Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region

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Abstract

We examined climatic effects on the geographic distribution and abundance of 34 dominant oceanic fishes in the southern California region using larval fish data collected from the 50-year long California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys. The oceanic species responses to environmental changes in their geographic distributions were not very pronounced, perhaps because they lived in the deep layer where temperature change was relatively small or because the environmental variation of the CalCOFI region is not strong enough (with an average temperature gradient of the upper 100 m around 91 km $^\circ C^{-1}$). Among the 34 taxa, 16 showed a significant distributional shift (median latitude or boundaries) in relation to environmental variables, and eight species significantly shifted their geographic distribution from the 1951–1976 cold period to the 1977–1998 warm period. Interestingly, the vertically migrating taxa more often showed a significant response to environmental variables than the nonmigrating mesopelagic taxa, reflecting the more significant increase in heat content of the upper ocean (< 200 m), compared with the deeper zone (300–500 m) where the mesopelagic fishes typically remain. Climate change has significant effects on the abundances of oceanic fishes. Twenty-four taxa exhibited a significant change in abundance in relation to environmental variables, and 25 taxa, including both warm and cold-water taxa, showed a significant increase in abundance from the cold to warm period. Analysis of physical data indicated that the surface-layer (20–200 m) warmed significantly and the isotherms approached shoreward from the cold to the warm period. We further show that the spatial distribution of coastal–neritic fish retreated shoreward and oceanic fish extended shoreward from the cold to warm period. Our results suggest intensified stratification of the southern California region during the warm period may create a suitable habitat for the oceanic species. Moreover, such an unfavorable condition (e.g. changes in food habitat) for coastal–neritic species might result in competitive release for the oceanic fishes to flourish.

Keywords: abundance, CalCOFI, competitive release, decadal, ecological traits, geographic distribution, interannual, ocean warming, stratification, time series

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Introduction

Climatic fluctuations have had profound impacts on the geographic distribution, abundance, and phenology of species (Beebee, 1995; Crick *et al.*, 1997; Mackas *et al.*, 1998; Beaugrand *et al.*, 2002; Stenseth *et al.*, 2002;

Parmesan & Yohe, 2003; Root *et al.*, 2003; Richardson & Schoeman, 2004; Perry *et al.*, 2005; Chiba *et al.*, 2006; Jonzen *et al.*, 2006; Menzel *et al.*, 2006). Studies of climatic effects on marine populations are increasingly gaining attention, as understanding these effects is an essential step towards conserving and managing marine resources (Botsford *et al.*, 1997; McCann *et al.*, 2003).

For fishes, climate change has significant influences on their abundances and distributions by affecting their survival, growth, reproduction, and migration, or through their responses to changes in food supply (Wood & McDonald, 1997; Beaugrand *et al.*, 2003; Hsieh *et al.*, 2005; Perry *et al.*, 2005). In the Northeast Pacific Ocean, changes in abundance and distribution of fish species in response to climate have been documented (Fiedler *et al.*, 1986; Yoklavich *et al.*, 1996; Beamish *et al.*, 1997; Benson *et al.*, 2002; Rodriguez-Sanchez *et al.*, 2002; Smith & Moser, 2003; Hsieh *et al.*, 2008). However, these studies are largely limited to coastal and neritic, commercially important species. While the oceanic fish are an important component of the ocean ecosystem (Beamish *et al.*, 1999), how they respond to climate changes is not well studied. Although El Niño effects on species composition were noted (Lea & Rosenblatt, 2000; Funes-Rodriguez *et al.*, 2006), long-term variability of abundances of selected species were examined (Smith & Moser, 2003), and decadal changes in distributions of oceanic fishes were illustrated in atlases (Moser *et al.*, 2001a), no systematic study has been carried out to examine these changes.

