# Ecological and life history traits explain a climate-induced shift in a temperate marine fish community

**Matthew McLean**[1,2,*], **David Mouillot**[2], **Arnaud Auber**[1]

[1]**IFREMER, Unité Halieutique de Manche et mer du Nord, 150 quai Gambetta, BP699, 62321 Boulogne-sur-Mer, France**
[2]**MARBEC, Université de Montpellier, CNRS, IFREMER, IRD, 34095 Montpellier Cedex, France**

ABSTRACT: A better understanding of community dynamics and ecosystem functioning can be achieved by describing how community functional structure responds to environmental change over both time and space and by identifying which functional groups best mediate community responses. Here, we used a trait-based approach in combination with a newly developed application of principal response curves to functionally characterize a rapid taxonomic shift in the eastern English Channel fish community in the late 1990s. We identified the functional groups with the greatest contributions to the overall shift in fish functional structure and uncovered significant trait–environment relationships. We found that pelagic species with rapid life history cycles, characterized by broadcast spawning, small offspring size, and early maturation, declined considerably in abundance following an increase in sea surface temperature associated with a warming phase of the Atlantic Multidecadal Oscillation, which was likely exacerbated by historical fishing pressure. In contrast, species with late maturation, high parental care, and few, well-developed offspring increased in abundance, reinforcing that fish community responses to climate warming are strongly mediated through life history traits. By examining how environmental factors drove a community shift at the trait level, we provide a mechanistic understanding of how fish functional structure responds to rapid environmental change.

KEY WORDS: Atlantic Multidecadal Oscillation · Climate warming · English Channel · Functional ecology · Principal response curves · Response traits

## INTRODUCTION

Sustainably managing natural resources requires a greater understanding of community dynamics and ecosystem functioning under changing environmental conditions (Kremen 2005, Carpenter et al. 2009, Cheung et al. 2016). Examining community dynamics on a species-by-species basis is useful for stock assessments and population management; however, such taxonomic approaches are less insightful for understanding ecological mechanisms and processes (Díaz & Cabido 2001, Mcgill et al. 2006, Mouillot et al. 2013). By contrast, trait-based ecology links community dynamics and ecosystem processes by identifying how organismal traits respond to environmental change (Mcgill et al. 2006, Winemiller et al. 2015, Gross et al. 2017), which can generate predictive relationships that are not taxon or ecosystem-specific (Díaz & Cabido 2001, Lavorel & Garnier 2002, Winemiller et al. 2015). This approach has gained progressive support and is now recognized as an essential step forward in community ecology and natural resource management (Hooper et al. 2005). Thus, a better understanding of community dynamics can be achieved by describing how community functional structure responds to environmental factors over both time and space and identifying which ecological traits best mediate community responses.

Rapid and pronounced shifts in community structure have been documented in many ecosystems world-

*Corresponding author: mcleamj@gmail.com

wide and are often related to rapid environmental change (Scheffer & Carpenter 2003, Beaugrand 2004, Vergés et al. 2014, Wernberg et al. 2016). In fish communities, such shifts have been documented in response to extreme climatic events and climate cycles that alter sea surface temperatures (SSTs) and oceanographic processes. For example, Wernberg et al. (2016) documented an increase in subtropical fishes following a heatwave along the southwestern coast of Australia and Reid et al. (2001) documented an increase in horse mackerel landings following a phase change of the North Atlantic Oscillation (NAO). Fluctuations of sardine and anchovy landings have also been linked to alternating cycles of the Pacific Decadal Oscillation (Chavez et al. 2003, Lindegren et al. 2013). Yet, such community shifts are classically examined using taxonomic approaches, which are limited in explaining biological responses and their consequences for ecosystem functioning (Reid et al. 2001, Chavez et al. 2003, Clare et al. 2015). Auber et al. (2015) previously documented a rapid shift in the eastern English Channel (EEC) fish community in re-sponse to a warming phase of the Atlantic Multi-decadal Oscillation (AMO), which induced substantial decreases in the abundance of several dominant species and moderate increases in some subordinate species. Such taxonomy-based findings can describe major ecosystem changes with potential impacts on ecosystem services but cannot identify the functional mechanisms that underpin how and why certain or-ganisms respond strongly to climatic changes while others are unaffected. Rather, greater understanding of fish community responses to rapid environmental change could be achieved by functionally charac-terizing community shifts and identifying the most responsive functional groups.

While a better understanding of community shifts can be achieved by describing spatiotemporal changes in functional groups, statistical methods for such studies are limited (Leps et al. 2006, Petchey & Gas-ton 2006, Violle et al. 2007). Auber et al. (2017) re-cently proposed a new application of principal response curves (PRCs) for examining community shifts between time frames. PRC analysis is a multi-variate method that simultaneously describes spatial and temporal changes in community structure and identifies the most responsive species (Van den Brink & Ter Braak 1999, Auber et al. 2017). Despite the util-ity of PRC analysis for describing community shifts, this method has been largely underused and has not yet been applied to ecological traits.

Here we used a trait-based approach with PRC analysis to functionally characterize the shift in the EEC fish community, specifically answering (1) do changes in taxonomic community structure corre-spond to a pronounced shift in functional structure, (2) which functional groups are most contributive to overall changes in functional structure, and (3) which environmental factors are most associated with changes in functional structure through time? By examining the underlying functional changes behind the taxonomic shift, we provide a mechanistic understanding of changes in fish functional structure in response to rapid environmental warming.

