inferred from taxonomically related species. Fecundity is the average total number of offspring produced per mature female per year, usually calculated as the number of oocytes in the ovary. Fecundity can either be determinate, where the annual potential fecundity is set before the onset of the spawning season, or indeterminate, where the species continuously produces eggs during the spawning season and the annual potential fecundity is not fixed. Since information on fecundity type and the number of batches spawned per year is largely lacking, the average total number of offspring produced per year for batch spawners is likely underestimated. The offspring size corresponds to the average size of the offspring released in the water (i.e., eggs for oviparous species or larvae/juveniles for ovoviviparous species). Parental care relates to the investment of the parents in the survival of their offspring. Parental care was transformed from categorical to continuous values, using a similar approach to Winemiller (1989), as follows: (1) pelagic egg, (2) benthic egg, (3) hidden brood, (4) guarded brood and (5) bearer. These three traits values were primarily derived from literature (Pecuchet, Lindegren, et al., 2016). For each species, only one value per trait was used assuming that inter-species variability is higher than intra-species variability. There were approximately 600 unique species or genera recorded in the surveys. Out of these, 258 species and 27 genera had complete information for all six traits and were used in the analysis. Although they represented only half of the entire species pool recorded in the surveys, the species retained were the most frequently occurring and most abundant ones. Hence, on average, across all the  $0.5^\circ$  grid cells, 95% of the species present and 97% of the individuals recorded in each grid cell had trait information.

## 2.3 | Life-history strategies

We used the unsupervised learning method of archetypal analysis (AA) to characterize European marine fish species. AA is similar to cluster analysis, but focuses on identifying extreme values that can be used as

archetypes rather than on the means or medians of a cluster (Cutler & Breiman, 1994). The core of the AA approach is the identification of points (archetypes) forming the corners of the convex hull volume encompassing the trait space (Mørup & Hansen, 2012): points are then represented by proportions based on the proximity of the point to each archetype. AA has several advantages compared with traditional cluster analysis such as  $k$ -mean and  $k$ -medoid, since these can result in an arbitrary grouping of neighbouring points when the data are continuous. For example, two data points which are at the limits of the space defined by two clusters might be categorized differently. Instead, AA gives similar values to the points that are close to each other in trait space (Hart et al., 2015), resulting in a continuous grouping instead of a categorical one (Cutler & Breiman, 1994). Therefore, AA is a suitable tool for identifying atypical species in a dataset, which makes it useful for characterizing life-history strategies based on traits.

Trait data were normalized before input to AA by  $\log_{10}$  transformation of fecundity, offspring size, body size and life span, and then all six traits were standardized (i.e., to a mean of 0 and a variance of 1) to ensure equal weights in the AA. The AA was performed on the traits matrix for a fixed number of strategies  $k = 1, 2, 3, \dots, 10$ , and the residuals sum of squares (RSS) of 10 iterations was calculated for each  $k$  using the package 'archetypes' in R (Eugster & Leisch, 2009). A robust, iteratively reweighted least-squares fitting algorithm was used to downweight the influence of the outliers (Eugster & Leisch, 2011). We used the 'elbow criterion' to select the optimal number of strategies permitting to minimize the RSS while minimizing the number of strategies. This is done visually by assessing the number corresponding to a significant drop in the RSS. The result of the AA, and notably the position in the traits space of the archetypes, was visualised using a principal components analysis (PCA) biplot performed on the six traits. The prevalence of the optimal strategies was then mapped as a proportion weighted by the relative abundances of the species or based on species presence only. The proportions were calculated as the mean of each life-history strategy from the species composition in each grid cell. Hence, each grid cell has:  $p\text{LHS1} + p\text{LHS2} + p\text{LHS3} = 1$ , where  $p$  is the proportion of the corresponding life-history strategy (LHS).

## 2.4 | Environmental predictors

Several environmental variables were collected to explain the observed spatial patterns of the life-history strategies. Annual, winter (January–March) and summer (July–September) mean sea temperature and salinity at the surface and bottom were obtained at a  $0.25^\circ$  grid resolution from the World Ocean Atlas (<http://www.nodc.noaa.gov/OC5/woa13>) for the period 2005–12 and averaged on a  $0.5^\circ$  grid. Surface and bottom temperature seasonality were calculated as the difference between the summer and winter mean temperatures. Chlorophyll data, used as a proxy for primary production, were obtained from the GlobColour database (<http://hermes.acri.fr/>) as monthly averages for the years 2002–12 on a  $0.5^\circ$  grid resolution. All the chlorophyll concentrations were log transformed prior to calculations. Several metrics were derived from the dataset, including mean annual chlorophyll concentration and mean chlorophyll concentration during spring (March–May).

Furthermore, chlorophyll variability during the year (a proxy for seasonality and resource stability) was calculated as the standard deviation of the mean chlorophyll concentration of each month across years, while variability of the chlorophyll concentration during the spring bloom (a proxy for resource predictability) was estimated as the standard deviation of mean spring chlorophyll concentrations between years. Minimum, maximum and variability (standard deviation) of depth were obtained for each 0.5° cell from ETOPO1 (<http://www.ngdc.noaa.gov/mgg/global>), whereas mean depth was calculated directly from the depth of the hauls performed.

