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

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Climatic 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 climatic 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 climatic change has had dramatic effects on community composition. Each assemblage contained a subset of dominant species whose abundances were 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 climatic change, possibly owing to additional local environmental determinants, interspecific ecological interactions and dispersal capacity. This will make species-level responses difficult to predict within geographically differentiated communities.

Keywords: fisheries; temperature; community structure; marine ecosystems

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 climatic change will have a significant impact on marine ecosystems in the North Atlantic because sea-surface temperatures (SSTs) are forecasted to increase by 0.5–4 °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 owing to the paucity of studies examining responses of whole communities to previous climatic 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 climatic forcing, and climate has had effects on both regional fisheries and the natural predators and prey of focal species (O'Brien *et al.* 2000; Chavez *et al.* 2003). However, with only a 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 dependants, 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 'bioclimatic envelopes' or 'climatic spaces', which are determined by the physiology of individuals (Pearson & Dawson 2003). The basis of this hypothesis is that changing climate should directly influence the 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 interspecific interactions, suggesting that individual-level climate-induced changes in survivorship, dispersal, fecundity and behaviour will cascade to the 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 climatic change (Davis *et al.* 1998). Thus, 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 (EC); estuarine, Bristol Channel (BC); separated by a minimum sea distance of 367 km). Both datasets are from the southwest of England, a region subjected to

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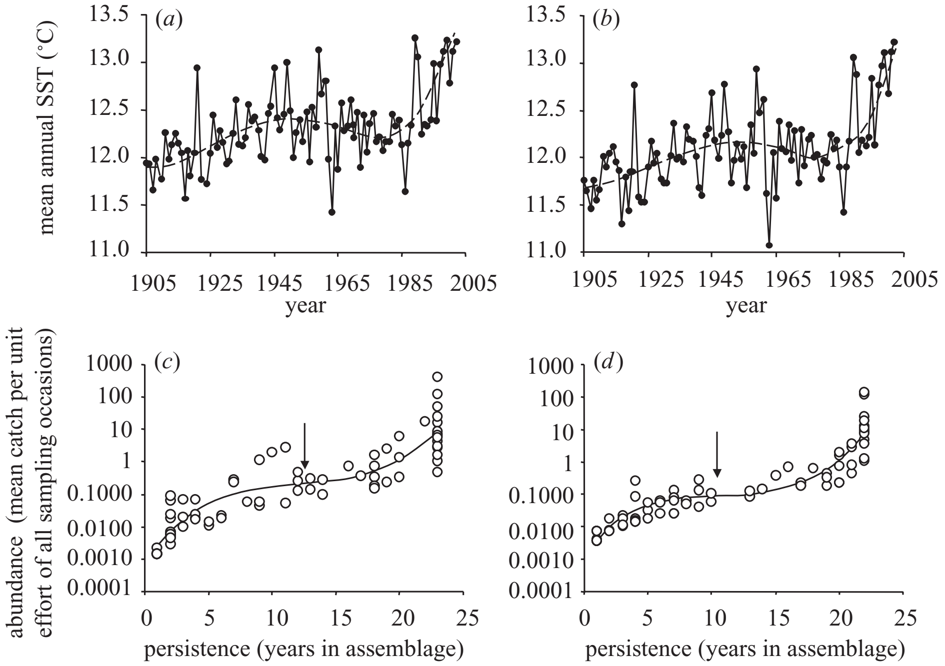

Figure 1. Mean annual SST between 1905 and 2002 for (*a*) the EC (50–51° N, 04–05° W) and (*b*) the BC (51–52° N, 03–04° W). Data from the UK Meteorological Office Hadley Centre; and smoothed with tenth-order polynomials. Plot of abundance against persistence for species in the (*c*) EC assemblage and (*d*) BC assemblage. Lines are third-order polynomials (EC: $r^2 = 0.83$; BC: $r^2 = 0.90$). The points of inflexion represent the break points between common and rare species, and are marked with arrows.

major climatic shifts (Russell *et al.* 1971; Southward 1980; Southward *et al.* 1995), with mean annual SSTs fluctuating within a range of 1.8 °C over the past century (figure 1). These trends are consistent with larger-scale patterns in temperatures in the Northern Hemisphere over the past 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.

(i) Are the observed changes in community composition related to regional temperature fluctuations?
(ii) Do species respond strongly to temperature, and if so what proportion of the community do they represent?
(iii) Are species responses predictable on the basis of their recorded latitudinal ranges?
(iv) Do the same species show congruent responses to climatic change in geographically differentiated assemblages?

