

Current Biology

A Climate-Driven Functional Inversion of Connected Marine Ecosystems

Highlights

- A climate oscillation caused rapid sea surface warming in two connected ecosystems
- r-selected pelagic fishes shifted abruptly northward from one ecosystem to the other
- The connected ecosystems underwent a rapid inversion in fish functional structure
- Future climate warming could trigger similar functional shifts in other ecosystems

Authors

Matthew McLean, David Mouillot, Martin Lindegren, ..., Paul Marchal, Anik Brind'Amour, Arnaud Auber

Correspondence

mcleamj@gmail.com

In Brief

McLean et al. show that climate-induced changes in fishes' distributions and abundances between two connected ecosystems caused inverse shifts in functional structure, primarily driven by pelagic species with rapid life histories. Future climate change could trigger similar functional shifts with profound consequences for ecosystem functioning.



A Climate-Driven Functional Inversion of Connected Marine Ecosystems

Matthew McLean,^{1,2,8,*} David Mouillot,^{2,3} Martin Lindegren,⁴ Georg Engelhard,^{5,6} Sébastien Villéger,² Paul Marchal,¹ Anik Brind'Amour,⁷ and Arnaud Auber¹

¹IFREMER, Unité Halieutique de Manche et mer du Nord, 150 quai Gambetta, BP699, 62321 Boulogne-sur-Mer, France

²MARBEQ, Université de Montpellier, CNRS, IFREMER, IRD, 34095 Montpellier Cedex, France

³Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811 Australia

⁴Centre for Ocean Life, c/o National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet Bygning 202, 2800 Kgs. Lyngby, Denmark

⁵Centre for Environment, Fisheries & Aquaculture Science (Cefas), Pakefield Road, Lowestoft NR33 0HT, UK

⁶School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

⁷IFREMER, Unité Ecologie et Modèles pour l'Halieutique, rue de l'île d'Yeu, BP 21105, 44311 Nantes Cedex 3, France

⁸Lead Contact

*Correspondence: mcleanmj@gmail.com

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SUMMARY

Sustainably managing natural resources under climate change requires understanding how species distribution shifts can impact ecosystem structure and functioning. While numerous studies have documented changes in species' distributions and abundances in response to warming [1, 2], the consequences for the functional structure of ecosystems (i.e., composition of species' functional traits) have received less attention. Here, using thirty years of fish monitoring, we show that two connected North Atlantic ecosystems (E. English Channel and S. North Sea) underwent a rapid shift in functional structure triggered by a climate oscillation to a prevailing warm-phase in the late-1990s. Using time-lag-based causality analyses, we found that rapid warming drove pelagic fishes with r-selected life history traits (e.g., low age and size at maturity, small offspring, low trophic level) to shift abruptly northward from one ecosystem to the other, causing an inversion in functional structure between the two connected ecosystems. While we observed only a one-year time-lag between the climate oscillation and the functional shift, indicating rapid responses to a changing environment, historical overfishing likely rendered these ecosystems susceptible to climatic stress [3], and declining fishing in the North Sea may have exacerbated the shift. This shift likely had major consequences for ecosystem functioning due to potential changes in biomass turnover, nutrient cycling, and benthic-pelagic coupling [4–6]. Under ongoing warming, climate oscillations and extreme warming events may increase in frequency and severity [7, 8], which could trigger functional shifts with profound consequences for ecosystem functioning and services.

RESULTS AND DISCUSSION

Here, we used over 30 years of fish-monitoring data and an extensive compilation of ecological traits to examine the dynamics of fish functional structure in the Eastern English Channel (EEC) and Southern North Sea (SNS) (Figure 1A) under a warming phase of the Atlantic Multidecadal Oscillation (AMO), a 60- to 80-year climate cycle affecting sea surface temperatures (SST) in the North Atlantic [9]. We characterized functional structure using ten traits (Table S1) related to life history, habitat use, and trophic ecology for 73 fish taxa in the EEC and 110 in the SNS. To examine the temporal dynamics of fish functional structure in the two ecosystems, we used a multidimensional functional-trait space where species' positions reflect their functional relatedness [10]. We then used Granger causality tests (see STAR Methods) to assess the influences of SST, AMO, chlorophyll-a, and fisheries landings on changes in fish functional structure through time, with cross-correlation analyses used to identify potential time lags between variables.

Warming was clearly reported in both ecosystems as annual SST increased by 0.28°C (±0.09) per decade in the EEC (1983–2015; $F_{1,31} = 10.36$; $p < 0.01$; Figure 1D) and 0.41°C (±0.1) per decade in the SNS (1983–2015; $F_{1,31} = 16.60$; $p < 0.001$; Figure 1B). Likewise, the AMO increased significantly over time ($F_{1,31} = 33.88$; $p < 0.0001$) as it entered a warming phase during the 1990s [9] (Figure 1B, D). While there was no significant trend in chlorophyll-a in the EEC, it significantly increased in the SNS by roughly 30% over the entire period ($F_{1,31} = 5.22$; $p < 0.05$; Figure 1B).

Demersal fisheries landings remained relatively stable in the EEC with no significant long-term change. By contrast, pelagic landings increased through time, notably between 2000 and 2005 ($F_{1,21} = 9.98$; $p < 0.01$; Figure 1E), while total landings also increased, largely tracking pelagic landings ($F_{1,21} = 5.2$; $p < 0.05$; Figure 1E). In the SNS, demersal landings progressively decreased ($F_{1,26} = 39.16$; $p < 0.0001$), while pelagic landings increased ($F_{1,26} = 7.24$; $p < 0.05$; Figure 1C); however, the increase in pelagic landings occurred primarily before 1990. While total landings in the SNS have progressively decreased since the mid-1990s, there was an initial spike in the early-1990s, leading to no significant long-term change.



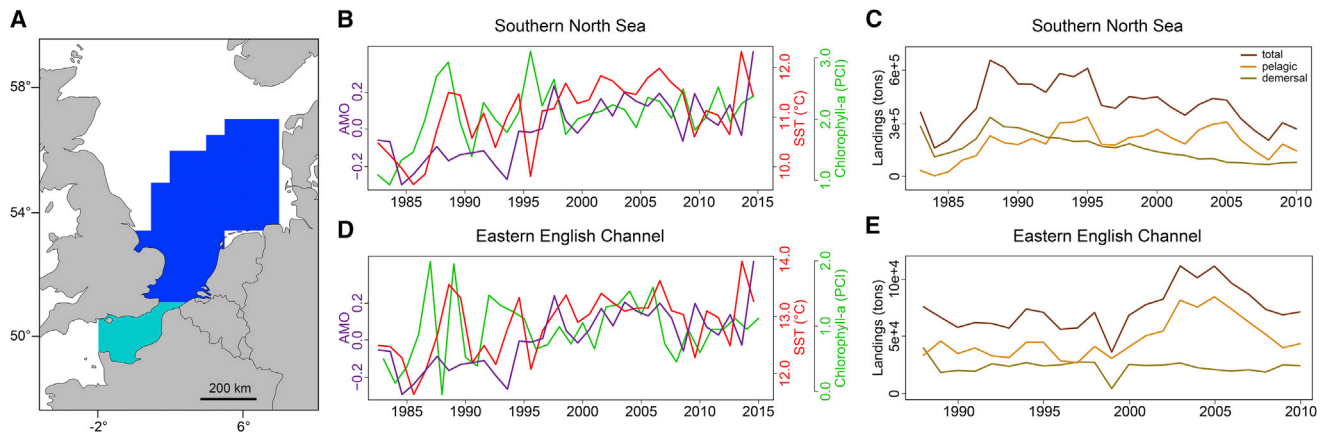


Figure 1. Map of the Two Study Ecosystems along with Their Long-Term Environmental and Fishing Variability