Fishing has an important impact on the composition of a community by favouring small and fast-growing species relative to large and slow-growing ones (De Juan, Thrush, & Demestre, 2007; Jennings, Alvsvåg, et al., 1999; Sguotti, Lynam, García-Carreras, Ellis, and Engelhard, 2016). Fishing intensity can thus be an important variable explaining the spatial prevalence of strategies. Unfortunately there are few extensive data on fishing effort, and these are only available for a subset of the area. As a proxy for bottom fishing intensity we used the ratio of the area of the seabed swept by bottom trawl fishing gear derived from vessel monitoring system (VMS) intensity data (ICES, 2015). The swept area ratio was calculated per  $0.05^\circ \times 0.05^\circ$  grid cell per year for vessels greater than 12 m long, and can be interpreted as the percentage of grid cell equivalent area swept per year. For this study, the swept area ratio was aggregated to the 0.5° grid cell and averaged over the four years 2009–12.

For the temporal case study in the North Sea, sea surface temperature data were gathered for the years 1980–2014 from a hydrographic analysis product (AHOI; Núñez-Riboni & Akimova, 2015). For each year, the mean temperature was calculated as the mean of all the months, and temperature seasonality was calculated as the difference between the summer and winter months. Fishing effort, calculated as the number of hours fished by beam trawlers or otter trawlers in the North Sea, was obtained for the years 1991–95 and 2003–12 (Engelhard, Lynam, García-Carreras, Dolder, & Mackinson, 2015; Jennings, Greenstreet, & Reynolds, 1999).

## 2.5 | Modelling the life-history strategies

The strategies of different species emerge from evolution of their life histories, and as such their prevalence has been hypothesized to be non-randomly distributed and intimately linked to the environment (Grime, 1977; Winemiller & Rose, 1992). We hence tested the hypothesis that the prevalence of a life-history strategy could be explained by environmental variables using generalized additive mixed models (GAMM), which allow for curvilinear relationships between the response and explanatory variables (Wood, 2006) (e.g., in case of an environmental optimum or saturation) and permit correction for spatial autocorrelation. In a previous analysis we reduced the number of environmental variables to avoid problems with correlation among predictors and retained only unclustered or not highly correlated ( $r < .8$ ) variables (Dormann et al., 2013). Eight abiotic variables were retained for the analysis: mean depth of the sampled hauls, maximum and variability of depth in each grid cell; mean and seasonality of sea surface

temperature; mean and variability of annual chlorophyll concentration and sea surface salinity (Appendix S2).

We modelled the life-history strategies as a function of the abiotic variables. The proportions of the different life-history strategies were logit transformed prior to the analysis to normalize the data and then fitted as the response variable with a Gaussian (normal) error distribution (Warton & Hui, 2011). Spatial autocorrelation was incorporated into this model with a Gaussian structure chosen from visual assessment of the variogram. The smoothing spline functions ( $s$ ) were constrained to four degrees of freedom ( $k = 4$ ), allowing for third-order relationships but restricting flexibility during model fitting. The strategy proportions were corrected for sampling effort by including the number of hauls performed in each grid cell as an additional explanatory variable smoother in each model and only grid cells with more than two hauls were included ( $n = 885$ ). All the possible models containing from zero to a maximum of three environmental variables were fitted and evaluated using the package 'MuMIn' in R (Barton, 2016), and the best model (defined as the one with the lowest Akaike information criterion, AIC) was retained. For each strategy the predictors of the best model were plotted against the response variable. Standard model checking diagnostics were applied. We calculated the relative variable importance (RVI) to assess the contribution of each variable to the performance of the final multivariate GAMM. RVI was quantified for each variable of the final models by randomly permuting the values of the variable of interest across grid cells and measuring the difference between the adjusted  $r^2$  of the newly fitted model compared with the original model, that is, measuring the drop in the quality of the model fit. Thus, a variable that caused a large decrease in model performance when randomized made a large contribution to the fit of the model.

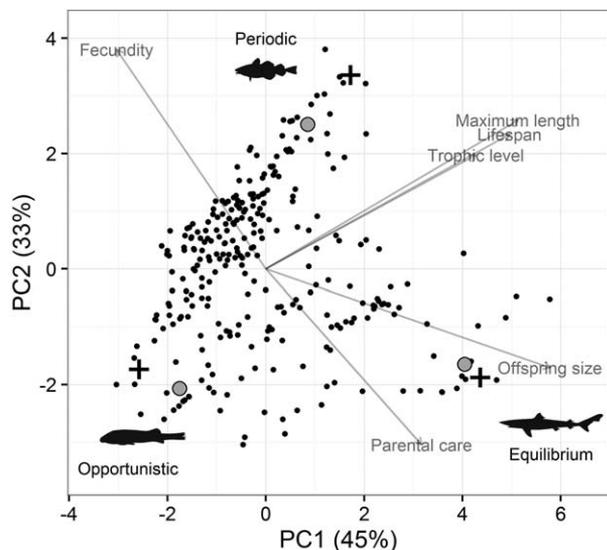
To explore the potential impacts of fishing on the prevalence of the different strategies, a second model which integrated both environmental variables and fishing intensity was performed on a sub-area of the study for which fishing data were available. The same environmental variables used in the main model were tested as explanatory variables alongside fishing intensity using the same GAMM method.

For the temporal study in the North Sea, changes in the life-history strategies and environmental variables were modelled using a linear model corrected for first-order temporal autocorrelation (i.e., AR1).

