

Regional climate warming drives long-term community changes of British marine fish

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Climate change has been implicated as the cause of abundance fluctuations in marine fish populations worldwide but the effects on whole communities are poorly understood. We examined the effects of regional climate change on two fish assemblages using independent datasets from inshore marine (English Channel, 1913–2002) and estuarine environments (Bristol Channel, 1981–2001). Our results show that climate change has had dramatic effects on community composition. In both assemblages the prominent patterns of community-level change were related to temperature. Each assemblage contained a subset of dominant species whose abundance was strongly linked to annual mean sea-surface temperature. Species' latitudinal ranges were not good predictors of species-level responses however, and the same species did not show congruent trends between sites. This suggests that within a region, populations of the same species may respond differently to climate change, possibly due to additional local environmental determinants, inter-specific ecological interactions and dispersal capacity. This will make species-level responses difficult to predict within geographically differentiated communities.

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1. INTRODUCTION

It is now clear that fluctuating climate affects the abundance and biogeography of organisms (Stenseth *et al.* 2002; Walther *et al.* 2002). Future climate change will have a significant impact on marine ecosystems in the North Atlantic because sea surface temperatures are forecasted to increase by 0.5 to 4°C over the next century (Hulme *et al.* 2002). Given our reliance on marine natural resources it is important that attempts are made to predict these changes (Wood & McDonald 1997). However, knowledge of how climate influences marine communities is at present limited due to the paucity of studies examining responses of whole communities to past climate change.

Fisheries investigations have traditionally selected data from species of commercial importance. Nevertheless, analyses of these long-term data show that individual populations of marine organisms are susceptible to climate forcing, and climate has had effects on both regional fisheries, and natural predators and prey of focal species (O'Brien *et al.* 2000; Chavez *et al.* 2003). However, with only few studies on changes in community structure, it is difficult to determine whether climate-induced responses are limited to these focal species and their immediate dependents, or whether they are symptomatic of wider changes.

There are two main hypotheses concerning how populations and therefore communities change in response to climate. One suggests that changes in species distributions and abundances depend on 'bioclimate-envelope' or 'climate space', which is determined by the physiology of individuals (Pearson & Dawson 2003). Under this scenario, changing climate should directly influence survivorship, dispersal, fecundity and behaviour of individuals, and these will directly transfer to species-level changes in abundance and distribution (Walther *et al.* 2002). Hence, future climate-induced changes may be predictable on the basis of current biogeographical information. An alternative viewpoint places greater emphasis on inter-specific interactions, suggesting individual-level, climate-induced changes in survivorship, dispersal, fecundity and behaviour will cascade to population and community levels, both directly and indirectly (Ottersen *et al.* 2001; Stenseth *et al.* 2002; Pearson & Dawson 2003). The complexity of ecosystems may generate counter-intuitive species-level responses to climate change (Davis *et al.* 1998). Under this scenario, within any one community, temperature-induced changes in community beta-diversity might be expected, although, additionally, spatially segregated populations of the same species might differ in their responses (Bertness *et al.* 1999).

To examine patterns of community changes in the marine environment, and to determine whether associations with climatic variables are congruent between populations in different areas, we analysed two independent datasets documenting long-term changes in whole marine fish assemblages within UK waters (inshore marine, English Channel; estuarine, Bristol Channel;

separated by 367km minimum sea distance). Both datasets are from the southwest of England, a region subjected to major climate shifts (Russell *et al.* 1971; Southward 1980; Southward *et al.* 1995), with mean annual sea surface temperatures fluctuating within a range of 1.8°C (Fig. 1). These trends are consistent with larger-scale patterns in Northern Hemisphere temperatures over the last century (Mann 2002), namely warming in the 1950s and in the 1990s to the present day, following relatively cooler periods in the early 1900s and 1970s.

We posed the following questions: (1) is observed variance in community composition related to regional temperature changes?; (2) do species respond strongly to temperature, and if so what proportion of the community do they represent?; (3) are species responses predictable on the basis of their recorded latitudinal ranges?; and (4) do the same species show congruent responses to climate change in geographically differentiated assemblages? The results demonstrate that climate change has had significant effects on British marine fish communities over the last century.

2. METHODS

(a) English Channel sampling

Abundance of 72 taxa were recorded within 707 'otter' trawls during 23 years from 1913 to 2002 (1913, 1919-22, 1950-57, 1968, 1976-79, 1983, 1985-86, 2001-02). Of the 72 taxa, six were multi-species groups, because records did not always identify individuals to species. For clarity, each of these multi-taxon groups is henceforth referred to as one species. Although the dataset contained more sampling years, only years with eight trawls or more were selected for inclusion in the data. Pelagic taxa were excluded as they were not recorded in all sampling years. The mean duration of each haul of the trawl was 52.0 min (\pm 14.5 min S.D.). They were undertaken at 30 to 50 m depth over a spatial scale of 42 x 19 km (50°10' - 50°20' N, 04°00' - 04°35' W). Six vessels were used for sampling, ranging in overall length from 18.3 to 39.0 m. Trawls were comparable in dimensions: headline length range, 16.2-19.8 m; groundrope length range, 19.8-27.4 m; main net stretched mesh diameter, 75-100 mm. All vessels used a fine-mesh cod end or a cover, and similar trawling speeds. The same net and vessel was used from 1976 to the present day. The mean number of hauls per year was 30.7 (\pm 16.2 S.D.). Trawls were not always evenly distributed throughout the year, on average samples we collected during 7.2 months of the year (\pm 3.0 S.D.). The annual mean catch per unit effort (CPUE) of each taxon was calculated as the average number of individuals caught per hour during all trawls in the sampling year.