The results demonstrate that climatic change has had significant effects on British marine fish communities over the past century.

2. MATERIAL AND METHODS

(a) *English Channel sampling*

The abundances of 72 taxa were recorded within 707 ‘otter’ trawls over eight time periods totalling 23 years from 1913 to 2002 (i.e. 1913, 1919–1922, 1950–1957, 1968, 1976–1979, 1983, 1985–1986 and 2001–2002). Out of the 72 taxa, six were multispecies groups, because records did not always identify individuals to species. For clarity, each of these multispecies groups is henceforth referred to as one species. Although the whole EC dataset collected by the Marine Biological Association of the UK (MBA) contained more sampling years, only years with eight trawls or more were selected for inclusion in the data. Pelagic taxa were excluded because they were not recorded in all sampling years. The mean duration of each haul of the trawl was 52.0 min (± 14.5 min s.d.). They were undertaken at depths of 30–50 m over a spatial scale of 42 km × 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 were used from 1976 to 2003. The mean number of hauls per year was 30.7 (± 16.2 s.d.). Trawls were not always evenly distributed throughout the year; on average, samples were collected during 7.2 months of the year (± 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*

The abundances of 81 species were recorded on 264 monthly sampling occasions at the cooling water filter screens at Hinkley Point B Nuclear Power Station, BC (51°12′ N, 03°8′ W), England from 1981 to 2002. The water intakes are placed between 1 and 5 m below the mean low water of spring tides, so the fish were sampled from water varying between 8 and 18 m in depth. A full description of the intake configuration and sampling methodology is given in Henderson & Seaby (1994, 1999). Quantitative sampling commenced in 1980, when 24 h 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 h catch (Henderson & Holmes 1990); monthly quantitative sampling commenced in January 1981. The total volume of water sampled per month was $3.24 \times 10^5\ m^3$, 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 over a 6-hour period and identified with respect to species; the number of individuals was recorded. The filter screens have a square mesh of 10 mm and retain fish of a standard length (SL) of greater than 25 mm, but 100% retention is attained for most species at a SL of greater than 40 mm.

(c) *Identifying core species*

Rarer species are, by 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 persistences of species (number of years in which species were present in the dataset) were plotted against the log of 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 the curves, the break point separating the persistence of core and rare species was determined (figure 1*c*,*d*). For the EC data, this point was at a persistence of 12.25 years, so the 33 taxa present during 13 years or more were considered to be core species. For the BC data, this point was at a persistence of 10.25 years, so the 33 taxa present for 11 years or more were considered to be core species. In total, core species comprised 99.43% of the 412 033 individuals in the EC dataset, and 99.42% of the 104 668 individuals in the BC 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 SST data used in our analyses were derived from the global ocean surface temperature (HadlSST 1.1) 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° latitude and longitude units dating back to 1870. The annual means for our study areas are shown in figure 1*a*,*b*, and these data correlate strongly with mean annual *in situ* measures taken in the EC by the MBA at International Council for the Exploration of the Seas 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 BC 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 tenth-order polynomial for data between 1905 and 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 $\log(x + 1)$-transformed. This will have reduced the scale of influence that different trawlers or seasonal differences in species catch abundance 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 summarize the major patterns of temporal changes in beta-diversity across the community. PCA was chosen over detrended component analysis (DCA) as an ordination technique because 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, whereas DCA assumes bell-shaped 'unimodal' responses (Jongman *et al.* 1995). Qualitative examination showed that the responses of species along the smoothed SST temporal gradient in both datasets was 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 of responses to climate of individual species, we calculated the univariate linear correlation coefficients between $\log(x + 1)$ mean annual CPUE and the 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 (MLRs). This was determined for each species using published data (Froese & Pauly 2003) and defined as the median point of the southern and northern range limits within the Northern Hemisphere. Where a taxon comprised more than one species, the median was calculated from the most northerly and southerly limits of species within the taxon within the region.

3. RESULTS

In the EC data, the PC1 captured 23.51% of the variation in community composition, while in the 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 responses to warming (EC: smoothed mean annual SST, $F_{1,21} = 35.34$, $r^2 = 0.63$, $p < 0.001$, figure 2*a*; non-smoothed mean annual SST, $F_{1,21} = 6.22$, $r^2 = 0.23$, $p < 0.05$; BC: smoothed mean annual SST, $F_{1,20} = 63.89$, $r^2 = 0.76$, $p < 0.001$, figure 2*b*; 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, $r = 0.94$, $n = 33$, $p < 0.001$, figure 2*c*; BC, $r = 0.96$, $n = 33$, $p < 0.001$, figure 2*d*).