## 3 | RESULTS

### 3.1 | Summarizing trait variability into life-history strategies

The optimal number of archetypes ( $k$ ) needed to encompass the spatial volume of trait-space was found to be three (Appendix S3). The largest drop in the RSS occurred when passing from two to three archetypes, and adding a fourth one did not significantly reduce the RSS. The three corresponding life-history strategies were represented in a biplot where the first two axes of the underlying principal component analysis (PCA) explained most of the trait variability (77%; Figure 1). The first axis (PC1) explained almost half of the total variability (45%) and was



**FIGURE 1** Plot of the first and second principal components (PC1 and PC2) based on a principal component analysis (PCA) on the six selected traits. Each species used in the study is represented by a black dot. The three extreme points (archetypes) that encompass the trait-space are represented by black crosses, corresponding to the equilibrium, opportunistic and periodic strategies, respectively. Furthermore, each of the strategies is illustrated by one characteristic species marked by grey dots, namely cod (*Gadus morhua*) a periodic species, sand goby (*Pomatoschistus minutus*) an opportunistic species, and school shark (*Galeorhinus galeus*) an equilibrium species

driven by offspring size, maximum length, life span and trophic level. The second axis was driven by fecundity and parental care. Several traits were clustered (maximum length, life span and trophic level), while others were negatively correlated (fecundity against parental care and offspring size). The three life-history strategies could be visualized as a triangle in trait space, with each extreme point representing a unique combination of trait characteristics (Figure 1). These strategies and their relations with traits corresponded closely to the theoretical model of Winemiller and Rose (1992), and are henceforth referred to as opportunistic, periodic and equilibrium strategies, respectively. The opportunistic strategy was characterized by species with small size, low trophic level and short life span but with relatively high fecundity and parental care, such as species of gobidae and ammodytidae, including the sand goby (*Pomatoschistus minutus*) and lesser sand eel (*Ammodytes tobianus*), as well as small pelagic fish, for example the European anchovy (*Engraulis encrasicolus*). The periodic strategy was characterized by species with medium to long life span, length and high trophic level, high fecundity but low parental care and offspring size, such as the sunfish (*Mola mola*), conger eel (*Conger conger*) and several species of gadoids including the blue ling (*Molva dypterygia*) and Atlantic cod (*Gadus morhua*). The equilibrium strategy was characterized by species with long length and life span and high trophic level, low fecundity but large offspring size and high parental care, such as rays and sharks, for example the marbled electric ray (*Torpedo marmorata*) and spiny dogfish (*Squalus acanthias*), as well as the rabbitfish (*Chimaera monstrosa*).

The species were not clustered around the end-points of the three strategies but instead demonstrated a continuum between the strategies (Figure 1). A species could therefore have characteristics of more than one strategy at the same time, and species were thus characterized by the proportion expressed by each of the strategies (Appendix S4). Both the opportunistic and the periodic strategies were prominent in the species pool, while few species showed an equilibrium strategy

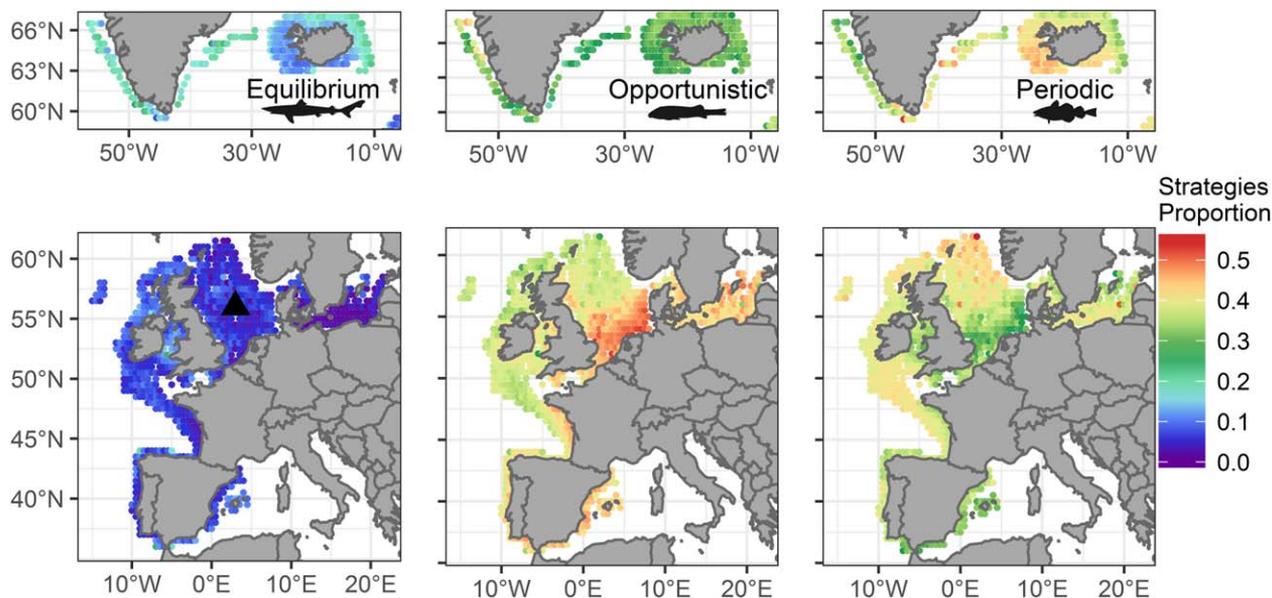
### 3.2 | Patterns of life-history strategies

The distribution of life-history strategies exhibited clear spatial patterns (Figure 2). The proportion of species showing the equilibrium strategy was generally much lower than for the periodic and opportunistic strategies, with values ranging between 0% and 36%. On the contrary, the proportions showing periodic and opportunistic strategies were never lower than 25% and 23%, and reached a maximum of 66% and 64%, respectively. The proportion of species showing the equilibrium strategy was highest at high latitudes, in Iceland and Greenland, as well as in the Balearic and Irish Seas. The opportunistic strategy displayed a north-west to south-east gradient, prevailing notably in the Baltic Sea, the southern North Sea and the Mediterranean while being less abundant in Iceland and Greenland. The periodic strategy did not exhibit strong spatial patterns as it had a relatively high prevalence in most of the studied area, notably south of Iceland, in the northern offshore of the North Sea and in the Celtic Sea.