(A–E) Locations of the Eastern English Channel (light blue area) and Southern North Sea (dark blue area) ecosystems (A) and their long-term dynamics in Atlantic Multidecadal Oscillation (AMO) (purple time series), sea surface temperature (red time series), and chlorophyll-*a* (green time series) (B and D), as well as demersal (dark yellow time series), pelagic (orange time series), and total (brown time series) fisheries landings (C and E).

We first examined temporal changes in fish functional structure using annual community-weighted mean trait values on principal component axes (see STAR Methods; Figure S1). Based on resulting dynamics, we then applied multivariate regression trees with analysis of similarity to identify whether there were significant shifts in fish functional structure and in which years they occurred. We identified a significant shift in 1997 in the EEC ($R^2 = 0.60$; $p < 0.01$) and in 1998 in the SNS ($R^2 = 0.39$; $p < 0.01$). These years were then used to examine changes in species abundances in functional space and compare trends between ecosystems. Functional space (Figure S2) revealed that these shifts were primarily driven by rapid changes in two species groups, one pelagic and one demersal (species clusters on left and right sides of functional space), which simultaneously decreased in the EEC and increased in the SNS (Figures 2A–2C), indicating a northward shift between ecosystems. Interestingly, despite major differences in habitat use and diet, both fish groups were characterized by *r*-selected life history traits such as low age and size at maturity, small offspring, and low trophic level (Figures 2A–2C). However, changes in pelagic fish abundances were much more pronounced, causing fish community centroids to move abruptly across the functional space, highlighting the inversion in functional structure between the two connected ecosystems (Figures 2D–2F; Figure S3): the EEC became relatively less dominated by *r*-selected pelagic fishes and more dominated by *K*-selected (e.g., high age and size and at maturity, large offspring, high trophic level) demersal fishes, while the SNS became relatively less dominated by *K*-selected demersal fishes and more dominated by *r*-selected pelagic fishes.

To further examine the contribution of life history traits to the shift in fish functional structure, we tested whether relationships between changes in species' abundances and traits differed between ecosystems. We thus used linear models to test the effect of the interaction between ecosystem and each life history trait (and trophic level) on changes in species' abundances before and after the functional shift. We found significant interaction terms for age at maturity (interaction coefficient = -2.18 ;

$F_{3,171} = 10.09$, $p < 0.01$), length at maturity (interaction coefficient = -1.92 ; $F_{3,179} = 9.1$, $p < 0.01$), offspring size (interaction coefficient = -0.58 ; $F_{3,175} = 8.16$, $p < 0.01$), parental care (interaction coefficient = -0.61 ; $F_{3,179} = 6.78$, $p = 0.05$), and trophic level (interaction coefficient = -6.2 ; $F_{3,179} = 6.7$, $p = 0.05$), indicating opposite trends between ecosystems: fishes with lower age and size at maturity, smaller offspring, lower parental care, and lower trophic level (*r*-selected traits) simultaneously decreased in the EEC and increased in the SNS regardless of whether they were pelagic or demersal (Figure 3).

A series of Granger causality tests then identified AMO as the only significant causal driver of changes in fish functional structure in the EEC ($F_{5,14} = 4.84$; $p < 0.01$; Figure 4A), while both AMO and SST were identified as significant causal drivers in the SNS (AMO $F_{1,50} = 13.33$; $p < 0.001$; SST $F_{2,44} = 6.86$; $p < 0.01$; Figure 4B). Neither chlorophyll-*a* nor fisheries landings had significant causal influence on fish functional structure in either ecosystem. Cross-correlation analysis then revealed a 1-year optimal time-lag (i.e., highest correlation) between changes in AMO and fish functional structure in both ecosystems (EEC $r = 0.78$; $p < 0.001$; SNS $r = 0.75$; $p < 0.0001$), and a 2-year optimal time lag between changes in SST and fish functional structure in the SNS ($r = 0.63$; $p < 0.001$).

Previous studies have documented pronounced changes in taxonomic community structure following rapid warming events where species shift poleward into adjacent ecosystems [11, 12]. Our results further indicate that climate-driven changes in species' abundances and distributions can lead to functional reorganization of entire species assemblages, particularly between connected ecosystems. However, not all impacted species concurrently decreased in the EEC and increased in the SNS, suggesting that the inversion in functional structure was driven not only by distribution shifts between ecosystems, but also by opposite trends in mortality, recruitment, and survivorship of functionally similar species. While we observed a pronounced shift in a single taxonomic group (fishes), shifts in fish communities have been documented alongside shifts in planktonic and benthic communities [11–13], and recent experiments