(b) Bristol Channel sampling

Abundance of 81 species were recorded in 264 monthly sampling occasions at the cooling water filter screens at Hinkley Point B Nuclear Power Station, Bristol Channel (51°12' N, 03°8' W), England from 1981 to 2002. The water intakes are placed between 1 and 5 metres below MLWS, so the fish were sampled from water varying between 8 and 18 metres in depth. A full description of the intake configuration and sampling methodology are given in Henderson & Seaby (1994; 1999). Quantitative sampling commenced in 1980 when 24-hour surveys of the diurnal pattern of capture were undertaken in October and November. From these surveys it was concluded that samples collected during daylight were representative of the 24-hour catch (Henderson & Holmes 1990) and monthly quantitative sampling commenced in January 1981. The total volume of water sampled per month was $3.24 \times 10^5 \text{ m}^3$, which has not varied over the 22-year period. Thus, the number of individuals caught during each sampling occasion was used as a measure of CPUE. To standardize for tidal influence, sampling dates were chosen for tides halfway between springs and neaps, with sampling commencing at high water. Fish were collected hourly from two filter screens for a 6-hour period, identified to species and the number of individuals recorded. The filter screens have a square mesh of 10 mm and start to retain fish greater than 25 mm standard length (SL), but 100% retention is attained for most species at SL greater than 40 mm.

(c) Identifying core species

Rarer species are by their nature undersampled, so trends are more difficult to identify than for common species. We present analyses based on the most abundant species in the assemblages by separating the most abundant or 'core' species from rare species using a modification of the method of Magurran & Henderson (2003). The persistence of species (number of years in which species were present in the dataset) were plotted against log transformed abundance (the average of all annual mean CPUE in sampling years). The resultant plots followed a sigmoid relationship enabling third order polynomials to be fitted. By identifying the point of inflexion of curves, the break point separating the persistence of core and rare species was determined (Fig. 1c & d). For the English Channel data, this point was at 12.25 years persistence, so the 33 taxa present in 13 years or more were considered core species. For the Bristol Channel data this point was at 10.25 years persistence, so the 33 taxa present in 11 years or more were considered core species. In total, core species comprised 99.43 % of the 412,033 individuals in the English Channel dataset, and 99.42% of the 104,668 individuals in the Bristol Channel dataset. Notably, the use of core species alone limits the analysis of the EC data to species that were consistently and commonly caught during the sampling period, irrespective of the trawler used.

(d) Temperature data

The sea surface temperature (SST) data used in our analyses were derived from the Global Ocean Surface Temperature (GISST) databank of the UK Meteorological Office Hadley Centre via the British Atmospheric Data Centre (<http://badc.nerc.ac.uk>). These data comprise monthly means for 1 degree latitude and longitude units dating back to 1870. The annual means for our study areas are shown in Fig.1a & b, and these data correlate strongly with mean annual *in-situ* measures taken in the English Channel by the MBA at ICES station E1 (50° 02' N, 04° 22' W) between 1903 and 1985 ($n = 83$, $r = 0.84$, $p < 0.001$), and measures taken in the Bristol Channel at Hinkley Point between 1981 and 2002 ($n = 22$, $r = 0.79$, $p < 0.001$). Given high inter-annual variability, data were then smoothed by fitting a 10th order polynomial for data between 1905-2002, enabling us also to focus on trends in temperature over the period.

(e) Community-level change

For each dataset we generated a matrix of annual mean CPUE for each species during each year, and these data were then $\log_{10}(x+1)$ transformed. This will have reduced the scale of influence that different trawlers or seasonal differences in species catch abundance will have had on inter-annual trends in the EC core species data. To condense multivariate variability into fewer dimensions and to identify patterns of temporal community change we used Principal Component Analysis (PCA). This was more suitable than a series of univariate analyses because within a single analysis PCA can summarise the major patterns of temporal changes in beta-diversity across the community. PCA was chosen over Detrended Component Analysis (DCA) as an ordination technique as our data more closely matched the assumptions concerning the distribution of species abundance responses along the temperature gradient. PCA assumes linear 'monotone' responses along environmental gradients, while DCA assumes bell-shaped 'unimodal' responses (Jongman *et al.* 1995). Qualitative examination showed the responses of species along the smoothed SST temporal gradient in both datasets to be predominantly monotone or very highly skewed, indicating that response curves extended beyond the short environmental gradients observed. Linear regression was used to examine the relationship between the PC1 (the axis encompassing most variation) and measures of annual mean SST.

(f) Species-level responses

To confirm that the loadings on the PC axes were indicative of the direction and scale responses to climate of individual species we calculated the univariate linear correlation coefficients between $\log_{10}(x+1)$ mean annual CPUE and smoothed mean annual SST temperature for each species. These values were then correlated with values from the PCA loadings of individual species. Additionally,

we used linear regression to test the hypothesis that species-level responses to climatic warming were directly related to their recorded median latitudinal ranges (MLR). This was determined for each species using published data (Froese & Pauly 2003), and defined as the median point of the southern and northern limits within the Northern Hemisphere. Where more than one species comprised a taxon, the median was calculated from the most northerly and southerly limits of species within the taxon within the region.

RESULTS

In the English Channel (EC) data, the first PC axis (PC1) captured 23.51 % of the variation in community composition, while in the Bristol Channel (BC) data PC1 captured 21.75%. In both cases these axes were significantly related to mean annual SST from the Hadley Centre, indicating that these axes represent the community level response to changes to warming (EC: smoothed mean annual SST, $F_{1,21} = 35.34$, $r^2 = 0.63$, $p < 0.001$, Fig 2a; non-smoothed mean annual SST, $F_{1,21} = 6.22$, $r^2 = 0.23$, $p < 0.05$. BC: smoothed mean annual SST, $F_{1,20} = 63.89$, $r^2 = 0.76$, $p < 0.001$, Fig 2b; non-smoothed mean annual SST, $F_{1,20} = 24.55$, $r^2 = 0.55$, $p < 0.001$). Annual PC1 scores for the BC data were also significantly related to non-smoothed mean annual SST calculated from *in-situ* measurements ($F_{1,20} = 19.19$, $r^2 = 0.49$, $p < 0.001$). PC1 loadings of individual species were strongly related to the correlations of CPUE with mean annual SST of those species, confirming that more positive PC1 loadings of species indicated higher abundance during warmer years (EC, $r = 0.94$, $n = 33$, $p < 0.001$, Fig 2c; BC, $r = 0.96$, $n = 33$, $p < 0.001$, Fig 2d).