We found the same overall spatial pattern when using presence data (Appendix S5) and the prevalence of strategies in the communities calculated using abundance and presence were highly correlated. A notable change was a shift to a lower prevalence for equilibrium strategies when using abundance compared with presence (Appendix S5). The spatial patterns were robust to different seasons, as seen for example in the North Sea (Appendix S6).

### 3.3 | Environmental predictors of life-history strategies

The best models with a maximum of three abiotic predictors explained 53%, 70% and 78% of the variability of the periodic, opportunistic and equilibrium strategies, respectively (Table 1). Sea surface temperature (SST) and SST seasonality were retained in all the final models. SST was the variable that explained most of the variability in the opportunistic strategy, with a positive relationship, while it followed a negative relationship for the equilibrium strategy (Figure 3). SST seasonality was the most important variable explaining the variability of the equilibrium strategy, and followed a negative relationship. On the other hand, the opportunistic strategy had a positive and saturating relationship with SST seasonality. Depth was also an important predictor of the equilibrium and periodic strategies, with a positive and hump-shaped relationship, respectively. Chlorophyll concentration was also retained in the opportunistic strategy and followed a positive relationship. The same explanatory variables were found when using presence only, with the exception of the equilibrium strategy for which chlorophyll concentration was retained instead of depth (Appendix S5). For the sub-area



**FIGURE 2** Proportion of the different life-history strategies equilibrium (left), opportunistic (middle) and periodic (right) in each 0.5° grid cell across the European seas calculated from species abundance. At each grid cell, the sum of the proportion of the three life-history strategies adds to 1. The top panel represents Greenland and Iceland while the bottom panel shows western Europe. On the bottom left panel, the black triangle represents the location of the North Sea, the ecosystem used in the temporal case study

where both environmental variables and fishing intensity were available, the best predictors of the opportunistic strategy were depth, temperature and temperature seasonality, explaining 78% of the variability, while for the periodic strategy they were depth, temperature and chlorophyll, explaining 63% of the variability. For the equilibrium strategy, fishing intensity, depth and SST were the most important variables, explaining 48% of the variability, with fishing demonstrating a negative relationship with prevalence (Appendix S7).

**TABLE 1** Variables and parameters of the best final generalized additive mixed models, with a maximum of three abiotic variables and corrected for the sampling effort

Life-history strategies	Best model	R <sup>2</sup>	RVI
Opportunistic	SST + SST seasonality + Chl	.78	
	SST		.38
	SST seasonality		.34
	Chl		.26
Periodic	SST + depth + SST seasonality	.53	
	SST		.13
	Depth		.12
	SST seasonality		.09
Equilibrium	SST seasonality + SST + depth	.70	
	SST seasonality		.20
	SST		.09
	Depth		.04

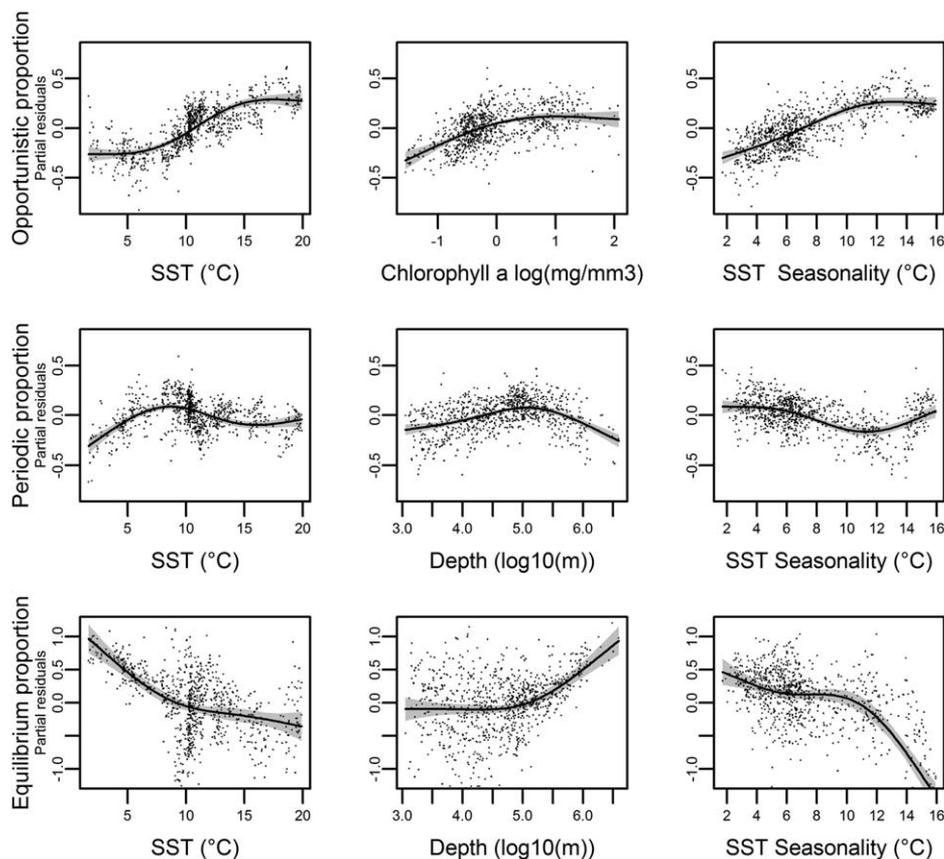
R<sup>2</sup> is the adjusted R<sup>2</sup> of the final model and RVI is the estimated relative variable importance of each variable present in the final model—it corresponds to the drop in the model R<sup>2</sup> when the variable is randomized. All variables in the final model are significant ( $p < .001$ ).