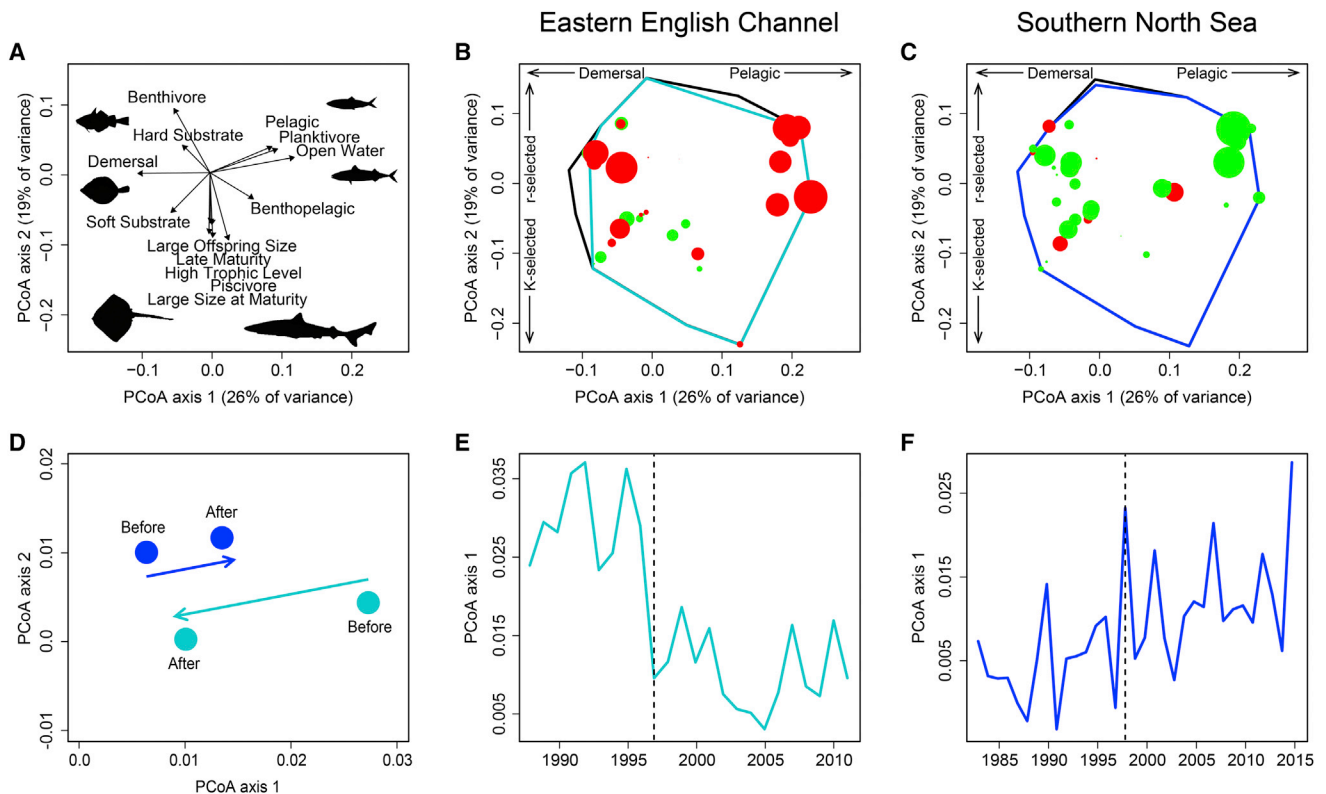


Figure 2. Inversion in Fish Functional Structure between the Eastern English Channel and Southern North Sea

(A–C) Multidimensional fish functional space showing functional-trait structure (A) along with changes in species' mean abundances in the EEC (B) and SNS (C) before and after the functional shift (EEC: 1997; SNS: 1998). (B and C) Red and green points indicate species that decreased or increased in abundance between the two periods, respectively, while point sizes are scaled by the log of absolute change in abundance. Polygons represent the functional space (i.e., convex hulls) containing all species in each ecosystem (EEC = light blue; SNS = dark blue; combined = black).

(D) Abundance-weighted fish community centroids for the periods before and after the functional shift in both ecosystems.

(E and F) Temporal dynamics of fish community centroids along the first axis of functional space with vertical lines indicating the functional shift. See also Figure S2, which shows the overall functional space for both ecosystems, Table S1, which lists the functional traits, Figure S3, which shows changes in the distribution and abundance of pelagic fishes in the two ecosystems, and Table S2, which shows changes in species' abundances before and after the functional shift.

show synchronous responses to warming across diverse phylogenetic and taxonomic groups [14]. As fishes are the dominant vertebrates in marine food webs and strongly influence ecosystem processes and stability [15, 16], this shift in fish functional structure was likely mirrored throughout the ecosystems, resonating across multiple taxonomic and trophic groups [17].

This functional shift was primarily characterized by inverse changes in the abundance of pelagic fishes, as although both demersal and pelagic fishes decreased in the EEC and increased in the SNS, the change in pelagic fishes was more pronounced. Previous studies have shown ecosystem changes driven by shifts between pelagic and demersal commercial fishery species in relation to climate change [18]. However, here, we characterized climate-driven changes in the functional structure of entire fish assemblages in two adjacent ecosystems. More interesting than the shift in pelagic and demersal dominance was the finding that the most impacted fishes were characterized by *r*-selected life history traits related to reproduction, population turnover, and generation time. By examining communities through the lens of functional traits, we found that, beyond habitat type or diet, species with *r*-selected life-history traits were most respon-

sive to temperature rise, reinforcing that life-history cycles determine fish responses to climate warming. Previous studies have shown that *r*-selected strategists are highly responsive to warming because short generation times favor faster population responses [2, 19–21]. However, no study has demonstrated the impacts of *r*-selected species responses on the functional structure of connected ecosystems over large temporal and spatial scales. Our results highlight that not only are *r*-selected species more responsive to climate change, but given their quick generation times, rapid sexual maturity, and high dispersal rates, their responses can abruptly shift the functional structure of marine ecosystems.

Large-scale climate oscillations can impact communities through changes in multiple ecological processes [22], and the speed of this shift was probably enhanced by oceanographic changes linked to the AMO, including large inflows of Atlantic water through the English Channel [23]. Thus, the rapid shift in distribution and spatial reallocation of *r*-selected pelagic fishes in the SNS may have resulted from both active migration in pursuit of warm water-masses, as well as passive advection of eggs and larvae. Variability in larval survival and recruitment success

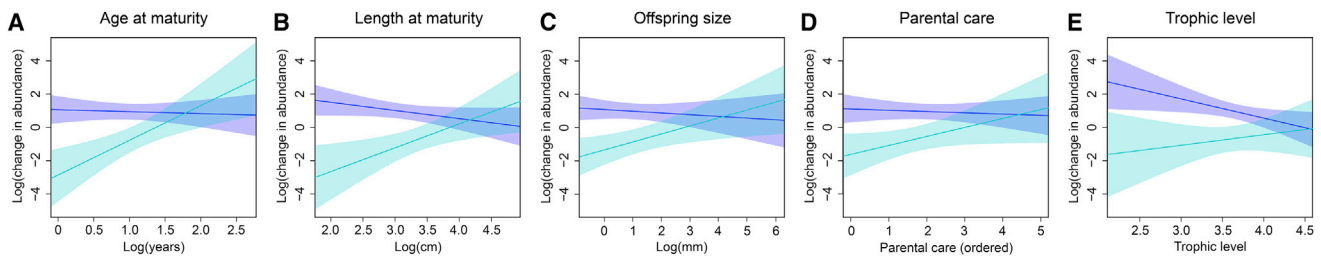


Figure 3. Inverse Relationships between Changes in Fish Abundances and Life History Traits in the Eastern English Channel, Light Blue, and Southern North Sea, Dark Blue

(A–E) Fishes with the largest decreases in the EEC and largest increases in the SNS had low age (A) and size at maturity (B), small offspring (C), low parental care (D), and low trophic level (E) (*r*-selected traits). See also [Table S1](#), which lists the functional traits, and [Table S2](#), which shows changes in species' abundances before and after the functional shift in each ecosystem.

could have also contributed to the rapid shift in abundance and distribution. Although chlorophyll-*a* was not identified as a driver of changes in functional structure, increased productivity in the SNS may have exacerbated the shift, as *r*-selected species can rapidly increase their populations in response to available resources. Additionally, associated changes in planktonic composition could have reinforced the transition [17]. In particular, long-term changes in dominance from large to small zooplankton may have benefitted pelagic fishes, which are less dependent on larger zooplankton than the planktonic life stages of demersal fishes [17].