We identified species responding strongly to temperature changes as those with PC1 values of greater or less than 0.2, that roughly corresponded with single species correlation coefficients of abundance with temperature of approximately 0.40 in both datasets (Fig 2; see Appendix). For the English Channel assemblage, 11 species responded strongly by increasing with warming (Fig. 3a). These were whiting (*Merlangius merlangus*), butterfly blenny (*Blennius ocellaris*), dragonet (*Callionymus lyra*), topknots (*Phrynorhombus* sp.), solenette (*Buglossidium luteum*), poor cod (*Trisopterus minutus*), lesser-spotted dogfish (*Scyliorhinus canicula*), greater pipefish (*Syngnathus acus*), thickback sole (*Microchirus variegatus*) and red bandfish (*Cepola macrophthalma*). In total these 11 species comprised on average 56.12% of the total individuals caught during sampling years (range 7.63% during 1968 to 94.90% during 2001). These species contributed substantially to the observed higher total \log_{10} CPUE of the assemblage in warmer years ($F_{1,21} = 32.32$, $r^2 = 0.70$, $p < 0.001$). For the Bristol Channel assemblage, we identified ten species responding strongly to temperature, one declining in abundance with warming (Fig. 3b), the sea snail (*Liparis liparis*), and nine increasing, sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), five-bearded rockling

(*Ciliata mustela*), cod (*Gadus morhua*), sand goby (*Pomatoschistus minutus*) bass (*Dicentrarchus labrax*), dover sole (*Solea solea*), plaice (*Platessa platessa*) and flounder (*Platichthys flesus*). These nine species comprised an average of 84.25% of the total individuals caught during sampling years (range 55.18% in 1982 to 97.27% in 1998). These species contributed substantially to the observed changes of higher total \log_{10} CPUE of the assemblage in warmer years ($F_{1,19} = 6.77$, $r^2 = 0.25$, $p < 0.02$).

In both assemblages median latitudinal ranges were not significantly associated with species responses to temperature, as measured by PC1 loadings (EC, $r^2 = 0.03$, $F_{1,31} = 0.94$, $p = 0.33$; BC, $r^2 = 0.03$, $F_{1,31} = 2.86$, $p = 0.10$), or linear correlations of annual mean CPUE with annual mean SST (EC, $r^2 = 0.01$, $F_{1,31} = 0.46$, $p = 0.25$; BC, $r^2 = 0.09$, $F_{1,31} = 3.11$, $p = 0.09$). There were also no significant associations between PC1 values of species present in both core assemblages ($n = 16$, $r = 0.12$, $p > 0.5$), or linear correlation coefficients of CPUE against SST ($n = 16$, $r = 0.12$, $p > 0.5$). This indicates that despite core assemblages showing similar macro-scale responses to temperature changes, overall, geographically distinct populations of the same species have responded differently to temperature fluctuations.

4. DISCUSSION

Climate-forced changes in sea surface temperature have had significant effects on the composition of the marine fish communities studied. In both assemblages, the first principal component, which captured the dominant changes in the community over the time period into a single variable, was significantly associated with sea temperature. The analyses showed that individuals belonging to the subset of the species that responded most strongly to temperature changes comprised on average more than 56% and 84% of the total individuals during any year in the English Channel and Bristol Channel, respectively. It would appear that fluctuations in sea surface temperature resulting from changing climate are the prominent drivers of the observed changes in species composition of these marine fish assemblages.

(a) Contrasting species-level responses

Over macro-geographic scales marine fish distributions are strongly linked to temperature gradients (e.g. Jacob *et al.* 1998). The ‘bioclimate envelope’ approach suggests that species replacement might take place as distributions are altered as they occupy favoured thermal niches, and that abundance trends would be predictable on the basis of preferred thermal regimes (Pearson & Dawson 2003). Our results suggest this is not entirely the case. Rather, abundance changes are not

predictable on the basis of species geographic ranges, and population abundance trends of species are not congruent between sites despite similar temperature regime changes.

The concept that species responses will be predictable on the basis of their physiological properties or geographic ranges is based upon the assumption that individuals are free-ranging throughout their biological distributions, and that populations have the capability to rapidly, and directly, shift distributions according to changes in climatic regimes. Such 'bioclimate envelope' responses for marine fish species seem unlikely on this assumption alone. Recent studies have shown that populations of marine fishes are much more geographically structured than ever previously thought. Electronic tagging and molecular methods have shown that dispersal of fish between geographically segregated sites can be extraordinarily low (e.g. Robichaud & Rose 2002; Knutsen *et al.* 2003), and population-specific migration routes and philopatry are present (Hunter *et al.* 2003). Therefore, we cannot assume panmixia of marine fish across the geographical range of species, and observed abundance shifts are probably not associated exclusively with distributional range changes, but also with abundance fluctuations within geographically restricted populations.

The lack of congruent species responses in this study may in part be linked to the differing sampling strategies and size classes of focal taxa at the two sampling locations. The English Channel site is an inshore ground dominated by adult and sub-adult individuals of the focal species, while the Bristol Channel site is a nursery ground. Thus, there is a possibility that temporal and spatial differences in behaviour of populations, rather than abundance, may have influenced the susceptibility of species to capture methods and therefore influenced the trends observed. However, even if sampling strategies were consistent and species showed equivalent catchability at all sites, there are likely to be strongly spatially contrasting differences in the structure and strength of the natural local ecological interactions, that will in turn influence responses to thermal regime changes. Anthropogenic disturbance intensity, particularly from fisheries and pollution that have had substantial influence on marine fish populations (Jennings & Kaiser 1998), is also likely to differ between the sampling sites. This may affect focal species directly, or indirectly through interspecific interactions. Thus, it appears likely that the combination of the differing sampling environments, species compositions and local ecological interactions of our study assemblages have also combined to generate the spatially contrasting species-level responses to thermal regime changes observed. This spatial-contrast-concept has been shown empirically with other species systems in both laboratory experiments (Davis *et al.* 1998) and in the field (Bertness *et al.* 1999). It seems that adequate prediction of spatial distribution and abundance changes in response to climate change will require complex models, incorporating additional spatial physical parameters, dispersal and inter-specific interactions.