SST, sea surface temperature; SST seasonality, seasonality in sea surface temperature; Depth, mean depth of the hauls performed; Chl, chlorophyll a concentration.

In the North Sea, during the period 1980–2014 the proportion of species showing the periodic strategy declined ( $p < .001$ ) while it increased for the equilibrium ( $p < .001$ ) and opportunistic ( $p < .001$ ) strategies (Figure 4). Although demonstrating significant temporal trends, the magnitudes of change in prevalence were rather moderate, amounting to a decrease in the periodic strategy from 46% in 1980 to 38% in 2014 and an increase in the equilibrium and opportunistic strategies from 7% to 12% and 47% to 50%, respectively. During the same time period SST increased ( $p < .01$ ), whereas for the recent period (1990–2012) fishing effort showed a marked decline, especially for beam trawlers ( $p < .05$ ).

#### 4 | DISCUSSION

The characterization of ecological communities by a set of biological traits is challenging because the selected traits are often correlated and therefore contain similar information. In this study, we show that several key traits of marine fish are correlated and that the variability of these traits could be reduced into three main components based on AA. AA has several advantages over traditional cluster analysis, especially when the data are continuous, as it gives similar values to the points that are close to each other in trait-space (Hart et al., 2015). Each point in the trait-space, for example a species, is defined as a convex combination (i.e., a proportion that sums to 1) of the archetypes (in this case, the three life-history strategies) rather than being assigned to a single class or cluster (Cutler & Breiman, 1994). Furthermore, the results of the AA are also easily interpretable thanks to the more pronounced contrasts between the extreme archetypes compared with cluster analysis. AA has been used in different research fields such as economics, astrophysics and pattern recognition for some years now



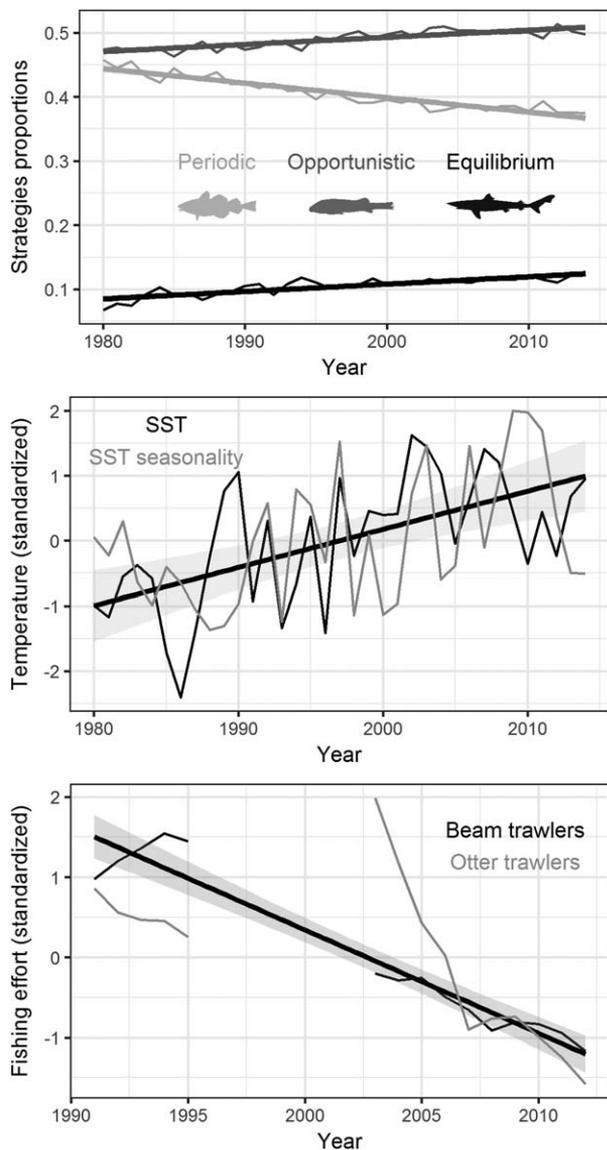
**FIGURE 3** Relationships between the proportion of life-history strategies in the different communities and their environmental predictors retained in the best generalized additive model. SST, sea surface temperature

(Bauckhage & Thureau, 2009), but has only recently been applied in biology and ecology (Hart et al., 2015). Using this novel approach the three main trait components identified are in good agreement with the theoretical model of Winemiller and Rose (1992), where the trait-space is encompassed by a triangular shape with end-points corresponding to a life-history strategy—opportunistic, equilibrium and periodic. At the community level the proportion of the strategies expressed followed a strong spatial pattern in European seas. These spatial patterns can be explained by abiotic variables, where each strategy prevails under different environmental conditions, largely depending on SST and its seasonality, as well as depth. The prevalence of the strategies is not fixed through time, and the last 30 years have seen a slight increase in the opportunistic and equilibrium strategies in the North Sea while the periodic strategy has decreased. These changes paralleled a period of change in the abiotic environment of the North Sea, with an increase in temperature and decrease in fishing effort.