To investigate the effects of climate, we studied the larval abundances and distributions of oceanic fish collected in the Southern California Current System (SCCS) by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys. The abundances and distributions of larvae are representative of biomass and locations of spawning adults because most larvae taken in plankton nets are in very early stages of development, although effects of physical advection and diffusion on eggs and larvae may partially obscure this relationship (Moser *et al.*, 2001b; Hsieh *et al.*, 2005, 2006). The CalCOFI sampling domain lies along the eastern boundary of the North Pacific subtropical gyre, in a latitudinally transitional region where subarctic and subtropical fauna meet (Valentine, 1966; Horn & Allen, 1978). In the east–west direction, the CalCOFI domain connects the California Current coastal upwelling system in the east to the open ocean Central Gyre Water in the west (Bograd & Lynn, 2003). Because the CalCOFI surveys were taken in this biogeographic boundary zone, the dynamics of the oceanic fish obtained from these surveys may be particularly sensitive to climate changes. In addition, associations of oceanic fishes and water masses in the Northeast Pacific are well known (Moser *et al.*, 1987; Smith & Moser, 2003). Because oceanic species are not under direct fisheries exploitation in the eastern North Pacific Ocean, their dynamics in abundance and geographic distribution mainly reflect their responses to climate (Smith & Moser, 2003; Hsieh *et al.*, 2005) or climate-mediated biological interactions. As such, the dynamics of oceanic fish may provide an opportunity to examine climatic effects on the southern California current ecosystem (CCE).

We first describe the environmental variation of the CalCOFI region. We then investigate whether oceanic fish show significant changes in their abundances and geographic distributions in response to climatic variations. Furthermore, we examine whether their sensitivities to climatic signals are related to their geographic affinities (e.g. cold water, warm water, or broadly distributed), adult habitats (e.g. mesopelagic or vertical migratory), and phylogeny. We then link the underlying dynamics associated with these changes to the variations in the physical environment. Although life history traits might affect sensitivities of fish in response to climatic variations (Hsieh *et al.*, 2005; Perry *et al.*, 2005), life history traits for oceanic species are generally poorly known and cannot be examined here.

Background on physical environmental variations

The CalCOFI sampling domain is located in the SCCS, which is part of the North Pacific eastern boundary upwelling system. Physical climate fluctuations in the SCCS beyond El Niño/Southern Oscillation (ENSO) timescales are connected to two large-scale modes of North Pacific climate variability. The first mode is the Pacific Decadal Oscillation (PDO; Mantua *et al.*, 1997), which emerges as the leading principal component (PC) of North Pacific sea surface temperature anomalies (SSTa) and of Northeast Pacific sea surface height anomalies (SSHa) (Chhak *et al.*, 2009). The second mode is the North Pacific Gyre Oscillation (NPGO; Di Lorenzo *et al.*, 2008), which emerges as the second principal component (PC2) of Northeast Pacific SSHa and SSTa.

During the positive phase of the PDO, the California coast is characterized by warmer than usual SSTa and higher SSHa along the coast. In the northern California Current System (north of $\sim 40°N$) these anomalies are connected to stronger downwelling conditions associated with increased Ekman transport towards the coast, which is driven by a deepening of the atmospheric Aleutian low (Chhak *et al.*, 2009). In the central and southern regions of the California Current (south of $\sim 40°N$) the SSTa and SSHa anomalies of the PDO are not linked to changes in the upwelling cell and cross-shelf transport (Chhak & Di Lorenzo, 2007) but rather to alongshore transport (Chhak *et al.*, 2009), although the