(b) Similar patterns of community-level shifts

Most species that responded strongly to temperature changes in this study increased in abundance with warming (Fig. 3). Only a single population, the sea snail *Liparis liparis* in the Bristol Channel, showed strong increases in abundance in cooler years (Henderson & Holmes 1990). Given the non-congruent species-level trends that were found in this study, and the intrinsic complexity of marine fish communities, it was therefore surprising to find the overall pattern in both assemblages of many of the dominant species increased with warming, whereas equivalent numbers of taxa did not undergo concomitant declines. These results suggest that a subset of species have increased in relative population abundance rapidly and opportunistically to warming, although the reverse did not occur. One explanation for this trend is that the abundance of many species within the community are limited by temperature-dependent resources, and upon warming the habitats can support a greater abundance of individuals of those species. Climate warming might, for example, have enhanced marine productivity, by lengthening the appropriate season, enabling opportunistic species to respond rapidly, either by changing their distributions to encompass our sampling sites, or by enhancing their local population abundance directly.

(c) Relevance to marine monitoring and prediction of climate-induced impacts

Given the considerable interest in monitoring the effects of climate on marine ecosystems, it is desirable to possess reliable indicator measures. Historically, the monitoring of marine fish stocks has primarily taken species-level approaches. However, our study suggests that direct extrapolations of local population trends to wider geographic scales may lead to erroneous predictions. Our finding of congruent community-level patterns of change driven by regional climate changes in geographically separated communities, suggests that monitoring the scale of beta-diversity change of local species assemblages may be a more robust measure of the scale of climatic impact. Such measures have been frequently used to assess the impact of other environmental changes on marine fish communities, such as fishing (Greenstreet & Hall 1996; Jennings & Kaiser 1998). Surprisingly, these have not, to our knowledge, been used to measure the impact of climatic change. We suggest that macro-scale measures of temporal change in community structure may be suitable indices of the extent of climatic influence on components of marine ecosystems. Nonetheless, further investigations into single-species responses will be necessary to identify the critical factors that combine to shape patterns of whole community change.

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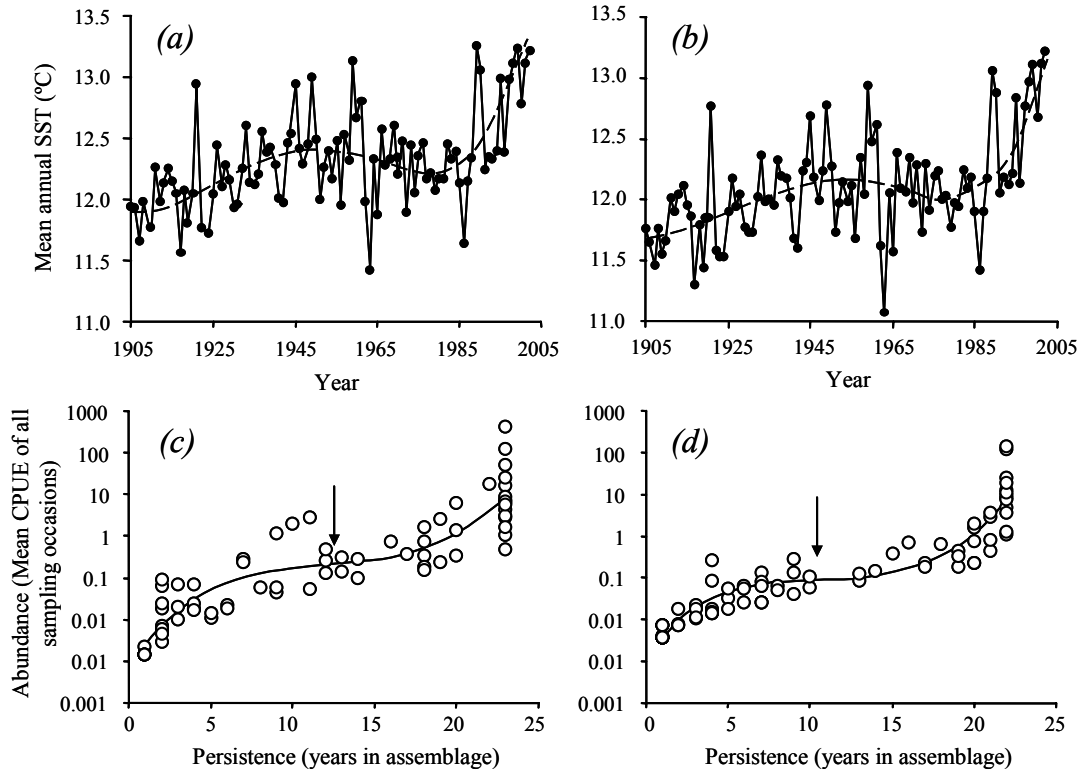


Figure 1 Mean annual sea surface temperature between 1905 and 2002 for **(A)** English Channel (50-51°N, 04-05°W) and **(B)** Bristol Channel (51-52°N, 03-04°W). Data from the UK Met Office Hadley Centre; and smoothed with 10th order polynomials. Plot of abundance against persistence for the **(C)** English Channel assemblage and **(D)** Bristol Channel assemblage. Lines are 3rd order polynomials (English Channel $r^2 = 0.83$; Bristol Channel $r^2 = 0.90$). The points of inflexion represent the break points between common and rare species, and are marked with arrows.