For large species, two distinctive strategies were dominant: either the periodic strategy producing many small offspring at the cost of offspring survival, or the equilibrium strategy producing few large offspring but with high survival. The periodic strategy is adopted mainly by bony fish species, for example large flatfish and gadoids, while the equilibrium strategy is mainly adopted by elasmobranchs, for example sharks and rays. These strategies reflect the evolutionary and environmental constraints and trade-offs shaping variability in life-history strategies (Neuheimer et al., 2015). High fecundity balances high pre-

adult mortality while longevity balances unfavourable periods for reproduction in typical poor environmental conditions (Gunderson, 1997; Longhurst, 2002). In contrast to the large species, the small and short-lived species, such as gobies and clupeids, largely follow the opportunistic strategy, producing many small offspring. The lifetime reproductive value of these short-lived species is often compensated by fast growth, early maturation and indeterminate spawning (Tsoukali, Olsson, Visser, & MacKenzie, 2016). The simpler, and often used, slow-fast continuum model was not appropriate here and would have failed to explain some of the trait variability. However, in smaller and extreme ecosystems, or in smaller samples of species with a wide geographical range, the slow-fast continuum model can sufficiently explain the life-history variation (Juan-Jordá, Mosqueira, Freire, & Dulvy, 2013; Wiedmann et al., 2014).

The prevalence of strategies in the communities was linked to the environment and its variability. Notably, we found that the opportunistic strategy prevailed in environments with high temperature and strong temperature seasonality while the equilibrium strategy prevailed in environments with lower and more stable temperatures. The opportunistic reproductive strategy, corresponding to the production of many small eggs, is favourable in seasonal environments to compensate for the short time when resources are available (Boyce, 1979) and in warm environments to balance the higher egg mortality resulting from thermal stress (Pepin, 1991). The strong negative relationship between the opportunistic strategy and temperature is verified by the recent



**FIGURE 4** Time series of relative proportions of equilibrium (black), opportunistic (dark grey) and periodic strategies (grey) in the North Sea from 1980 to 2014 (top panel). The lower panels show the concomitant trends in sea surface temperature (SST) and SST seasonality for 1980–2014 (middle) and fishing effort by otter- and beam trawlers for 1991–95 and 2003–12 (bottom). The regression lines and their confidence interval (shaded area) are displayed when the temporal pattern is significant at  $p < .05$ . Due to different scales, the fishing effort and temperature variables were standardized to facilitate the comparison

distributional shift of mostly small and short-lived species in response to warming (Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015; Perry, Low, Ellis, & Reynolds, 2005), where these opportunistic seasonal migrants take advantage of newly disturbed conditions in such areas (Collie, Wood, & Jeffries, 2008). The opportunistic species are physiological generalists; they are the first to respond to disturbance and can quickly attain high densities thanks to their life-history characteristics (e.g., high fecundity, short generation time and wide dispersal ability; Levinton, 1970). The opportunistic strategy prevails in lower latitudes in areas with high thermal seasonality and primary productivity, while the equilibrium

strategy prevails in higher latitudes and in areas with comparatively lower seasonality. According to MacArthur (1960), opportunistic species are considered not to be resource limited and thrive in environments where the population size is below the carrying capacity of the habitat, while communities composed of equilibrium species are often resource-limited and at, or near, the carrying capacity of the environment.

Abiotic variables explained a lower degree of variability in the prevalence of the periodic strategy. This is probably due to its relatively moderate spatial contrast compared with the more pronounced spatial pattern of the equilibrium and opportunistic strategies throughout the study areas. Since we assess the prevalence of strategies in communities as proportions, the three strategies are related to each other: as the proportion of one strategy increases that of the other declines. Therefore, the moderate response of the periodic strategy to the environment might also be due to the fact that its relative proportion is affected by the more pronounced changes in the opportunistic and equilibrium strategies.

Fishing can affect community composition by affecting the relative abundance of both commercial and non-commercial species, as well as by physical impacts on the seabed (Hiddink et al., 2006; Myers & Worm, 2003). The impacts of fishing on individual species is dependent on their traits and life-history strategies (Jennings, Alvsvåg, et al., 1999; Winemiller, 2005). As fishing increases disturbance, it will most likely benefit opportunistic species while disadvantaging equilibrium species (Jennings, Alvsvåg, et al., 1999; Stevens, Bonfil, Dulvy, & Walker, 2000). In our study, we found a negative effect of fishing effort on the prevalence of the equilibrium strategy. This negative relationship is expected, as equilibrium species (e.g., sharks and rays) are particularly vulnerable to fishing and habitat disturbance due to their low productivity arising from their life-history characteristics (e.g., low fecundity and slow growth) (Dulvy et al., 2008; Sguotti et al., 2016). Although the variability explained by the final model was low, the negative relationship with fishing is supported by the temporal changes in the equilibrium strategy in the North Sea, where it has increased since the 1980s, in synchrony with a general decrease in fishing effort. Recent findings showing that the decline in fishing effort in the North Sea and the neighbouring Kattegat coincided with an increase in the number of large fish in the communities (Engelhard et al., 2015; Fock, Kloppmann, & Probst, 2013; Lindegren, Blenckner, & Stenseth, 2012) also support this explanation.