## METHODS

### Fish community data

The fish community of the EEC (area VIId defined by the International Council for the Exploration of the Sea, ICES) has been sampled every October since 1988 during the Channel Ground Fish Survey (CGFS). Here, we focused on the period of 1988–2011. The CGFS sampling scheme is spatially strati-fied by subdividing the EEC into 15′ longitude × 15′ latitude rectangles where at least one 30 min haul is made during daylight hours at an average speed of 3.5 knots. A high (3 m) vertical opening bottom trawl (GOV) with a 10 mm stretched-mesh-size codend is used. The stratified sampling scheme manages to complete 90 to 120 hauls per year depending on weather conditions, and we removed all sites that had not been visited for at least 3 consecutive years (Auber et al. 2017). After each haul, all captured fishes are identified and the number of individuals per species is counted. Abundance indices at each sampling station were obtained from the ICES data portal and were standardized to ind. km$^{-2}$ (ICES).

### Ecological traits

Ecological trait data for 73 taxa (67 species and 6 genera not identified to species level) were collected from FishBase (Froese & Pauly 2012), the Ocean Bio-geographic Information System (www.iobis.org/), the Global Biodiversity Information Facility (https://www.gbif.org/), Engelhard et al. (2011), Pecuchet et al. (2017), and a search of primary literature. Nine eco-logical traits were used for this study related to life history, habitat use, and trophic ecology (Table 1). Traits were chosen if they were (1) readily avail-able, (2) deemed accurate by comparison of multiple sources, and (3) potentially implicated in the response

Table 1. Ecological traits and their corresponding functional groups (i.e. trait attributes)

| Ecological trait | Functional (trait) groups |
| --- | --- |
| Length at maturity (cm) | 2.65–11.03, 11.04–18.69, 18.70–26.63, 26.64–40.13, ≥40.14 |
| Age at maturity (yr) | 0.33–1.39, 1.40–2.31, 2.32–2.99, 3.0–4.49, ≥4.5 |
| Parental care | Pelagic egg, benthic egg, clutch hider, live bearer |
| Offspring size (mm) | 0.34–0.89, 0.90–1.09, 1.10–1.39, 1.40–2.67, ≥2.68 |
| Fecundity (offspring female$^{-1}$) | 2–879, 880–9999, 10000–106399, 106400–406589, ≥406590 |
| Water column position | Demersal, reef-associated, benthopelagic, pelagic |
| Temperature preference (°C) | 4.62–10.41, 10.42–11.29, 11.30–11.72, 11.73–12.49, ≥12.5 |
| Trophic guild | Detritivore, planktivore, benthivore, carcinophage, benthopiscivore, piscivore |
| Trophic level | 2.2–3.23, 3.24–3.39, 3.4–3.69, 3.7–3.99, ≥4 |

of communities to environmental change. Categorical or binary traits included parental care, water column position, and trophic guild, while continuous traits included length and age at maturity, fecundity, offspring size, temperature preference, and trophic level. Temperature preference was calculated as the median temperature of a species across its global range of observations for which data were available.

When combining species' abundances and traits, ecologists generally have 2 choices: calculate community-weighted mean (CWM) trait values or use the abundances of functional groups. The advantage in using CWM trait values is that continuous data are not broken into categories and thus no information is lost; however, examination of the underlying changes in trait values is not possible. For instance, CWM trait values could reveal that, on average, maximum length of fishes decreased over time, but could not reveal whether this was driven by an increase in small fishes, a decrease in large fishes, or both. To characterize the EEC fish community shift in terms of changes in the actual abundance of different functional groups, we categorized continuous traits, making all traits categorical. Continuous traits were therefore put into 5 groups by using quintiles of the continuous trait data for all individuals with each trait (Table 1). The abundances of all functional groups (i.e. each trait category or attribute) were then $\log_{10}(x+1)$ transformed.

**Environmental factors**

Environmental factors included both ocean-wide climate oscillations and local environmental parameters. The NAO is an intradecadal alternation of atmospheric mass over the North Atlantic, which is known to influence SSTs and oceanographic processes (Dickson 2000). The NAO index used here is based on the difference of normalized sea-level atmospheric pressure between Lisbon, Portugal, and Reykjavik, Iceland (Dickson 2000). The annual NAO index for the period 1988–2011 was obtained from the NOAA (https://www.ncdc.noaa.gov/tele-connections/nao/). The AMO refers to a 60–80 yr cycle of North Atlantic SST (Edwards et al. 2013). The AMO index is computed as a monthly area-weighted mean of SST anomalies over the North Atlantic (from 0° to 70° N), which is detrended to remove the effect of global warming. This index is correlated to air temperature and rainfall over the Northern Hemisphere, and positive phases are associated with warm, dry conditions, while negative phases are associated with cool, wet conditions (Enfield et al. 2001). AMO values were also obtained from NOAA (https://www.esrl.noaa.gov/psd/data/timeseries/AMO/).