Although we found that changes in fish functional structure were primarily driven by climate, fishing is a well-known driver of population dynamics and the relative abundances of target versus non-target species in these ecosystems. North Atlantic ecosystems have been intensively fished since industrialization in the 20th century [24], and progressive overfishing, particularly in the EEC, has led to a long-term shifting baseline as historically abundant species such as spurdog, cod, and ling have been replaced by small pelagics and commercially untargeted elasmobranchs [25]. Thus, moderate to low exploitation of many small, fast-growing species compared to the historically high fishing pressure on many commercially important demersal species likely rendered these ecosystems more susceptible to climate warming, as they became dominated by species with environmentally sensitive life-history traits [25–27]. While fishing was not identified as a main driver of the functional shift, pelagic landings have increased in the EEC while overall landings have decreased in the SNS [28]. Hence, the decrease in pelagic fishes in the EEC in parallel to an increase in the SNS was potentially exacerbated by fishing, as pelagic harvesting in the EEC may have prevented recovery while reduced harvesting in the SNS may have facilitated the increase. However, as inverse changes in functional structure between ecosystems were primarily driven by a northward shift of *r*-selected pelagic fishes in only 1–2 years, it is unlikely that fishing was a main driver, as fisheries impacts tend to manifest progressively over longer periods [24]. Yet, we cannot dismiss that both historical overfishing and contemporary changes in fishing pressure likely contributed to the increase and spatial reallocation of pelagic fishes in the SNS, either directly or through indirect changes in trophic interactions and predation pressure [27].

Given widespread phenological mismatches among marine organisms under climate change [29], it is also possible that

long-term changes in seasonal movements of pelagic and demersal fishes could have influenced our findings. Fisheries monitoring campaigns are routinely conducted during the same month each year. Therefore, year-to-year changes in fish community structure could be impacted by phenological mismatches between community patterns and fisheries campaigns. Phenological shifts could arise from behavioral adaptations such as changes in depth distribution and spawning timing, as well as resource fluctuations and changes in hydrodynamic connectivity [29]. Thus, while simultaneous and inverse changes between ecosystems indicate an abrupt shift in species' distributions and abundances (Figure S3), phenological changes could also explain the observed shift in functional structure.

As this functional shift was triggered by a warming phase of a natural climate oscillation, a future cooling phase could potentially act in reverse to our findings, with species shifting southward between ecosystems. Past studies have documented fluctuations in pelagic landings under alternating phases of climate cycles. For example, warm phases of the El Niño are correlated to higher landings of sardine in the North Pacific, while cool phases favor anchovies [30]. However, the North Sea has been identified as a global warming hotspot [31], and fisheries have become increasingly dominated by species with warm temperature preferences [32]. Additionally, studies have shown that both the AMO and global warming are influencing sea surface temperatures in the North Atlantic [9], and human-induced amplification of the AMO is already evident [33]. Thus, although a cooling phase of the AMO could slow (or slightly reverse) warming in these ecosystems, the long-term trends are likely to continue, particularly given the expected increase in marine heat waves in the near future [8, 34].

This functional shift could have major implications for ecosystem functioning, services, and governance [35, 36]. Declining abundances of pelagic planktivorous species in the EEC likely reduced carbon and nutrient sequestration from the pelagic food web leading to diminished benthic-pelagic coupling [37, 38]. Furthermore, a decrease in *r*-selected species could have shifted the ecosystem from a state of high biomass turnover and rapid nutrient cycling toward an alternative state with slower turnover and higher biomass accumulation [4–6]. This would have a major impact on trophic structure and fisheries productivity, requiring a change in management to account for biomass shifts across trophic levels and reduced surplus

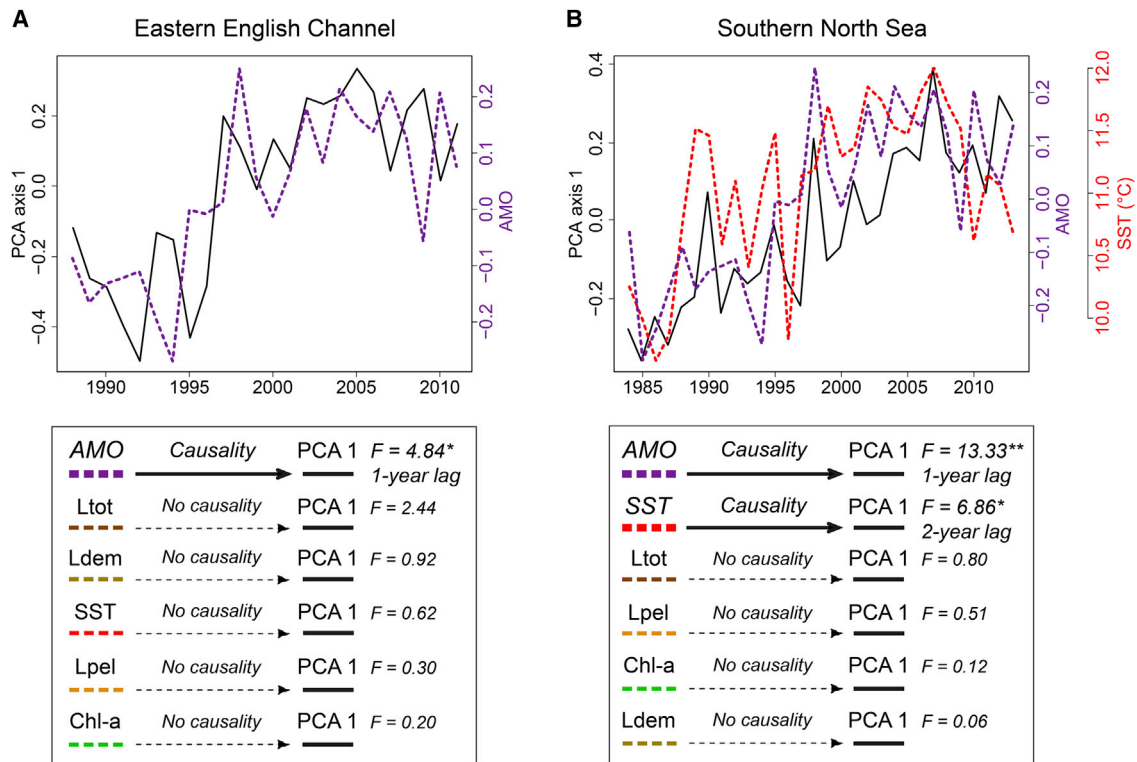


Figure 4. Ranked Drivers of Changes in Fish Functional Structure

(A and B) Causal influences of the Atlantic Multidecadal Oscillation (AMO), sea surface temperature (SST), chlorophyll-a (Chl-a), pelagic landings (Lpel), demersal landings (Ldem), and total landings (Ltot) on fish functional structure in the Eastern English Channel (A) and Southern North Sea (B) as revealed by Granger causality tests. Significant causal drivers are plotted alongside PCA axis 1 in both ecosystems. $** = p < 0.001$, $* = p < 0.01$. Optimal time lags are indicated for significant drivers. See also Figure S1, which shows the full PCA analysis.

production [6]. By contrast, the SNS shifted toward pelagic dominance, likely having inverse impacts, such as increased input of pelagic-derived energy and connectivity between food webs [37, 38]. In parallel, this would have shifted the ecosystem toward a state of higher turnover, lower biomass accumulation, and lower overall stability. Yet, increases in overall abundance, particularly in pelagic stocks, could enhance fisheries production [4, 6]. Ultimately this functional shift caused these ecosystems to become more like historical versions of each other, with the SNS resembling the EEC of the early-1990's and vice versa. Examining historical ecosystem functioning and fisheries patterns in these ecosystems could therefore help guide resource management, which will be crucial for future ocean governance and adaptation capacity [36].