Life-history strategies permit trait information to be reduced to a few ecologically meaningful components. Our empirical findings for marine fish communities clearly support the theoretical framework of Winemiller and Rose (1992) demonstrating three main life-history strategies of fish: opportunistic, equilibrium and periodic. The proportions of these strategies showed pronounced spatio-temporal patterns across European seas in response to varying environmental conditions. This highlights the underlying ecological mechanism whereby fitness is optimized through natural selection, conditioned on the key trade-offs between growth, feeding and reproduction that ultimately determine the success or failure of a given life-history strategy under certain environmental conditions. However, our study also shows that while marine fish communities can be characterized by three life-history

strategies, a significant fraction of species do not stick strictly to any given strategy but rather reflect a combination of strategies. Interestingly, this is particularly evident for a number of small pelagic species primarily distributed along the axis from opportunistic to periodic strategies (e.g., sprat, herring and mackerel). Although size is arguably a strong predictor of the position of species along a life-history continuum (Brown & Sibly, 2006), it should be worthwhile to explore other more proximate traits explaining the presence and success of these intermediate strategies (Sibly & Brown, 2007). In terms of marine fish, one such trait might be swimming performance, which determines the range and extent of migratory behaviour and that ultimately allows species to successfully explore, forage and reproduce in very different habitats across pronounced environmental gradients. This may suggest that while for sedentary species it may be advantageous to more closely follow a given strategy, highly mobile species may rather optimize fitness through intermediate strategies, reflecting a compromise between the traits and trade-offs suitable across a large range of environments. Finally, we wish to stress that life-history strategies can be incorporated into various types of studies, for example to investigate population dynamics (Mims & Olden, 2012), colonization (Olden, Leroy Poff, & Bestgen, 2006), fisheries management (King & McFarlane, 2003) or biological succession (Silvertown & Franco, 1993). Due to their strong dependence on the environment, life-history strategies can therefore be a suitable management tool for deconstructing and characterizing community composition and monitoring changes in communities in response to exploitation and climate change.

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## DATA ACCESSIBILITY

The species list, their reproductive traits and their literature sources used for this study are available from the Pangaea database: <https://doi.pangaea.de/10.1594/PANGAEA.868610>

## REFERENCES

- Barton, K. (2016). Package MuMIn: Multi-model inference. Retrieved from <http://cran.r-project.org/web/packages/MuMIn/MuMIn>
- Bauchhage, C., & Thureau, C. Making archetypal analysis practical, in: Proceedings of the 31st DAGM Symposium on Pattern Recognition, Springer-Verlag, Berlin, Heidelberg, 2009, 272–281.
- Bellwood, D. R., Hoey, A. S., & Choat, J. H. (2003). Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. *Ecology Letters*, 6, 281–285.
- Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K. E., ... Purvis, A. (2007). The fast-slow continuum in mammalian life history: An empirical reevaluation. *The American Naturalist*, 169, 748–757.
- Boyce, M. S. (1979). Seasonality and patterns of natural selection for life histories. *The American Naturalist*, 114, 569–583.
- Brown, J. H., & Sibly, R. M. (2006). Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences USA*, 103, 17595–17599.
- Cadotte, M., Albert, C. H., & Walker, S. C. (2013). The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters*, 16, 1234–1244.
- Charnov, E. L., Gislason, H., & Pope, J. G. (2013). Evolutionary assembly rules for fish life histories. *Fish and Fisheries*, 14, 213–224.
- Collie, J. S., Wood, A. D., & Jeffries, H. P. (2008). Long-term shifts in the species composition of a coastal fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 1352–1365.
- Cutler, A., & Breiman, L. (1994). Archetypal analysis. *Technometrics*, 36, 338–348.
- Diaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646–655.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.
- Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A., ... Valenti, S. (2008). You can swim but you can't hide: The global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18, 459–482.
- Engelhard, G. H., Lynam, C. P., García-Carreras, B., Dolder, P. J., & Mackinson, S. (2015). Effort reduction and the large fish indicator: Spatial trends reveal positive impacts of recent European fleet reduction schemes. *Environmental Conservation*, 42, 227–236.
- Eugster, M. J. A., & Leisch, F. (2009). From spider-man to hero – archetypal analysis in R. *Journal of Statistical Software*, 30, 1–23.
- Eugster, M. J. A., & Leisch, F. (2011). Weighted and robust archetypal analysis. *Computational Statistics and Data Analysis*, 55, 1215–1225.
- Flynn, D. F. B., Mirotnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem–function relationships. *Ecology*, 92, 1573–1581.
- Fock, H. O., Kloppmann, M. H. F., & Probst, W. N. (2013). An early footprint of fisheries: Changes for a demersal fish assemblage in the German Bight from 1902–1932 to 1991–2009. *Journal of Sea Research*, 85, 325–335.
- Franco, M., & Silvertown, J. (1996). Life history variation in plants: An exploration of the fast-slow continuum hypothesis. *Proceedings of the National Academy of Sciences USA*, 351, 1341–1348.