Local environmental parameters included SST, salinity, chlorophyll a (chl a), and dissolved oxygen. Mean annual SST data were derived from the Hadley Centre for Climate Prediction and Research's freely available HadISST1 database (Rayner et al. 2003). Mean annual chl a data came from the Sir Alister Hardy Foundation for Ocean Science Continuous Phytoplankton Recorder database (SAHFOS 2017). Surface salinity and dissolved oxygen were extracted from outputs of the NORWegian ECOlogical Model (NORWECOM, www.ii.uib.no/~morten/norwecom.html, Skogen et al. 1995). NORWECOM is a coupled 3-dimensional physical, biochemical model for the North Sea and the English Channel that provides monthly averages of environmental parameters at a geographical resolution of 0.1°. For salinity and dissolved oxygen, data were averaged across months and spatial locations to obtain mean annual values for the entire EEC. Non-algal suspended matter was obtained from satellite data (Gohin 2011) for each survey, which were then averaged across years to obtain mean annual values.

### Fishing pressure

Fishing pressure was assessed using 3 different fishing mortality indices: $F_{pelagic}$, $F_{demersal}$, and $F_{benthic}$, for pelagic, demersal, and benthic species, respectively. These were estimated annually as the 1-yr-lagged landing-weighted average fishing mortality rates for stocks assessed by ICES working groups, namely mackerel and herring for pelagic, cod and whiting for demersal, and plaice and sole for benthic. The fishing mortality rates of these 6 stocks (the only stocks analytically assessed in the EEC) were considered representative of the global fishing pressure on the EEC fish community, as these species account for more than 60% of total landings in the EEC (Auber et al. 2015). The 1 yr lagging accounted for the fact that annual instantaneous fishing mortality rates of a given year are expected to affect the abundance of fish stocks the year after (Auber et al. 2015). Each fishing mortality index was calculated as the average fishing mortality of the 2 corresponding stocks weighted by their landings. We considered pelagic, demersal, and benthic fishing mortality to account for mixed types of fishing gear, and to encompass the totality of fishing pressure throughout all habitat zones in the EEC. The EEC is a mixed-gear fishery where pelagic stocks are generally targeted by mid-water trawls and demersal and benthic stocks are targeted by a mix of otter trawls, beam trawls, nets, pots, and dredges (Pascoe & Coglan 2002, Ulrich et al. 2002). Thus, by computing 3 different fishing mortality indices, we account for fishing pressure across several stocks and gear types, within the limitations of ICES-assessed stocks. Fishing mortality rates of the different stocks, as well as landing statistics, were extracted from the ICES Stock Assessment Summary database and Catch Statistics database (www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx).

### Data analysis

#### PRCs

Temporal and spatial changes in fish functional structure were assessed using PRC analysis. PRC is a special case of partial redundancy analysis with a single tested factor as the explanatory variable and a single dimension of repeated observations as the co-variable (Van den Brink & Ter Braak 1999). Auber et al. (2017) recently adapted the PRC analysis to examine spatiotemporal changes in community structure, specifically between 2 time periods (i.e. a 'baseline period' and a 'tested period'), by using spatial sites as repeated observations and time as a tested factor. The PRC analysis generates canonical regression co-efficients ($c_{dt}$) for each sampling site, as well as contribution weights ($b_k$) for each species (or functional group in this study). The absolute values of $c_{dt}$ quantify, at each sampling site, the magnitude of change between the 2 tested time periods, and the absolute values of $b_k$ quantify the contribution of each functional group to the overall change of community structure; groups with weights near zero have little or no response, while groups with high weights have strong responses. For a given functional group; the sign (+/−) of $c_{dt}$ indicates the type of community response and is interpreted by comparing with the sign (+/−) of $b_k$. When the signs of $b_k$ and $c_{dt}$ are identical, the abundance of the corresponding functional group is higher in the tested period than the baseline period, and when the signs of $b_k$ and $c_{dt}$ are opposite, the abundance is higher in the baseline period than the tested period. For a complete description of the original PRC method and the new application of the PRC method, see Van den Brink & Ter Braak (1999) and Auber et al. (2017), respectively.

In correspondence with the taxonomic community shift in the EEC (Auber et al. 2015), we considered the years 1988 to 1997 as the pre-shift period (baseline period), and 1998 to 2011 as the post-shift period (tested period). We then applied the PRC analysis to examine changes in functional community structure at each site between the 2 time periods and to identify the functional groups with the highest contributions to overall change. The PRC analysis was performed using the function 'prc' in the R package 'vegan'. Significant changes in functional structure between the 2 periods were then tested at each sampling site using Monte-Carlo permutation tests designed to correct for the increase in the family-wise type-1-error rate due to multiple comparisons across sampling sites (see Auber et al. 2017 for full details and R code).