We identified species responding strongly to temperature changes as those with PC1 values of greater or less

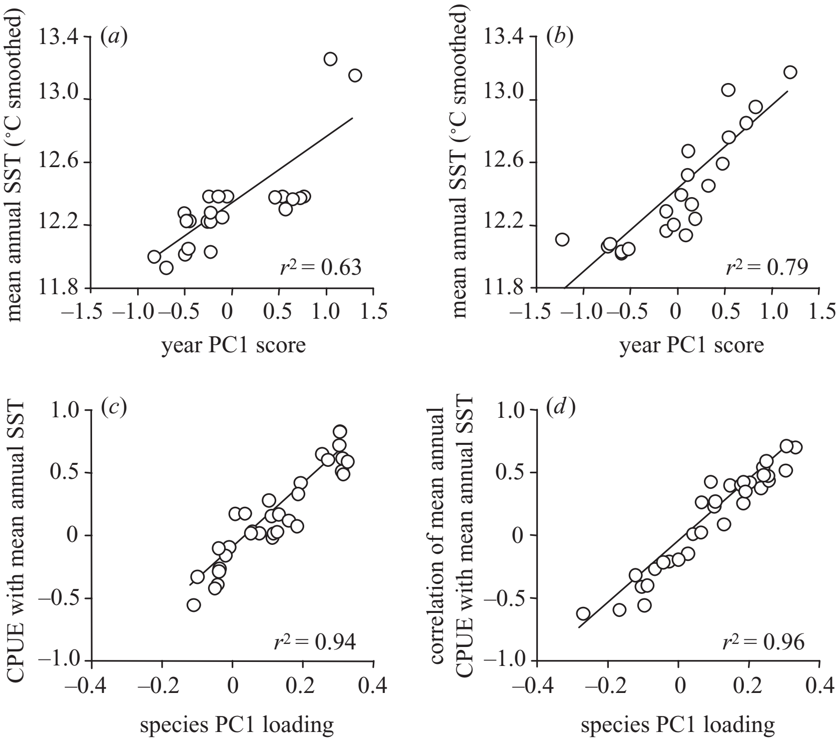

Figure 2. Relationship of PC1 with smoothed annual mean SST for core species from (*a*) the EC and (*b*) the BC. Relationships verifying that PC1 loadings of species are reliable measures of core species responses to smoothed annual mean SST for core species from (*c*) the EC and (*d*) the BC. All relationships $p < 0.001$.

than 0.2, which roughly corresponded to single species correlation coefficients of abundance with temperature of *ca.* 0.40 in both datasets (figure 2; see electronic Appendix A available on The Royal Society's Publications Web site). For the EC assemblage, 9 species responded strongly by increasing with warming (figure 3*a*). These were 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 macropthalma*). In total, these 9 species comprised, on average, 57.43% of the total individuals caught during sampling years (range of 7.63% during 1968 to 94.93% during 2001). These species contributed substantially to the observed higher total log(CPUE) of the assemblage in warmer years ($F_{1,21} = 32.32$, $r^2 = 0.70$, $p < 0.001$). For the BC assemblage (figure 3*b*), we identified 10 species responding strongly to temperature, one declining in abundance with warming (the sea snail, *Liparis liparis*), and nine increasing (sprat, *Sprattus sprattus*; whiting, *M. 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 of 55.18% in 1982 to 97.27% in 1998). These species contributed substantially to the observed changes of higher total log(CPUE) of the assemblage in warmer years ($F_{1,19} = 6.77$, $r^2 = 0.25$, $p < 0.02$).

In both assemblages, MLRs 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 SST 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 57% and 84% of the total individuals during any year in the EC and BC, respectively. It would appear that fluctuations in SST 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-geographical scales, marine fish distributions are strongly linked to temperature gradients (Jacob *et al.* 1998). The 'bioclimatic envelope' approach