- Froese, R., & Pauly, D. (Eds.) (2012). *FishBase*. Retrieved from <http://www.fishbase.org>
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111, 1169–1194.
- Grizzetti, B., Bouraoui, F., & Aloe, A. (2012). Changes of nitrogen and phosphorus loads to European seas. *Global Change Biology*, 18, 769–782.
- Gunderson, D. R. (1997). Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 990–998.
- Halpern, B., & Floeter, S. (2008). Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*, 364, 147–156.
- Hart, Y., Sheftel, H., Hausser, J., Szekely, P., Ben-Moshe, N. B., Korem, Y., ... Alon, U. (2015). Inferring biological tasks using Pareto analysis of high-dimensional data. *Nature Methods*, 12, 233–235.
- Hiddink, J. G., Jennings, S., Kaiser, M. J., Queirós, A. M., Duplisea, D. E., & Piet, G. J. (2006). Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 721–736.
- ICES (2015). *Report of the Working Group on Spatial Fisheries Data (WGSFD)*, 8–12 June 2015, ICES Headquarters, Copenhagen, Denmark. ICES CM 2015/SSGEPI:18.
- Jennings, S., Alvsvåg, J., Cotter, A. J., Ehrich, S., Greenstreet, S. P., Jarre-Teichmann, A., ... Smedstad, O. (1999). 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.
- Jennings, S., Greenstreet, S. P. R., & Reynolds, J. D. (1999). 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.
- Juan, S. D., Thrush, S. F., & Demestre, M. (2007). Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Marine Ecology Progress Series*, 334, 117–129.
- Juan-Jordá, M. J., Mosqueira, I., Freire, J., & Dulvy, N. K. (2013). Life in 3-D: Life history strategies in tunas, mackerels and bonitos. *Reviews in Fish Biology and Fisheries*, 23, 135–155.
- King, J. R., & McFarlane, G. A. (2003). Marine fish life history strategies: Applications to fishery management. *Fisheries Management and Ecology*, 10, 249–264.
- 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.
- Levinton, J. S. (1970). The paleoecological significance of opportunistic species. *Lethaia*, 3, 69–78.
- Lindegren, M., Blenckner, T., & Stenseth, N. C. (2012). Nutrient reduction and climate change cause a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. *Global Change Biology*, 18, 3491–3503.
- Litchman, E., Ohman, M. D., & Kiorboe, T. (2013). Trait-based approaches to zooplankton communities. *Journal of Plankton Research*, 35, 473–484.
- Longhurst, A. (2002). Murphy's law revisited: Longevity as a factor in recruitment to fish populations. *Fisheries Research*, 56, 125–131.
- MacArthur, R. (1960). On the relative abundance of species. *The American Naturalist*, 94, 25–36.
- Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J., & McGill, B. (2015). Rapid biotic homogenization of marine fish assemblages. *Nature Communications*, 6, 8405.
- 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.
- McIntyre, S., Lavorel, S., Landsberg, J., & Forbes, T. D. A. (1999). Disturbance response in vegetation towards a global perspective on functional traits. *Journal of Vegetation Science*, 10, 621–630.
- Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, 93, 35–45.
- Mims, M. C., Olden, J. D., Shattuck, Z. R., & Poff, N. L. (2010). Life history trait diversity of native freshwater fishes in North America. *Ecology of Freshwater Fish*, 19, 390–400.
- Mørup, M., & Hansen, L. K. (2012). Archetypal analysis for machine learning and data mining. *Neurocomputing*, 80, 54–63.
- Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283.
- Neuheimer, A. B., Hartvig, M., Heuschele, J., Hylander, S., Kjørboe, T., Olsson, K., ... Andersen, K. H. (2015). Adult and offspring size in the ocean over 17 orders of magnitude follows two life-history strategies. *Ecology*, 96, 3303–3311.
- Nichols, J. D., Conley, W., Batt, B., & Tipton, A. R. (1976). Temporally dynamic reproductive strategies and the concept of R- and K-selection. *The American Naturalist*, 110, 995–1005.
- Núñez-Riboni, I., & Akimova, A. (2015). Monthly maps of optimally interpolated in situ hydrography in the North Sea from 1948 to 2013. *Journal of Marine Systems*, 151, 15–34.
- Olden, J. D., Leroy Poff, N., & Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs*, 76, 25–40.
- Oli, M. K. (2004). The fast-slow continuum and mammalian life-history patterns: An empirical evaluation. *Basic and Applied Ecology*, 5, 449–463.
- Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., ... Payne, M. R. (2016). Reproductive traits (fecundity, egg diameter, parental care) of marine European fish. doi:10.1594/PANGAEA.868610
- Pecuchet, L., Törnroos, A., & Lindegren, M. (2016). Patterns and drivers of fish community assembly in a large marine ecosystem. *Marine Ecology Progress Series*, 546, 239–248.
- Pepin, P. (1991). Effect of temperature and size on development, mortality and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 503–518.
- 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.
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5, 402–411.
- Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9, 741–758.
- Pianka, E. R. (1970). On r- and K-selection. *The American Naturalist*, 104, 592–597.
- Schleuter, A. D., Daufresne, M., Massol, F., Argillier, C., Monographs, S. E., & August, N. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80, 469–484.
- Sguotti, C., Lynam, C. P., García-Carreras, B., Ellis, J. R., & Engelhard, G. H. (2016). Distribution of skates and sharks in the North Sea: 112 years of change. *Global Change Biology*, 22, 2729–2743.

- Shiple, B., Vile, D., & Garnier, E. (2006). From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, 314, 812–814.
- Sibly, R. M., & Brown, J. H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences USA*, 104, 17707–17712.
- Silvertown, J., & Franco, M. (1993). Plant demography and habitat: A comparative approach. *Plant Species Biology*, 8, 67–73.
- Stevens, J., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57, 476–494.
- Tsoukali, S., Olsson, K. H., Visser, A. W., & MacKenzie, B. R. (2016). Adult lifetime reproductive value in fish depends on size and fecundity type. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1405–1412.
- 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.
- Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, 92, 3–10.
- Wiedmann, M. A., Primicerio, R., Dolgov, A., Ottesen, C. A M., & Aschan, M. (2014). Life history variation in Barents Sea fish: Implications for sensitivity to fishing in a changing environment. *Ecology and Evolution*, 4, 3596–3611.
- Winemiller, K. O. (1989). Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia*, 81, 225–241.
- Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 872–885.
- Winemiller, K. O., Fitzgerald, D. B., Bower, L. M., & Pianka, E. R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, 18, 737–751.
- Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218.
- Wood, S. N. (2006). *Generalized additive models: an introduction with R*. Boca Raton, FL: CRC Press.

### BIOSKETCH

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### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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