specific dynamics need further investigation. Changes in the upwelling cells south of $\sim 40°$N are more strongly correlated to the NPGO (Di Lorenzo *et al.*, 2008), which has been shown to capture the dominant low frequency fluctuations of salinity and nutrient upwelling in the CalCOFI region. Physically, the NPGO is associated with changes in strength of the eastern and central branches of the North Pacific gyres (e.g. intensification/weakening of the North Pacific Current) and of the Kuroshio–Oyashio Extension (Ceballos *et al.*, accepted) These circulation changes of the NPGO are driven by variations in the atmospheric winds associated with the North Pacific Oscillation (NPO) – the second dominant mode of sea level pressure variability in the North Pacific (Linkin & Nigam, 2008). In the SCCS, the NPO atmospheric variations project on the alongshore components of the winds more strongly than the Aleutian Low, therefore controlling the cross-shelf transport variation (Chhak *et al.*, 2009). Although correlations of physical and biological variables in the CalCOFI domain have been linked to PDO and NPGO, the mechanism responsible for these correlations need further investigation.

Materials and methods

Fish data

To examine climatic effects on the abundances and distributions of oceanic fishes, we studied 34 dominant taxa collected in the CalCOFI surveys (Hsieh *et al.*, 2005). We used only data landward of station 90 of the standard CalCOFI grid in this study (54 stations
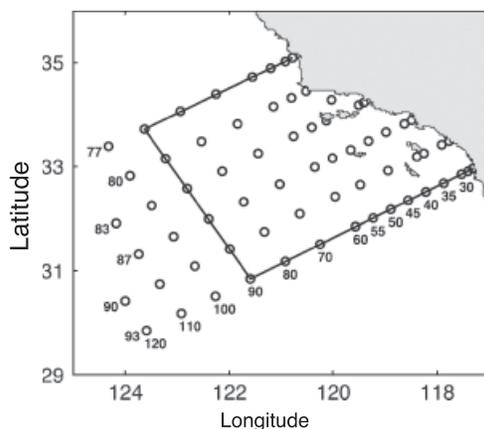

Fig. 1 Map showing the spatial pattern of California Cooperative Oceanic Fisheries Investigations stations. Only stations within the solid lines (station 90 and inshore) were used in this study because the stations outside the box were sampled with less consistency.

within the inner box illustrated in Fig. 1) in order to avoid statistical bias due to missing data (offshore stations were not sampled during some cruises) in examining the spatial distribution of fish. The CalCOFI sampling frequency was quarterly from 1961 to 1965 and 1985 to the present, but was higher than quarterly from 1951 to 1960 and 1966 to 1984; we used only the quarterly data in this study so that the variance associated with the spatial data is not biased due to differences in annual sampling effort.

We determined the distribution-center (median latitude and longitude) of each year for each taxon, first, by averaging the station values of abundance (number of larvae under $10 \, m^2$ of sea surface) across the principal seasons (estimated following the procedure of Hsieh *et al.*, 2006) in which the larvae occurred, and then, calculating the distribution-center as the abundance-weighted median of the annual map. Thus, a time series of the distribution-center was obtained for each taxon. We used abundance-weighted median in order to guard against potential outliers; however, abundance-weighted mean was also calculated. In addition, the southern/northern boundary was calculated as the minimum/maximum latitude in which a species occurred within the study area for each year. The annual abundance was calculated by averaging the station values during the principal seasons in which the larvae occurred.

Environmental data

For environmental effects, we examined local variables as well as large-scale climate indices. Local variables include averaged sea surface temperatures (SSTs) of the CalCOFI region (the inner box of Fig. 1), the first principal component (PC1) of the spatial-explicit SST data, heat content for the upper layer (20–200 m) and deeper layer (300–500 m) from lines 80 and 90 (sensu Fig. 1), buoyancy frequency at the pycnocline depth from lines 80 and 90, and the macrozooplankton biovolume of the studied region. Climate indices include PDO, Southern Oscillation Index (SOI), NPGO, and North Pacific Index (NPI). When analyzing the environmental data, only the quarterly data corresponding to the fish data were used.