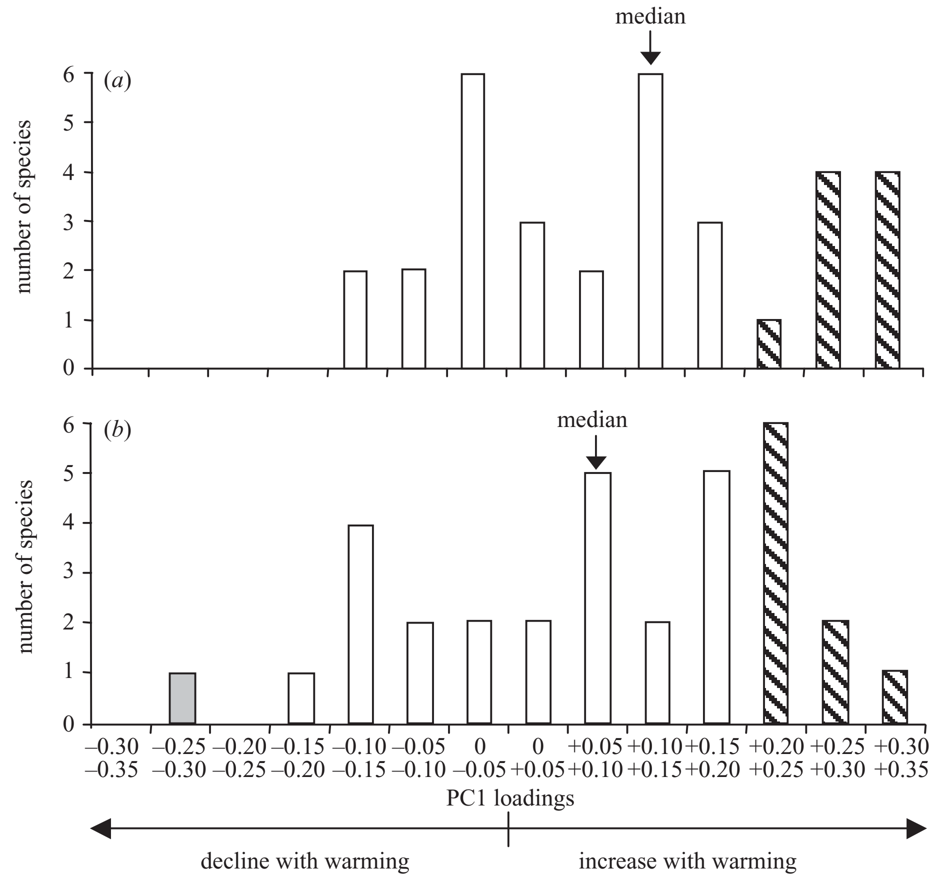

Figure 3. Frequency distributions of responses to smoothed mean annual SST of core species from (*a*) the EC and (*b*) the BC. Congruent patterns were derived when correlations between log(x + 1)-transformed CPUE and smoothed annual mean SST were used as indicators of species-level responses. Grey bar, strong decline with warming; striped bars, strong increases with warming.

suggests that species replacement might take place as distributions alter to occupy favoured thermal niches, and that abundance trends would be predictable on the basis of preferred thermal regimes (Pearson & Dawson 2003). Our results suggest that this is not entirely the case. Rather, abundance changes are not predictable on the basis of species' geographical 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 geographical ranges is based upon the assumption that individuals are free-ranging throughout their biological distributions and that populations have the capability rapidly and directly to shift distributions according to changes in climatic regimes. Such 'bioclimatic envelope' responses for marine fish seem unlikely on this assumption alone. Recent studies have shown that populations are much more geographically structured than previously thought. Electronic tagging and molecular methods have shown that dispersal between geographically segregated sites can be extraordinarily low (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 EC site is an inshore ground dominated by adult and sub-adult individuals of the focal species, whereas the BC 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 methods of capture 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, which 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 differing sampling environments, species compositions and local ecological interactions of our study assemblages have combined to generate the spatially contrasting species-level responses to thermal regime changes observed. This spatial-contrast concept has been demonstrated 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 climatic change will require complex models, incorporating additional spatial physical parameters, dispersal and interspecific interactions.

(**b**) *Similar patterns of community-level shifts*

Most species that responded strongly to temperature changes in this study increased in abundance with warming (figure 3). Only a single population, the sea snail (*Liparis liparis*) in the BC, showed strong increases in abundance during climatic cooling (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 that the overall pattern in both assemblages of many of the dominant species increasing with warming, whereas equivalent numbers of taxa did not undergo concomitant declines. These results suggest that a subset of species have increased in population abundance rapidly and opportunistically to warming, although the reverse did not occur. One explanation for this trend is that the abundances of many species are limited by temperature-dependent resources, and the habitats can support a greater abundance of individuals of those species upon warming. Climatic 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 climatic impacts*

Given the considerable interest in monitoring the effects of climate on marine ecosystems, it is desirable to find 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 geographical scales may lead to erroneous predictions. Our finding of congruent community-level patterns of change driven by regional climatic fluctuations suggests that measures of beta-diversity may be more robust indicators of climatic impact. Such measures have been used frequently to assess the impact of other environmental changes, such as fishing, on marine fish communities (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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