#### Influence of environmental factors and fishing mortality

We identified the influences of environmental factors on temporal changes in fish functional structure using RLQ and fourth-corner analyses, where we considered environmental factors across years rather than across sites. RLQ is a method that integrates environmental data (R), species abundance data (L),

and species' ecological traits (Q) to examine how environmental factors influence trait variation (Dray et al. 2014). RLQ examines the co-inertia between 3 separate ordination analyses (i.e. R, L, and Q), while fourth-corner analysis assess statistical associations between each environmental factor and each functional group individually (Dray & Legendre 2008, Dray et al. 2014). Thus RLQ analysis was first used to reveal major environmental drivers of temporal variation in fish functional structure, while fourth-corner analysis then identified significant correlations between individual functional groups and environmental factors. For both the RLQ and fourth-corner analyses, species abundance data were the mean time series of species composition averaged over the entire EEC, thus the species abundance table (L) consisted of species mean abundances in columns and years in rows. While RLQ is generally applied to spatial data, as the analysis functions through co-inertia of 3 individual ordinations, alternative species abundance structures, including temporal, are permissible (see Dolédec et al. 1996, Dray & Legendre 2008). Temporal environmental drivers included in RLQ analysis were mean annual AMO, NAO, SST, salinity, chl *a*, oxygen, and fishing mortality (pelagic, demersal, and benthic). Thus the environmental table consisted of mean environmental factors in columns and years in rows. A potential concern with RLQ and fourth-corner analysis was the influence of temporal autocorrelation among variables. Autocorrelation can bias statistical tests by inflating type-1 error, leading to spurious correlations. However, RLQ analysis is purely descriptive and does not test for significant relationships (see Thuiller et al. 2006). To account for potential autocorrelation in fourth-corner analysis, which does test for significant relationships, we used both the standard fourth-corner analysis and an extended version of fourth corner that integrates Moran spectral randomization (MSR) to account for autocorrelation (Wagner & Dray 2015). MSR is a constrained randomization procedure that compares observed values against a null model that preserves the autocorrelation of the data (Wagner & Dray 2015). Due to missing environmental data in 2009, 2010, and 2011, RLQ and fourth-corner analysis were calculated for the time series 1988–2008.

## RESULTS

The PRC analysis revealed that sampling sites explained 34% of spatiotemporal variance in fish functional structure, which is represented by the horizontal axis in Fig. 1a (showing site-to-site variation in community structure), while time explained 13.4%, 71% of which is represented by the first canonical axis of the PRC analysis (vertical axis in Fig. 1a). All sites in the EEC were characterized by positive $c_{dt}$ values, indicating that the type of community change was the same at every site (Fig. 1a). However, $c_{dt}$ values were highly variable across sites, indicating that while all sites experienced the same type of change, the magnitude of change was spatially heterogeneous (Fig. 1). Monte-Carlo permutation tests further revealed that 36 out of 79 sites had a significant change in fish functional structure between the 2 time periods (Fig. 1b).

The $b_k$ values revealed that changes in fish functional structure were primarily driven by decreases in the abundance of species with small offspring size (0.9–1.1 mm), pelagic egg release (broadcast spawning), planktivory, pelagic water column position, and low age at maturity (1.4–2.3 yr), as the absolute values of $b_k$ were much higher for functional groups with negative values (decreasing) (Fig. 1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m606p175_supp.pdf). Concurrently, there was an increase in clutch hiders (i.e. high parental care) and species with high age at maturity (3.0–4.5 yr), moderate trophic level (3.25–3.4), high temperature preference (≥12.5°C), and low fecundity (2–880) (Figs. 1 & S2). Thus, the taxonomic shift in the EEC fish community in the late 1990s was generally characterized by a strong decrease in pelagic and planktivorous species with opportunistic, '*r*-selected' life history traits, and a moderate increase in species with equilibrium, '*K*-selected' life history traits.

## Influence of environmental factors

RLQ analysis identified AMO, demersal and pelagic fishing mortality, SST, and NAO as the primary drivers of temporal variability in fish functional structure, as AMO and fishing mortality had the highest correlations with the first RLQ axis, and SST and NAO were both highly correlated with the first RLQ axis and had the highest correlations with the second RLQ axis (Figs. 2 & 3).