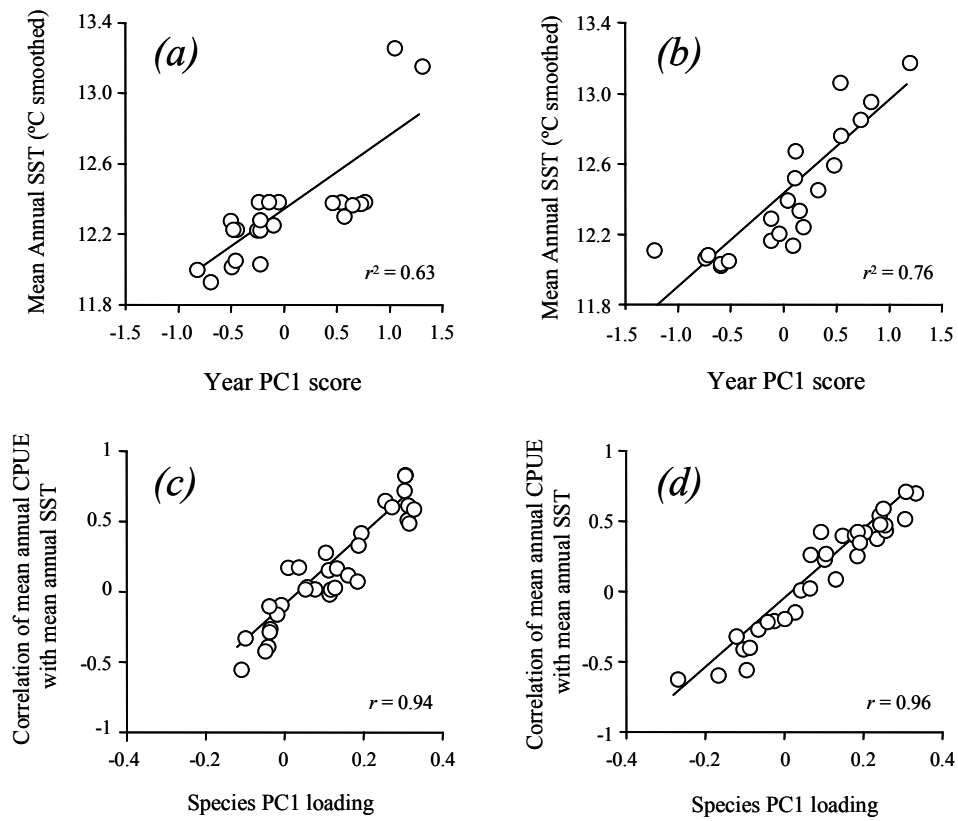


Figure 2 Relationship of PC1 with smoothed annual mean sea surface temperature for core species from **(A)** English Channel and **(B)** Bristol Channel. Relationships verifying that PC1 loadings of species are reliable measures of core species responses to smoothed annual mean SST for core species from **(C)** English Channel and **(D)** Bristol Channel. All relationships $p < 0.001$.

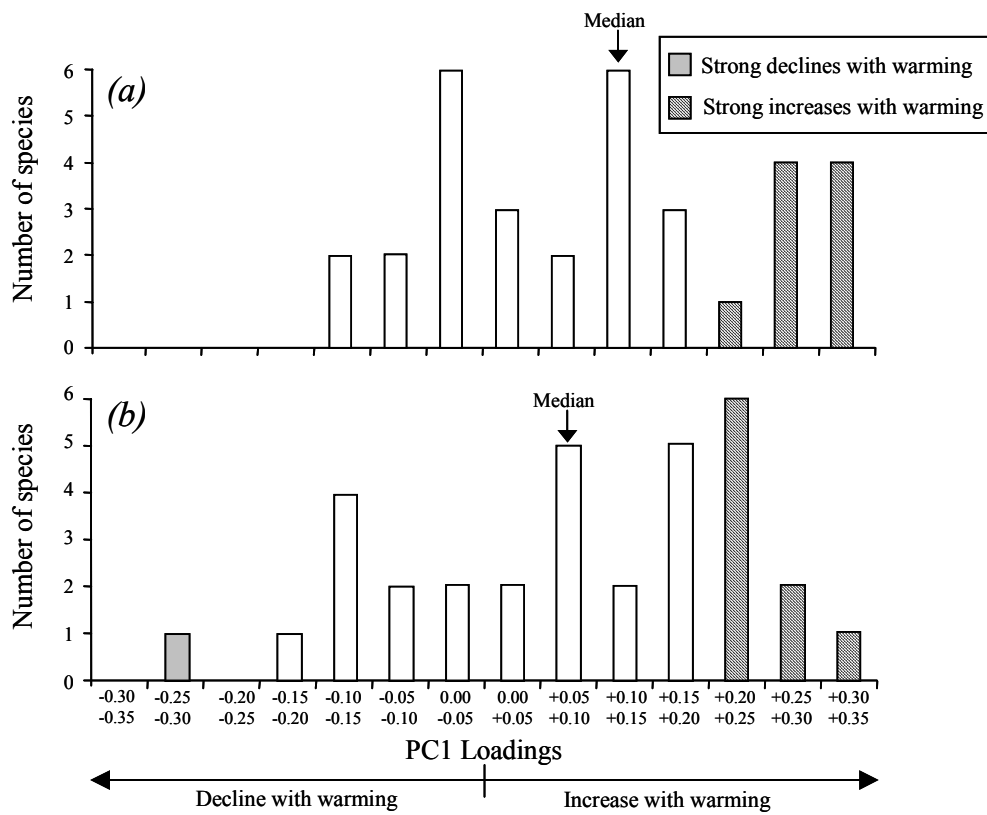


Figure 3 Frequency distributions of responses to smoothed mean annual sea surface temperature of core species from (A) English Channel and (B) Bristol Channel. Congruent patterns were derived when correlations between $\log_{10}(x+1)$ transformed CPUE and smoothed annual mean SST were used as indicators of species-level responses.