Climate oscillations and warm extremes are predicted to increase in frequency and severity under ongoing climate change [7, 33, 34, 39]. In particular, El Niño events are expected to double in frequency given current trends in greenhouse gas emissions [7]. Future climate change is therefore likely to cause functional shifts and reorganization of ecosystems with unknown consequences [13, 35]. While immediate drastic measures have been recommended to abate human-induced climate change [40], our results provide insight for pre-emptive conservation planning under current climate projections. Marine resource management, particularly in connected ecosystems with large latitudinal gradients, must prepare for changes in ecosystem

functioning and services, and future ocean governance must anticipate such rapid functional shifts [36].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- METHOD DETAILS
 - Fish survey methods
 - Environmental and fishing data
 - Functional traits and functional space
- QUANTIFICATION AND STATISTICAL ANALYSIS
 - Data analysis
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and two tables and can be found with this article online at <https://doi.org/10.1016/j.cub.2018.09.050>.

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AUTHOR CONTRIBUTIONS

M.M., D.M., and A.A. conceived the idea for the study. M.M. and A.A. collected the data. M.M. performed the analyses with input from all authors. M.M. led manuscript writing, and all authors edited the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Fish community data	International Council for the Exploration of the Sea (ICES) [41, 42],	http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx
Atlantic Multidecadal Oscillation data	[43]	https://www.esrl.noaa.gov/psd/data/timeseries/AMO/
Sea surface temperature data	[44]	https://www.metoffice.gov.uk/hadobs/hadisst/
Chlorophyll-a data	[45]	https://www.cprsurvey.org/about-us/sir-alister-hardy-and-the-continuous-plankton-recorder-cpr-survey/
Fisheries landings data	[28]	http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx
Functional trait data	[21]	https://doi.pangaea.de/10.1594/PANGAEA.868610
Functional trait data	[46]	https://academic.oup.com/icesjms/article/68/3/580/658004#supplementary-data
Functional trait data	[47]	http://www.fishbase.org/

CONTACT FOR REAGENT AND RESOURCE SHARING

The data used in this study are all freely and publically available. Further information and requests for data should be directed to and will be fulfilled by the lead contact, Matthew McLean (mcleamj@gmail.com).

METHOD DETAILS

Fish survey methods

Fish abundance data for the EEC came from the Channel Ground Fish Survey (CGFS) [41], an annual monitoring campaign that uses stratified random sampling to survey fish communities at 90 to 120 stations across ICES (International Council for Exploitation of the Sea) area VIId each October. During each survey, a 3-m vertical opening bottom trawl (i.e., GOV trawl) with a 10-mm mesh codend is towed for 30 min at an average speed of 3.5 knots. In each survey, fishes are identified and counted, and resulting abundances are standardized to numbers of individuals per km². The data included the period from 1988 to 2011. Fish monitoring data for the SNS came from the International Bottom Trawl Survey (IBTS) [42], a similar annual campaign conducted in February in approximately 150, 1° longitude by 0.5° latitude survey rectangles covering the entire North Sea. The IBTS also uses a GOV trawl, which is towed for 30 min at an average speed of 4 knots. IBTS abundance estimates are also standardized to numbers of individuals per km². These data were available from 1983 to 2015 for ICES areas IVa, IVb and IVc. A potential concern with these surveys is that the survey gear is not well-adapted for sampling pelagic fishes, and changes in the depth distribution of pelagic fishes could influence survey findings. However, sampling methods have remained consistent through time, thus potential sampling biases have not changed and community changes documented in the surveys should reflect changes in community structure. Furthermore, the IBTS survey campaign has been previously shown effective for examining the temporal dynamics of both demersal and pelagic fishes [48], and the IBTS surveys are reliably used for pelagic stock assessment. A second potential concern was the possibility that differences in community structure in the two ecosystems could result from different sampling seasons. However, our study focused on global trends in each ecosystem throughout the overall time series. Therefore, temporal changes in community structure highlighted inter-annual and not seasonal variation within each ecosystem individually.

As both fish communities and environmental conditions in the North Sea are highly stratified with depth [49] and because the northern North Sea is open to the North Atlantic Ocean, the SNS was selected via k-means clustering of spatial fish functional structure for the overall time series. The resulting clustering for the SNS strongly corresponded both to the 50-m depth contour, which has previously been documented as a natural boundary for the SNS [49], and to taxonomic clustering. Furthermore, the resulting clustering corresponded to a previous investigation of spatial fish functional structure across the North Sea [21], highlighting the consistent division of taxonomic and functional structure near the 50-m depth contour. Furthermore, changes in fish functional structure were examined throughout the entire North Sea, and similar trends were repeatedly found, indicating that functional changes in the North Sea were spatially consistent and robust to the choice of geography. Finally, because the IBTS survey occurs in February, at the beginning of each year, fish monitoring data from the SNS were matched to the environmental data from the previous year, so that fish data were not matched with environmental data that had not yet occurred (in the ten months following the fish surveys).

Environmental and fishing data

The AMO refers to a 60–80 year natural climate cycle affecting sea surface temperature across the entire North Atlantic Ocean [50]. Unsmoothed data for the AMO came from the US National Oceanic and Atmospheric Administration [43]. Mean annual sea surface temperature data were derived from the Hadley Centre for Climate Prediction and Research's freely available HadISST1 database [44]. Mean annual chlorophyll-*a* data came from the Sir Alister Hardy Foundation for Ocean Science's Continuous Phytoplankton Recorder database [45].

Fisheries landings data for the period 1983–2010 came from the ICES Catch Statistics Database [28]. Fisheries landings (tons per year) were first extracted for all available species for ICES division VII_d for the EEC and divisions IV_c and IV_b for the SNS. To calculate pelagic landings, demersal landings, and total landings, data were combined for all available i) pelagic species (EEC: $n = 9$; SNS: $n = 13$), ii) demersal species (EEC: $n = 47$; SNS: $n = 44$), and iii) and for all overall species (EEC: $n = 55$; SNS: $n = 58$) that were observed during the CGFS and IBTS surveys. Thus, we derived pelagic, demersal, and total fisheries landings data that best reflected the actual fish communities of the EEC and SNS assessed during fisheries monitoring campaigns. Landings data were thus favored over fishing mortality indices, which are often based on a few representative species, while landings data were available for over 50 species per ecosystem, and are therefore better adapted for community-level analyses. Prior to all statistical analyses, fisheries landings data were \log_{10} transformed.