Initial fourth-corner analysis, without MSR, indicated that AMO had positive relationships with demersal species and species with high age at maturity (3.0–4.5 yr), and negative relationships with pelagic and planktivorous species and species with low trophic level (2.2–3.25), low age at maturity (1.4–2.3 yr), and low temperature preference (10.4–11.3°C) (p < 0.05, Fig. 4). In contrast, NAO was positively cor-
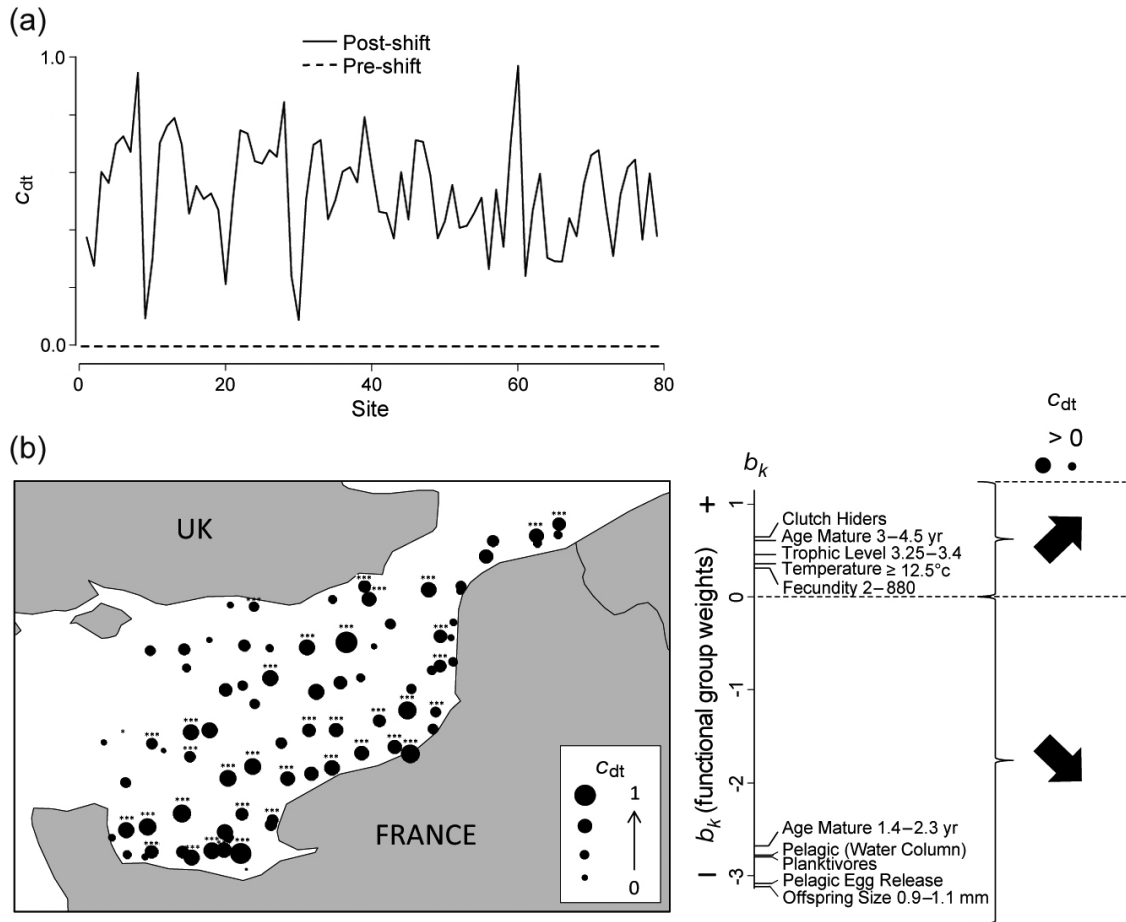
Fig. 1. (a) Principal response curve showing changes in fish community structure across sampling sites (*x*-axis) between the baseline period (1988–1997) (pre-shift) and tested period (1998–2011) (post-shift). (b) Map showing the amplitude of temporal changes in fish functional structure (i.e. $c_{dt}$ values) at each sampling site and the trend (increase or decrease) of abundance for the most contributive functional groups (diagram to the right of map). Functional groups are ranked by their contribution weight ($b_k$) coefficients. For clarity, only traits with $b_k$ coefficients in the first or last decile are shown. Sampling sites with significant change are shown by asterisks (***p < 0.001; **0.001 < p < 0.01; *0.01 < p < 0.05)
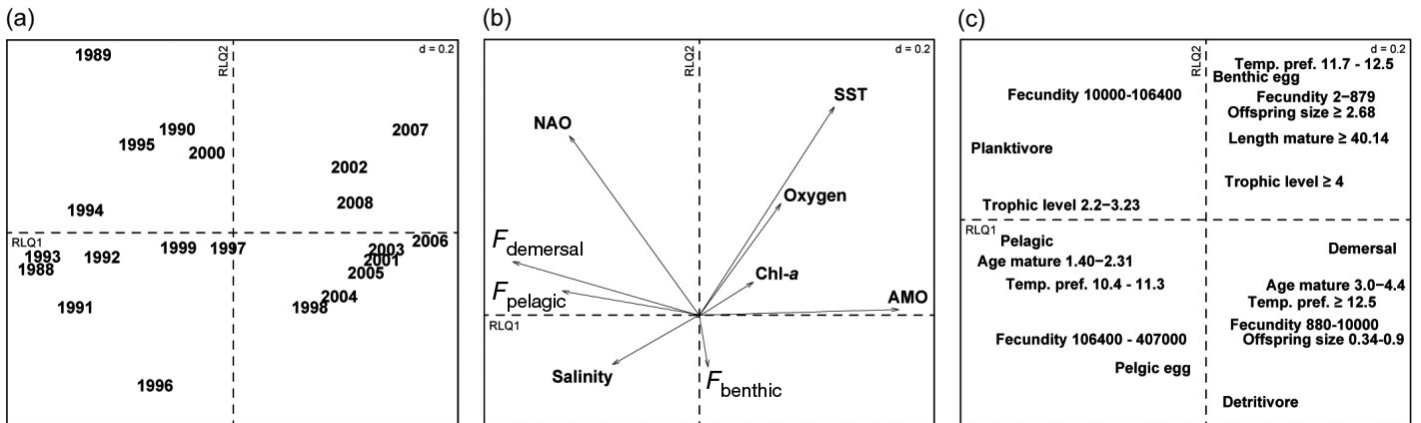