Appendix Page 1: English Channel Core Species

Species name	Common name	Total caught in samples	CPUE (mean catch per hour per haul)	Persistence (years)	Median latitude (degrees N)	PC1 loading	Correlation of $\log_{10}(x+1)$ transformed mean annual CPUE with smoothed SST
<i>Arnoglossus</i> sp.	scaldfishes	11797	18.04036596	22	35	0.174	0.1036864
<i>Blennius ocellaris</i> L.	butterfly blenny	184	0.291807203	13	35	0.306	0.5148717
<i>Buglossidium luteum</i> (Risso)	solenette	426	0.742011124	16	49.5	0.261	0.6305387
<i>Callionymus lyra</i> L.	dragonet	71557	118.8627321	23	50.5	0.301	0.5400638
<i>Cepola macrophthalmalma</i> (L.)	red bandfish	1293	2.524884337	19	35	0.296	0.8608017
<i>Chelidonichthys cuculus</i> (L.)	red gurnard	29324	48.10210826	23	35.5	0.15	0.147355
<i>Chelidonichthys gurnardus</i> (L.)	grey gurnard	5679	8.755525821	23	37.5	-0.029	-0.1298837
<i>Chelidonichthys lastoviza</i> (Bonnaterre)	streaked gurnard	830	1.606219085	18	45	-0.052	-0.359974
<i>Chelidonichthys lucerna</i> (L.)	tub gurnard	152	0.231117531	19	35.5	-0.049	-0.0731652
<i>Conger conger</i> (L.)	conger eel	208	0.323569238	20	33	0.103	0.0143196
<i>Dicentrarchus labrax</i> (L.)	sea bass	61	0.097218906	14	39.5	0.025	0.2038669
<i>Gadus morhua</i> L.	Atlantic cod	219	0.364613604	17	56.5	0.101	0.183186
<i>Limanda limanda</i> (L.)	dab	4234	6.56761198	23	54	-0.11	-0.2973572
<i>Lophius</i> sp.	anglerfishes	1054	1.64558684	23	49	-0.048	-0.2571411
<i>Merlangius merlangus</i> (L.)	whiting	15768	25.21581183	23	53.5	0.184	0.4456421
<i>Merluccius merluccius</i> (L.)	hake	2585	4.234994667	23	42.5	0.122	0.1968009
<i>Microchirus variegatus</i> (Donovan)	thickback sole	2948	5.874316254	20	37.5	0.294	0.8584174
<i>Microstomus kitt</i> (Walbaum)	lemon sole	1903	3.044078261	23	55	0.118	0.0588992
<i>Molva molva</i> (L.)	common ling	158	0.271444209	14	50	-0.001	0.200007
<i>Mullus surmuletus</i> L.	red mullet	462	0.700471476	18	34.5	0.176	0.361564
<i>Phrynorhombus</i> sp.	topknots	819	1.393207076	20	44.5	0.317	0.616133
<i>Pleuronectes platessa</i> L.	plaice	1800	2.798339629	23	45	0.043	0.0493195
<i>Pollachius pollachius</i> (L.)	pollack	107	0.174129972	18	58	-0.018	-0.0667766
Rajidae	skates	3258	5.379353341	23	35	-0.12	-0.5238653
<i>Scophthalmus maximus</i> (L.)	turbot	104	0.153677313	18	50	-0.046	-0.2364885
<i>Scophthalmus rhombus</i> (L.)	brill	282	0.45388876	23	47	0.067	0.0486834
<i>Scyliorhinus canicula</i> (L.)	lesser-spotted dogfish	9382	15.96698334	23	37.5	0.244	0.6757865
<i>Scyliorhinus stellaris</i> (L.)	nurse hound	176	0.330395677	18	38	0.093	0.3078074
<i>Solea solea</i> (L.)	Dover sole	674	1.069202447	23	37.5	-0.059	-0.3918196
<i>Syngnathus acus</i> L.	greater pipefish	75	0.136963696	13	35.5	0.292	0.7456933
<i>Trisopterus luscus</i> (L.)	pouting	4352	6.976392262	23	43.5	0.046	0.0606486
<i>Trisopterus minutus</i> (L.)	poor cod	231540	406.5361168	23	47	0.302	0.6437528
<i>Zeus faber</i> L.	John Dory	3870	6.235274973	23	31.5	0.106	0.0459323

Arnoglossus sp. includes: *A. imperialis* (Rafinesque), *A. laterna* (Walbaum) and *A. thori* Kyle.

Lophius sp. includes: *L. budegassa* Spinola and *L. piscatorius* L.

Phrynorhombus sp. includes: *P. regius* (Bonnaterre) and *P. norvegicus* (Günther)

Rajidae includes: *Raja montagui* Fowler, *R. brachyura* Lafont, *R. clavata* L., *R. microocellata* Montagu, *R. undulata* Lacepède, *Leucoraja naevus* (Müller & Henle) and *L. fullonica* (L.).