Functional traits and functional space

We selected ten functional traits known to influence species responses to environmental changes and impacts on ecosystem processes, particularly in these ecosystems [46, 51] (Table S1). Functional traits incorporated life history, trophic ecology, and habitat associations. Functional trait data came primarily from FishBase [47] but also from primary literature when data were unavailable or inconsistent on FishBase. We compiled functional trait data for 129 taxa (116 species and 13 unspecified genera). The multidimensional functional space was then created by applying principal coordinates analysis (PCoA) to a Gower similarity matrix of the taxa by functional trait table, and was primarily examined by plotting the first two principal coordinate axes [10], which cumulatively explained 45% of the total variance. Functional space was additionally examined using the third and fourth principal coordinates axes which cumulatively explained 22% of the total variance, thus the first four axes of functional space accounted for 67% of the total variance and additional axes were not examined. Community centroids within functional space were then computed for each year by the abundance-weighted positions of all taxa on the first two principal coordinate axes [52], and centroid movements along the first axis were used to visually examine changes in functional trait structure through time (Figure 2e, f).

QUANTIFICATION AND STATISTICAL ANALYSIS

Data analysis

All data analysis was conducted using R-statistics (Ver. 3.3.2; R Core Team) [53]. Temporal Changes in environmental variables and fisheries landings were first assessed by simple linear regressions of each variable against time.

For each ecosystem, temporal dynamics of fish functional structure were examined by first generating tables of community-weighted mean trait values using the standardized (i.e., scaled) functional traits and $\log_{10}(x+1)$ of taxa abundances for each year, which were then ordinated using principal component analysis (Figure S1). The first PCA axes of the resulting ordinations were then used as the metrics of fish functional structure for Granger causality analyses. Multivariate regression trees [54] were used to determine whether there were marked shifts in fish functional structure in each ecosystem over time, and to identify the years when they occurred. By considering time as a constrained variable, multivariate regression trees perform chronological clustering suitable for detecting shifts in multivariate time series. Multivariate regression trees are assessed by finding the optimal partitions that minimize relative error and explain the greatest amount of variation [55]. Significant differences in fish functional structure between the resulting time periods (before and after the functional shifts) were then tested by applying analysis of similarity with 999 permutations to the community-weighted mean functional trait matrices with time period as the tested factor.

To examine the contribution of life history traits to changes in fish functional structure beyond the shift in pelagic and demersal dominance, we built linear models testing the effect of the interaction of ecosystem and life history traits on changes in species' abundances before and after the shift in each ecosystem. These models revealed whether the relationships between changes in species' abundances and trait values differed between the ecosystems, e.g., lower age at maturity lead to greater decreases in abundance in the EEC but greater increases in abundance in the SNS. For each model, trait values (not including trophic level and parental care) and changes in species' abundances were \log transformed for normality and linearity.

We began by testing the influence of all environmental and fishing variables on fish functional structure (PCA axis 1 of temporal functional dynamics; Figure S1C and S1D) using multiple linear regression to identify the most influential variables. Initial multiple regression models identified AMO as the only significant driver of fish functional structure in the in the EEC, while both demersal landings and SST were identified as significant drivers in the SNS. However, an issue with analyzing time series data with standard statistical models such as multiple linear regressions or generalized linear models is that such models ignore i) temporal autocorrelation and ii) potential time lags between correlated processes and thus do not consider whether changes in one variable occur before or after another in temporal sequence. A cause cannot occur after its effect in temporal sequence, and thus standard regression models only reflect correlation without considering predictive relationships where changes in a causal driver precede and thus predict

changes in an effect. For example the shift in fish functional structure in the EEC occurred in 1997, while pelagic landings sharply increased in 2000, suggesting a secondary effect, as the shift in community structure occurred prior to changes in fishing.

Granger causality tests [56] were therefore performed in order to differentiate between simple correlations and apparent causal relationships between environmental and fishing variables and fish functional structure. A recently developed method for examining causality in non-linear time series, convergent-cross-mapping (CCM) [57], was first attempted in lieu of Granger Causality; however, reliable results could not be obtained as CCM can be unreliable for time series of only thirty time steps, and methods for applying CCM to shorter time series are only beginning to emerge [58]. Granger causality analysis is a linear modeling method that identifies apparent causality by satisfying two criteria: i) a causal factor should precede an effect, and ii) incorporating historical values of a causal factor leads to significantly improved prediction of an effect [56]. If a variable is identified as significant by Granger causality, it is said to “Granger cause” the effect variable, as true causality can never be proven in the absence of controlled experiments [56]. Prior to Granger causality analyses, all variables were made stationary by taking first differences to account for temporal autocorrelation. In the SNS, analyses were applied for the time series ranging from 1983 to 2013, as data were not available for all environmental drivers in 2014 and 2015. Granger causality was executed in the R package *vars*, which uses Akaike’s Information Criterion (AIC) to identify the optimal number of historical predictor values for generating linear models.

Finally, cross correlation analyses were applied following Granger causality to determine the time-lags of effect between significant environmental drivers and fish functional structure in both ecosystems. The results of cross correlations were interpreted by identifying the optimal significant time-lags of environmental variables that had the highest correlation with fish functional structure.

DATA AND SOFTWARE AVAILABILITY

Fish community data for both the EEC and SNS are available on <http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx>. AMO data are available on <https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>. SST data are available on <https://www.metoffice.gov.uk/hadobs/hadisst/>. Chlorophyll-a data can be accessed via <https://www.cprsurvey.org/about-us/sir-alister-hardy-and-the-continuous-plankton-recorder-cpr-survey/>. Fisheries landings data are available on <http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx>. Functional trait data are available on <http://www.fishbase.org> and from the supplemental databases of [21] <https://doi.pangaea.de/10.1594/PANGAEA.868610> and [46] <https://academic.oup.com/icesjms/article/68/3/580/658004#supplementary-data>.