Fig. 2. RLQ biplots showing (a) temporal variation and (b) associations between environmental factors and (c) functional groups. For clarity, only functional groups with the greatest correlations (first or last decile) to the first and second RLQ axes are plotted in (b). AMO: Atlantic Multidecadal Oscillation; SST: sea surface temperature; $F_{pelagic}$: pelagic fishing mortality; $F_{demersal}$: demersal fishing mortality; $F_{benthic}$: benthic fishing mortality; Temp. pref.: temperature preference. The first 2 RLQ axes preserved 87 % of environmental variation and 71 % of trait variation
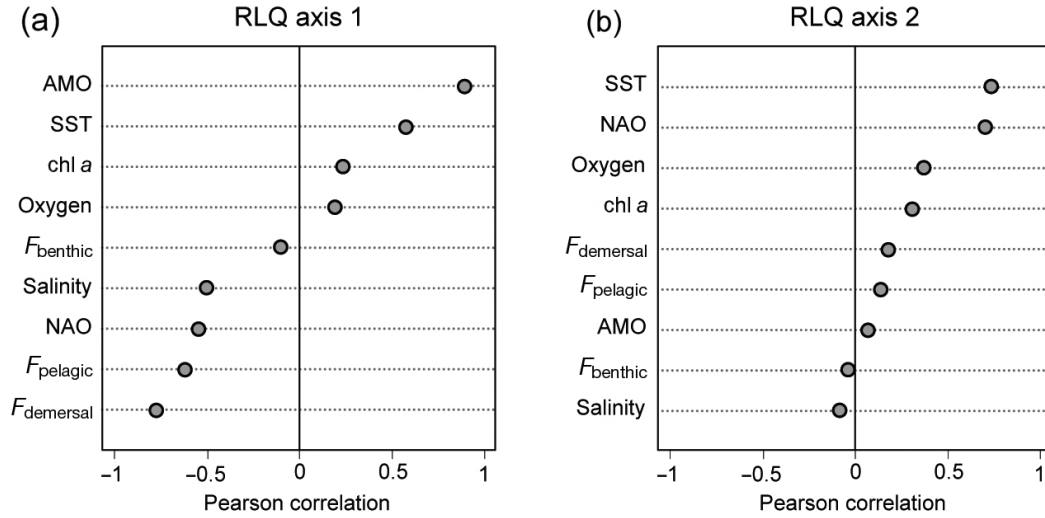
Fig. 3. Contribution of environmental factors to temporal variation in fish functional structure according to Pearson correlations between environmental factors and the (a) first and (b) second axes of the RLQ analysis. See Fig. 2 for definitions of acronyms

related with planktivores and negatively correlated with species with high temperature preferences (≥12.5°C). SST was positively correlated with species with the largest length at maturity (≥40.1 cm), lowest fecundity (2–880), largest offspring size (≥2.7 cm), and reef-associated species, and negatively correlated with species with low temperature preference (10.4–11.3°C) (p < 0.05, Fig. 4). Dissolved oxygen had a single, positive association with high-trophic-level species (≥4) (p < 0.05, Fig. 4). Pelagic and demersal fishing mortality had nearly identical relationships with functional groups; however, pelagic mortality had fewer significant associations. Both pelagic and demersal mortality were positively associated with

pelagic and planktivorous species, and negatively associated with demersal species and species with high age at maturity (3.0–4.5 yr) (p < 0.05, Fig. 4). Demersal fishing mortality was also positively related to species with the lowest trophic level (2.2–3.25) and lowest age at maturity (1.4–2.3 years) (p < 0.05, Fig. 4). However, re-running the fourth-corner analysis with MSR to account for temporal autocorrelation revealed that only AMO and SST had significant associations with any of the functional groups, indicating potential spurious correlations for fishing mortality, oxygen, and NAO due to high autocorrelation (Fig. 4). The relationships between AMO, SST, and functional group dynamics remained nearly identi-
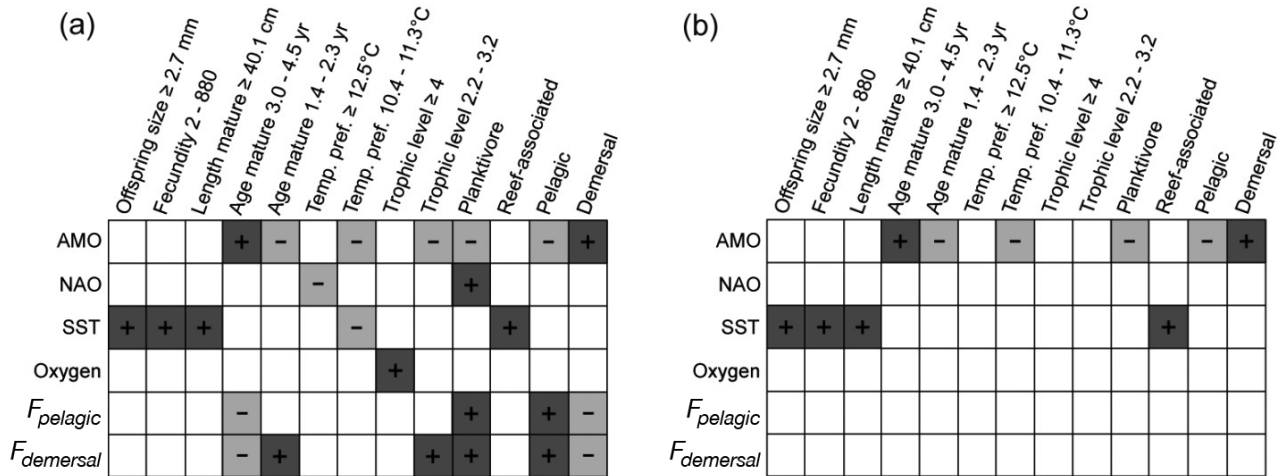


Fig. 4. Results of fourth-corner analyses of trait−environment correlations (a) without and (b) with Moran spectral randomization (white: no significant relationship; dark grey: positive relationship; light grey: negative relationship. See Fig. 2 for definitions of acronyms

cal, with only the associations between AMO and low trophic level, and between SST and low temperature preference no longer significant.