Appendix Page 2: English Channel Rare Species

Species name	Common name	Total caught in samples	CPUE (mean catch per hour per haul)	Persistence (years)
<i>Agonus cataphractus</i> (L.)	pogge	15	0.023338048	4
<i>Callionymus maculatus</i> Rafinesque	dragonet	1191	1.892917863	10
<i>Callionymus reticulatus</i> Valenciennes	reticulated dragonet	46	0.065770863	4
<i>Capros aper</i> (L.)	boarfish	458	1.10660805	9
<i>Chirolophis ascanii</i> (Walbaum)	Yarrel's blenny	1	0.001414427	1
<i>Ciliata mustela</i> (L.)	five-bearded rockling	1	0.002121641	1
<i>Ctenolabrus rupestris</i> (L.)	goldsinny	12	0.017680339	2
<i>Cyclopterus lumpus</i> L.	lumpsucker	2	0.002828854	2
<i>Diplecogaster bimaculata</i> (Bonnaterre)	two-spotted clingfish	11	0.016973126	4
<i>Echiichthys vipera</i> (Cuvier)	lesser weever	7	0.013302351	5
<i>Enchelyopus cimbrius</i> (L.)	four-bearded rockling	31	0.065299387	3
<i>Gaidropsarus mediterraneus</i> (L.)	shore rockling	5	0.007072136	2
<i>Gaidropsarus vulgaris</i> (Cloquet)	three-bearded rockling	3	0.005657709	2
<i>Galeorhinus galeus</i> (L.)	tope shark	7	0.00990099	3
<i>Glyptocephalus cynoglossus</i> (L.)	witch	13	0.018387553	6
Gobiidae	gobys	153	0.24115983	7
<i>Hippoglossus hippoglossus</i> (L.)	halibut	1	0.001414427	1
<i>Labrus bergylla</i> Ascanius	ballan wrasse	21	0.084587486	2
<i>Labrus mixtus</i> L.	cuckoo wrasse	11	0.024045262	2
<i>Lepadogaster lepadogaster</i> (Bonnaterre)	cornish sucker	2	0.004557599	2
<i>Lepidorhombus whiffiagonis</i> (Walbaum)	megrin	62	0.12633762	12
<i>Lipophrys pholis</i> (L.)	shanny	4	0.005657709	2
<i>Melanogrammus aeglefinus</i> (L.)	haddock	25	0.042311578	9
<i>Micromesistius poutassou</i> (Risso)	blue whiting	162	0.265899447	7
<i>Mustelus asterias</i> Cloquet	starry smooth-hound	14	0.021923621	6
<i>Mustelus mustelus</i> (L.)	smooth-hound	13	0.018205698	4
<i>Pagellus</i> sp.	red sea-bream	162	0.242803872	12
<i>Phycis blennoides</i> (Brünnich)	greater fork-beard	14	0.01980198	3
<i>Platichthys flesus</i> (L.)	flounder	273	0.467721058	12
<i>Pollachius virens</i> (L.)	saithe	3	0.004732891	2
<i>Raniceps raninus</i> (L.)	tadpole fish	1	0.001414427	1
<i>Serranus cabrilla</i> (L.)	comber	33	0.051037247	11
<i>Spondyliosoma cantharus</i> (L.)	black sea bream	31	0.055162659	9
<i>Squalus acanthias</i> L.	spurdog	1880	2.665086791	11
<i>Squatina squatina</i> (L.)	angel shark	8	0.011032532	5
<i>Torpedo marmorata</i> Risso	spotted electric ray	1	0.001414427	1
<i>Trachinus draco</i> L.	greater weever	1	0.001414427	1
<i>Trisopterus esmarkii</i> (Nilsson)	norway pout	42	0.059405941	2
<i>Zeugopterus punctatus</i> (Bloch)	topknot	32	0.056127512	8

Gobiidae includes: *Buenia jeffreysii* (Günther), *Crystallogobius linearis* (Düben), *Gobius niger* L., *Pomatoschistus minutus* (Pallas) and *P. pictus* (Malm).

Pagellus sp. includes: *P. erythrinus* (L.) and *P. bogaraveo* (Brünnich).

Appendix Page 3: Bristol Channel Core Species

Species name	Common name	Total caught in samples	CPUE (mean catch per sampling event)	Persistence (years)	Median latitude (degrees N)	PC1 loading	Correlation of log ₁₀ (x+1) transformed mean annual CPUE with smoothed SST
<i>Agonus cataphractus</i> (L.)	pogge	127	0.4763	21	57.5	0.173	0.279586
<i>Alosa fallax</i> (L.)	twait shad	444	1.6527	20	48.5	0.017	-0.119812
<i>Anguilla anguilla</i> (L.)	European eel	303	1.1370	22	47.5	-0.178	-0.566209
<i>Aphia minuta</i> (Risso)	transparent goby	366	1.2690	22	47.5	-0.037	-0.181179
<i>Callionymus lyra</i> L.	dragonet	61	0.2322	17	50.5	0.174	0.452851
<i>Chelidonichthys lucerna</i> (L.)	tub gurnard	34	0.1280	13	37.5	-0.054	-0.18911
<i>Ciliata mustela</i> (L.)	five-bearded rockling	865	3.0175	21	58	0.243	0.497696
<i>Ciliata septentrionalis</i> (Collett)	Northern rockling	53	0.1895	19	54	0.18	0.375193
<i>Chelidonichthys gurnardus</i> (L.)	grey gurnard	172	0.6495	18	45	0.192	0.447592
<i>Clupea harengus</i> L.	Atlantic herring	601	2.0344	20	57	0.136	0.42522
<i>Conger conger</i> (L.)	conger eel	238	0.8525	21	33	0.167	0.426057
<i>Cyclopterus lumpus</i> L.	lumpsucker	109	0.4091	15	65	-0.133	-0.292722
<i>Dicentrarchus labrax</i> (L.)	sea bass	2236	8.1803	22	39.5	0.238	0.615378
<i>Entelurus aequoreus</i> (L.)	snake pipefish	60	0.2273	20	51	0.054	0.050671
<i>Gadus morhua</i> L.	Atlantic cod	943	3.5748	21	56.5	0.245	0.462009
<i>Gasterosteus aculeatus</i> L.	three spined stickleback	40	0.1478	14	47.5	0.081	0.453445
<i>Limanda limanda</i> (L.)	dab	1342	5.0651	22	54	-0.1	-0.370112
<i>Liparis liparis</i> (L.)	common sea snail	2642	9.7144	22	64.5	-0.28	-0.598121
<i>Liza ramada</i> (Risso)	thin-lipped grey mullet	1012	3.7369	22	42	0.055	0.288179
<i>Merlangius merlangus</i> (L.)	whiting	32692	120.9551	22	53.5	0.293	0.542721
<i>Merluccius merluccius</i> (L.)	hake	198	0.7352	16	42.5	-0.107	-0.529197
<i>Platichthys flesus</i> (L.)	flounder	2189	8.0787	22	45	0.295	0.736547
<i>Pleuronectes platessa</i> L.	plaice	124	0.4454	19	45	0.231	0.505405
<i>Pollachius pollachius</i> (L.)	pollock	88	0.3340	19	58	0.031	0.036319
<i>Pomatoschistus minutus</i> (Pallas)	sand goby	6815	25.4389	22	40	0.229	0.569149
<i>Raja clavata</i> L.	thornback ray	64	0.2419	20	49	-0.01	-0.162737
<i>Scyliorhinus canicula</i> (L.)	lesser-spotted dogfish	25	0.0911	13	37.5	0.094	0.294812
<i>Solea solea</i> (L.)	Dover sole	3926	13.2963	22	37.5	0.321	0.729381
<i>Sprattus sprattus</i> L.	sprat	37379	140.6865	22	49.5	0.223	0.403148
<i>Syngnathus rostellatus</i> (Nilsson)	Nilsson's pipefish	49	0.1854	17	35.5	0.09	0.254568
<i>Trisopterus esmarkii</i> (Nilsson)	Norway pout	220	0.7826	20	60.5	-0.078	-0.243982
<i>Trisopterus luscus</i> (L.)	pout	3544	11.4627	22	43.5	0.119	0.11459
<i>Trisopterus minutus</i> (L.)	poor cod	5122	19.0316	22	47	-0.115	-0.383544