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Supplemental Information

**A Climate-Driven Functional Inversion
of Connected Marine Ecosystems**

Matthew McLean, David Mouillot, Martin Lindegren, Georg Engelhard, Sébastien Villéger, Paul Marchal, Anik Brind'Amour, and Arnaud Auber

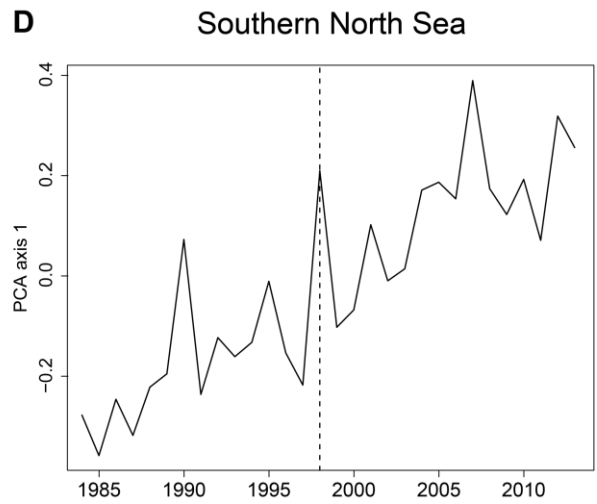
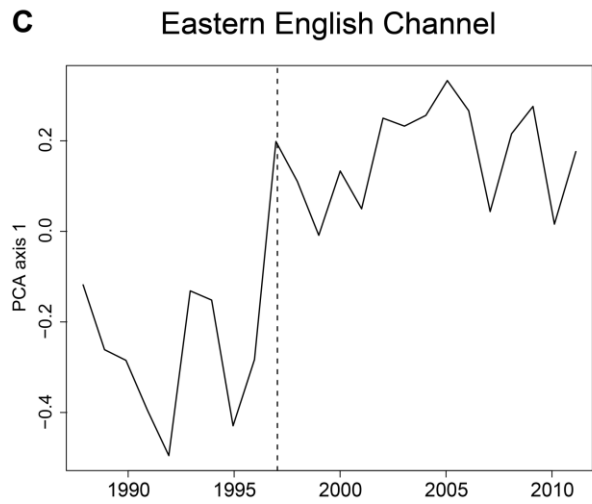
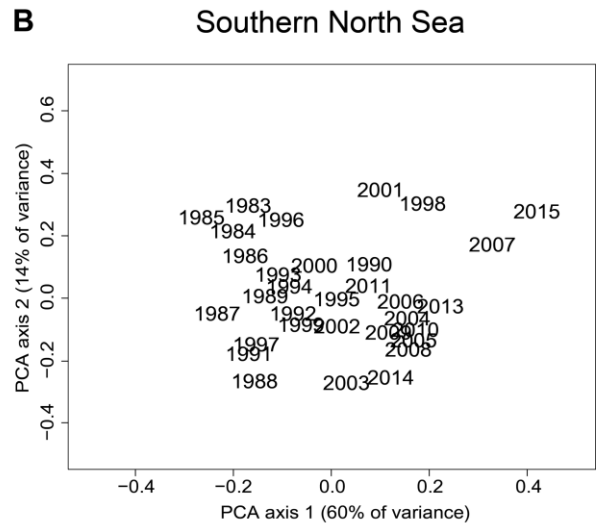
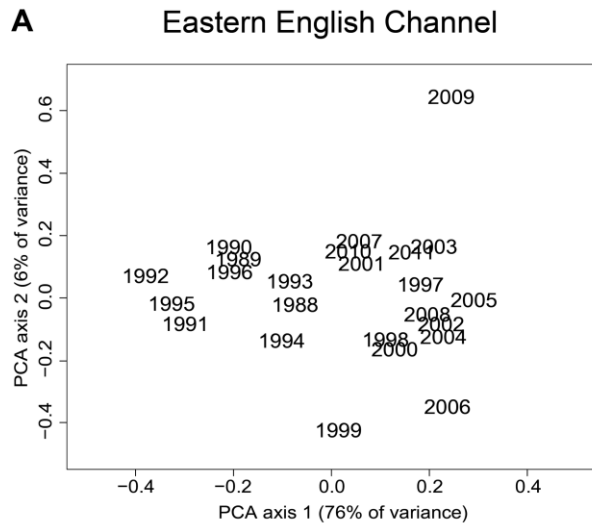


Figure S1. Temporal changes of fish functional structure in the Eastern English Channel (EEC) and Southern North Sea (SNS), related to Figure 4. Principal component plots showing temporal changes in fish functional structure in the EEC (A) and SNS (B). PCA axes 1 (C, D) were used for Granger causality analyses.

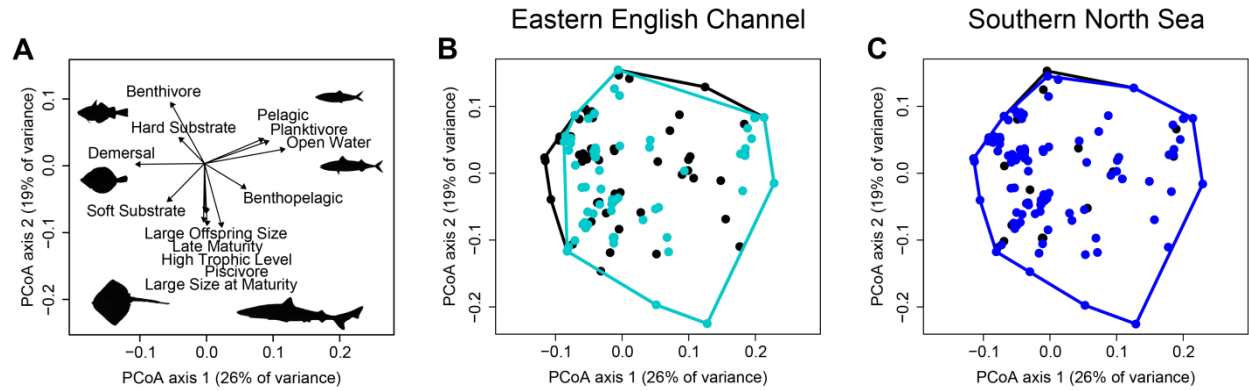


Figure S2. Multidimensional fish functional in the Eastern English Channel (EEC) (B) and Southern North Sea (SNS), related to Figure 2. (B, C). Points represent each species while polygons represent the functional space (i.e., convex hulls) containing all species in each ecosystem (EEC = light blue; SNS = dark blue; combined = black).