## DISCUSSION

Here, we found that a previously documented taxonomic shift in a temperate marine fish community also corresponded to a considerable shift in fish functional structure. This is a major finding as community functional structure can be relatively unaffected by temporal species replacement or turnover (Villéger et al. 2010, Clare et al. 2015). Examining the taxonomic shift through the lens of ecological traits provided more pronounced results and greater insight into the biological mechanisms behind the shift. We found that the shift was characterized by a large decrease in the abundance of pelagic, planktivorous species with low temperature preferences and opportunistic, 'r-selected' life histories such as low age and size at maturity and low trophic level, and a concurrent increase in species with moderate to high temperature preferences and equilibrium, 'K-selected' life histories such as high size and age at maturity, few large offspring, and high parental care. Interestingly, we found significant temporal change in functional community structure at roughly half of all sites (36 of 79), whereas Auber et al. (2017) found significant temporal change for only 13 sites when using PRC analysis with taxonomic data, highlighting that changes in community structure are better identified using ecological traits regardless of species identity.

The finding that the type of community change was similar across all sites indicates a regionally consistent response across the entire EEC. Indeed, we found that changes in fish functional structure are strongly correlated with the AMO and associated increases in sea surface temperature. While sea surface temperature has been progressively rising in the North Atlantic during the past few decades, the switch from a cool to a warm phase of the AMO led to unusually rapid warming (Ting et al. 2009, Moore et al. 2017). This rapid warming likely amplified ongoing 'tropicalization' throughout the channel, causing an abrupt decrease of species sensitive to higher SSTs, and a concurrent increase in tolerant species (Rijnsdorp et al. 2009, Cheung et al. 2013, Vergés et al. 2014). Indeed, we identified increases in species with high temperature preferences as contributive to the overall change in fish functional structure, and also identified correlations between AMO, SST, and temperature preference. While the NAO was also correlated with changes in fish functional structure, the NAO is a regional index of atmospheric pressure that was associated with ocean warming in the late 1980s (Reid et al. 2001), but has progressively declined in parallel with the AMO increase.

While the AMO appeared to be the primary driver of changes in fish functional structure, RLQ analysis also identified substantial correlation between fishing mortality and functional group dynamics. However, both demersal and pelagic fishing pressure declined in parallel with decreasing fish abundances, and both fishing indices had identical relationships with the abundance of small pelagic fishes. Thus, fishing mortality was likely not a primary driver of changes in fish functional structure, as pelagic fishing mortality declined in parallel with a pronounced decrease in small pelagic fishes. The community shift being characterized by a rapid decrease in species with fast life history cycles also indicates an environmental response rather than progressive fishing impacts (Perry et al. 2005, Rijnsdorp et al. 2009). However, given that demersal fishing pressure was positively correlated with pelagic and planktivorous fishes and negatively correlated with demersal fishes, it is likely that historically high demersal fishing increased the relative abundance of pelagic fishes with rapid growth and generation times, rendering the community more susceptible to climate stress (Thurstan et al. 2010, Molfese et al. 2014, Auber et al. 2015, McLean et al. in press). Indeed, the English Channel has been heavily exploited for decades, particularly following intense industrialization of commercial fisheries in the early to mid-1900s (Pauly et al. 2002). Long-term overfishing and fishing down the food web in the English Channel have progressively shifted the ecosystem from historical dominance by large demersal species such as cod and ling toward increased dominance by small pelagic and demersal species with higher fishing tolerances, and commercially untargeted species such as catsharks (McHugh et al. 2011, Molfese et al. 2014). Thus, while the rapid shift in fish functional structure appeared most strongly associated with climate-driven ocean warming, the long history of exploitation in the EEC clearly reinforced this shift by rendering the ecosystem susceptible to a climatic disturbance. Furthermore, the observed functional shift also reflects reduced contemporary fishing effort, as we observed an increase in larger and higher-trophic-level species through time (Pauly et al. 2002). Altogether it appears that historical overfishing in combination with rapid environmental change induced a major shift in fish functional structure, as the EEC was dominated by spe-

cies with environmentally sensitive life history traits in the early 1990s, which were highly responsive to the shift in AMO.