Appendix Page 4: Bristol Channel Rare Species

Species name	Common name	Total caught in samples	CPUE (mean catch per sampling event)	Persistence (years)
<i>Ammodytes marinus</i> (Raïtt)	lesser sandeel	1	0.0038	1
<i>Ammodytes tobianus</i> L.	small sand eel	17	0.0603	10
<i>Atherina boyeri</i> Risso	sand smelt	19	0.0682	8
<i>Balistes capriscus</i> Gmelin	triggerfish	1	0.0038	1
<i>Belone belone</i> (L.)	garfish	1	0.0038	1
<i>Buglossidium luteum</i> (Risso)	solenette	2	0.0076	1
<i>Centrolabrus exoletus</i> (L.)	rock cook	2	0.0076	1
<i>Chelon labrosus</i> (Risso)	thick-lipped grey mullet	75	0.2806	4
<i>Crystallogobius linearis</i> (Düben)	crystal goby	9	0.0335	5
<i>Ctenolabrus rupestris</i> (L.)	goldsinny	5	0.0184	4
<i>Engraulis encrasicolus</i> (L.)	anchovy	6	0.0227	3
<i>Gaidropsaurus vulgaris</i> (Cloquet)	three-bearded rockling	5	0.0184	3
<i>Glyptocephalus cynoglossus</i> (L.)	witch	1	0.0038	1
<i>Gobius niger</i> L.	black goby	18	0.0682	6
<i>Gobius paganelus</i> L.	rock goby	3	0.0076	1
<i>Hyperoplus lanceolatus</i> (Le Sauvage)	greater sand eel	4	0.0155	4
<i>Labrus bergylta</i> Ascanius	ballan wrasse	15	0.0569	6
<i>Labrus mixtus</i> L.	cuckoo wrasse	3	0.0114	3
<i>Lampetra fluviatilis</i> (L.)	river lamprey	7	0.0269	6
<i>Liza aurita</i> (Risso)	golden mullet	24	0.0913	4
<i>Lophius piscatorius</i> L.	anglerfish	15	0.0565	5
<i>Maurolicus muelleri</i> (Gmelin)	pearlside	31	0.1140	10
<i>Micromesistius poutassou</i> (Risso)	blue whiting	57	0.0152	4
<i>Microstomus kitt</i> (Walbaum)	lemon sole	2	0.0079	2
<i>Molva molva</i> (L.)	ling	3	0.0117	3
<i>Mullus surmuletus</i> L.	red mullet	88	0.3011	9
<i>Nerophis lumbriciformis</i> Jenyns	worm pipefish	1	0.0038	1
<i>Parablennius gattorugine</i> (L.)	tompot blenny	4	0.0152	4
<i>Petromyzon marinus</i> L.	marine lamprey	1	0.0041	1
<i>Pollachius virens</i> (L.)	saithe	1	0.0038	1
<i>Pomatoschistus microps</i> (Krøyer)	common goby	40	0.1439	7
<i>Pomatoschistus pictus</i> (Malm)	painted goby	17	0.0537	8
<i>Raja brachyura</i> Lafont	blonde ray	1	0.0038	1
<i>Raja microocellata</i> Montagu	small-eyed ray	2	0.0076	2
<i>Raniceps raninus</i> (L.)	tadpole fish	4	0.0152	4
<i>Salmo salar</i> L.	Atlantic salmon	7	0.0262	7
<i>Sardina pilchardus</i> (Walbaum)	European pilchard	5	0.0189	2
<i>Scophthalmus maximus</i> (L.)	turbot	22	0.0844	7
<i>Scophthalmus rhombus</i> (L.)	brill	19	0.0682	7
<i>Spinachia spinachia</i> (L.)	fifteen-spined stickleback	5	0.0186	5
<i>Spondylisoma cantharus</i> (L.)	black sea bream	7	0.0262	7
<i>Symphodus melops</i> (L.)	corkwing wrasse	2	0.0076	2
<i>Syngnathus acus</i> L.	greater pipefish	36	0.1371	9
<i>Trachinus vipera</i> Cuvier	lesser weaver	1	0.0038	1
<i>Trachurus trachurus</i> (L.)	scad	11	0.0417	9
<i>Trigla lyra</i> L.	piper gurnard	2	0.0076	1
<i>Zeugopterus punctatus</i> (Bloch)	topknot	1	0.0038	1
<i>Zeus faber</i> L.	John Dory	2	0.0076	2