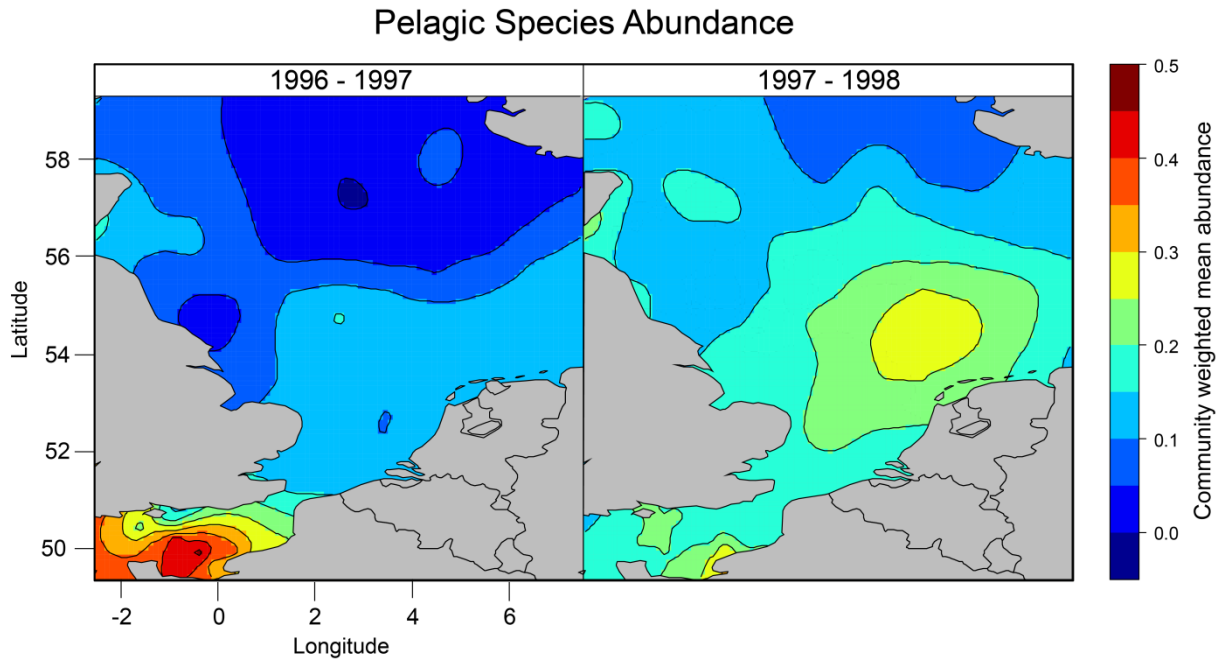


Figure S3. Kriging-interpolated map of the community-weighted mean abundance of all pelagic species in the Eastern English Channel (EEC) and Southern North Sea (SNS) for the years 1996 – 1997 and 1997 – 1998, related to Figure 2. For this figure the year 1998 in the SNS was combined with 1997 for the EEC, and 1997 in the SNS was combined with 1996 in the EEC to demonstrate the rapid northward shift of pelagic species, and because the SNS survey of a given year actually occurs only four months after the EEC survey of the year before.

Table S1. Functional traits used to characterize fish functional structure, related to Figure 2 and 3.

Functional Trait	Category	Type	Units
Length at maturity	Life history	Numeric	Total length (cm)
Age at maturity	Life history	Numeric	Years
Parental care	Life history	Ordered factor [S1]	1 = pelagic egg, 2 = benthic egg, 3 = clutch hider, 4 = clutch guarder, 5 = live bearer
Fecundity	Life history	Numeric	Number of offspring
Offspring size	Life history	Numeric	Total length or diameter (cm)
Trophic guild	Trophic ecology	Factor [S2]	Benthivore, benthopiscivore, carcinophage, detritivore, ectoparasite, piscivore, planktivore, scavenger
Trophic level	Trophic ecology	Numeric [S2]	Level (unit-less)
Water column position	Habitat use	Factor [S2]	Bathydemersal, bathypelagic, benthopelagic, demersal, epipelagic, mesopelagic, pelagic, reef-associated
Substrate preference	Habitat use	Factor	Soft, hard, or open-water
Thermal preference	Habitat use	Numeric	Degrees Celsius

Table S2. Changes in mean abundance before and after the shift for all species that co-occur in both ecosystems, related to Figure 2 and Figure 3.

	Eastern English Channel	Southern North Sea
Species	ΔAbundance (Ind./km²)	ΔAbundance (Ind./km²)
<i>Agonus cataphractus</i>	-2.30	22.03
<i>Alosa spp.</i>	0.06	5.90
<i>Amblyraja radiata</i>	0.08	5.66
<i>Anguilla anguilla</i>	-0.60	0.02
<i>Arnoglossus spp.</i>	1.14	19.47
<i>Buglossidium luteum</i>	12.30	160.80
<i>Callionymus spp.</i>	-56.82	9.95
<i>Chelidonichthys cuculus</i>	-92.34	-0.26
<i>Chelidonichthys lucerna</i>	-6.96	0.14
<i>Clupea harengus</i>	-827.46	11579.96
<i>Dicentrarchus labrax</i>	33.28	1.43
<i>Engraulis encrasicolus</i>	-225.51	235.84
<i>Eutrigla gurnardus</i>	-2.56	640.92
<i>Gadus morhua</i>	-12.37	-96.03
<i>Galeorhinus galeus</i>	-7.01	0.03
<i>Hyperoplus lanceolatus</i>	-48.09	7.70
<i>Labrus bergylta</i>	0.28	0.01
<i>Leucoraja naevus</i>	-0.25	0.03
<i>Limanda limanda</i>	-298.50	627.53
<i>Liza ramada</i>	0.28	0.01
<i>Lophius piscatorius</i>	0.15	0.10
<i>Melanogrammus aeglefinus</i>	0.01	-50.57
<i>Merlangius merlangus</i>	-406.82	266.26
<i>Microchirus variegatus</i>	-0.07	0.28
<i>Micromesistius poutassou</i>	3.73	0.01
<i>Microstomus kitt</i>	-17.38	17.38
<i>Molva molva</i>	-0.32	-0.14
<i>Mullus surmuletus</i>	54.61	1.34
<i>Myoxocephalus scorpius</i>	0.01	16.66
<i>Platichthys flesus</i>	3.83	-5.92
<i>Pleuronectes platessa</i>	-47.48	273.42
<i>Pollachius pollachius</i>	-4.51	-0.10
<i>Raja brachyura</i>	1.70	0.29
<i>Raja clavata</i>	9.11	-13.71
<i>Raja montagui</i>	-3.50	1.24

<i>Raja undulata</i>	0.08	0.00
<i>Sardina pilchardus</i>	-1207.36	17.11
<i>Scomber scombrus</i>	-1075.73	3.70
<i>Scophthalmus maximus</i>	1.32	0.49
<i>Scophthalmus rhombus</i>	0.92	0.08
<i>Scyliorhinus canicula</i>	105.76	40.89
<i>Scyliorhinus stellaris</i>	15.91	-0.02
<i>Solea solea</i>	0.72	-2.07
<i>Spondyliosoma cantharus</i>	81.95	-0.15
<i>Sprattus sprattus</i>	-3911.04	35611.78
<i>Squalus acanthias</i>	-0.77	-0.83
<i>Syngnathus spp.</i>	0.17	28.41
<i>Trachinus draco</i>	2.30	0.58
<i>Trachurus trachurus</i>	-24025.56	40.30
<i>Trigla lyra</i>	-1.64	-1.77
<i>Trigloporus lastoviza</i>	3.38	0.00
<i>Trisopterus luscus</i>	-2170.73	-46.86
<i>Trisopterus minutus</i>	-13835.40	-203.41
<i>Zeus faber</i>	5.62	0.13

Supplemental references

- S1. Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H.O., Gil de Sola, L., Punzón, A., Sólmundsson, J., and Payne, M.R. (2017). From traits to life-history strategies: Deconstructing fish community composition across European seas. *Glob. Ecol. Biogeogr.* 26, 812–822.
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