While high temperature preference was identified as an influential trait, temperature preference is a 'soft' (i.e. easily measured but less informative) trait that serves as a proxy for 'hard' (i.e. informative but difficult to measure) physiological traits influencing species' distributions and habitat preferences (Leps et al. 2006, Violle et al. 2007, Pakeman 2011). More interesting was the finding that increasing and decreasing species contrast strongly in life history traits related to offspring survival, population growth, and generation time. Species with *r*-selected life histories follow type III survivorship curves, where many small offspring are produced and given little to no parental investment (Pianka 1970, Gadgil & Solbrig 1972, Southwood et al. 1974). This strategy employs the trade-off that while survivorship is extremely low among progeny, larval dispersal and population turnover are high, allowing populations to quickly respond to unfavorable environmental conditions (Pianka 1970, Gadgil & Solbrig 1972, Southwood et al. 1974). Alternatively, *K*-selected strategists make large energetic investments in few, well-developed offspring. While such a strategy limits dispersal and colonization abilities, progeny are strong competitors and have high individual fitness (Pianka 1970, Gadgil & Solbrig 1972, Southwood et al. 1974). Beyond the classical distinction of *r*- and *K*-selected strategies, recent work using ecological traits suggests a continuum of 3 life history strategies where *r*-selected species are considered 'opportunistic' and *K*-selected species can be split into 'periodic' and 'equilibrium' based on trade-offs in fecundity, parental care, and offspring size (Winemiller & Rose 1992, King & McFarlane 2003, Pecuchet et al. 2017). Opportunistic species are characterized by low size and trophic level and short lifespans, but with high fecundity (Winemiller & Rose 1992, King & McFarlane 2003, Pecuchet et al. 2017). Both periodic and equilibrium species have larger size, higher trophic level, and longer lifespans, but periodic species have high fecundity and low parental care, whereas equilibrium species have low fecundity and high parental care (Winemiller & Rose 1992, King & McFarlane 2003, Pecuchet et al. 2017). In the context of the 3-strategy life history continuum, our results suggest that opportunistic species are the most susceptible to rapid environmental change, notably warming, due to their shorter life cycles, while equilibrium species with few, well-developed offspring and longer life cycles, appear less responsive. Previous studies examining

the relationship between life history strategies and climate change have shown that opportunistic species can be highly impacted by climate warming because short generation times enable rapid population responses (Jiguet et al. 2007, Hoffmann & Sgro 2011, Pearson et al. 2014). For example, Perry et al. (2005) and Devictor et al. (2012) documented faster and more pronounced distribution shifts among species with faster life cycles and smaller size in fishes, birds and butterflies, while Simpson et al. (2011) showed that smaller fish species responded faster to warming across European shelf seas.

While previous studies have documented rapid responses in opportunistic species, few examples have shown that such responses can drive major community shifts in entire species assemblages over large temporal and spatial scales (Perry et al. 2005, Devictor et al. 2012). Here, our results suggest that temperature warming, amplified during the late 1990s by the combination of human-made climate change and the AMO (Ting et al. 2009), led to an abrupt decrease in opportunistic species with fast life histories throughout the EEC, likely as an evolutionary response to a rapidly changing environment (Pianka 1970, Stearns 1989, Bradshaw & Holzapfel 2006). It further appears that this decrease allowed equilibrium species to expand their populations under new environmental conditions. However, although opportunistic species are highly responsive to environmental change and can thus be heavily impacted over short timescales, over evolutionary time opportunistic species should have higher capacity to adapt given their rapid evolutionary responses (Rijnsdorp et al. 2009).

Among potential explanations for the shift in functional structure, temperature rise likely affected larval and juvenile mortality rates through changes in dispersion and recruitment (Blaxter 1991, Drinkwater et al. 2014, Young et al. 2018) or through match-mismatches with food sources (Kristiansen et al. 2011, McQueen & Marshall 2017). In addition, as proposed by Auber et al. (2015), this community shift may have been influenced by density-dependent interactions such as predation and competition. Temperature rise is also known to drive species emigrations, and the community shift could have resulted from the rapid displacement of existing individuals (Pinsky et al. 2013, Day et al. 2018, McLean et al. in press). Finally, while opportunistic species can rapidly track environmental changes, allowing quick recovery when conditions return to normal, the community has not returned to the initial pre-shift state, suggesting environmental conditions are no longer favorable for the impacted species, inhibiting their recovery.

While we found interesting patterns linking eco-logical and life history traits to rapid environmental change, our study has several important limitations. As we examined changes in the abundance of functional groups, our results are influenced by both trait choice and categorization (Leps et al. 2006, Mcgill et al. 2006, Violle et al. 2007). Such methods remain subjective, and there is no universal approach for choosing traits or defining groups. Binning species also leads to a necessary loss of trait information and can potentially combine species with different environmental responses. Our approach further cannot account for intraspecific trait variability, and thus cannot examine how changes in ontogeny or population demographics influence functional structure (Petchey & Gaston 2006, Violle et al. 2007). We also used RLQ analysis to examine the potential drivers of temporal changes in fish functional structure; however, RLQ is unable to identify statistical significance due to potential autocorrelation, and can only reveal associations among variables.

By using a trait-based approach, we were able to uncover the ecological characteristics linking species that drove a rapid shift in the EEC fish community. These findings increase our understanding of how organisms respond to environmental change and help anticipate how ecosystems might change in the future. Growing evidence shows it is essential to adopt a trait-based approach as it provides better understanding of biological mechanisms and because global change will have drastic impacts on biodiversity, which will be mediated through species' functional characteristics.

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