The temperature data are obtained from the CalCOFI database (http://www.calcofi.org/newhome/data/data. htm). Where available, this database includes vertical profile data (temperature and salinity) taken at 0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, and 500 m for each station. With these data, the average SST within our study region (Fig. 1, the inner box) was calculated for each quarter. Using the spatial-explicit data, the PC1 of CalCOFI SST was computed to represent the dominant spatial variation of the SST. For calculating the water column properties (buoyancy frequency and heat

content), only data from lines 80 and 90 were used, because vertical profiles are less complete compared with surface data, particularly in the early period. To minimize spatial aliasing, each profile was interpolated by a piecewise cubic spline method to 1 m resolution (Kim & Miller, 2007). With these interpolated data, the pycnocline depth for each profile was calculated as the depth with the maximum vertical gradient of density. We then calculated the buoyancy frequency at the pycnocline depth as an indicator to the strength of stratification of the CalCOFI region, which might affect nutrient dynamics and thus primary production (Kim & Miller, 2007). Although it is desirable to investigate directly chlorophyll concentrations (surrogate for phytoplankton biomass), data of chlorophyll are only available since 1984. Instead, we investigated macrozooplankton biovolume from the studied domain as a proxy to food availability to fishes. Note that the macrozooplankton biovolume excludes large gelatinous zooplankton. The details of this zooplankton dataset have been described in Lavaniegos & Ohman (2007), and the effects of changes in zooplankton sampling methods of CalCOFI were corrected following the procedures of Ohman & Smith (1995). For each quarter, spatial data of zooplankton biovolume (mL m^{-2}) were log10 transformed and then averaged into quarterly mean value. Furthermore, because the oceanic fish examined here can be categorized into vertical migrators and deep-dwellers (Hsieh et al., 2005), we calculated heat content for the upper layer between 20 and 200 m where migrating species occur at night and that for the deep layer between 300 and 500 m where nonmigrating mesopelagic fishes typically reside.

The SOI is based on atmospheric pressure differences between Tahiti and Darwin (Trenberth, 1984), indicating the state of the ENSO. The PDO is based on the PC1 of SST in the Pacific (Mantua et al., 1997). The NPI is the area-weighted sea level pressure over the region 30–65°N, 160°E–140°W (Trenberth & Hurrel, 1994). The PDO and NPI track the leading patterns of SST variability and North Pacific sea-level pressure, respectively. The NPGO is the PC2 of SSHa and tracks closely to the PC2 of SST anomaly, which is linked to wind-driven upwelling and horizontal advection in the California region (Di Lorenzo et al., 2008).

To show the variation of environmental variables, we plotted the time series of annual anomalies of those variables. To do so, we removed the long-term quarterly mean and averaged the quarterly anomalies into annual anomalies. Correlation analyses were used to investigate relationships among the environmental variables. To account for serial dependence in time series data in the correlation analyses, we calculated the correlation coefficients using the estimated generalized least
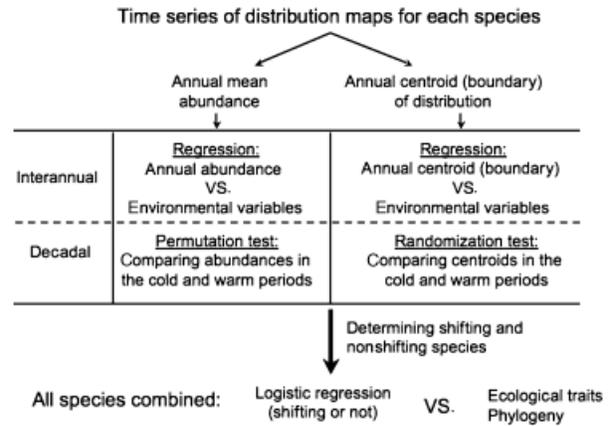

Fig. 2 Schematic illustrating the statistical procedures. For each fish species, we analyzed their mean abundance and geographic distribution in response to environmental factors on both interannual and decadal scales. We then defined shifting and nonshifting species according to whether the species showed a significant correlation with environmental variables on either interannual or decadal scale. A meta-analysis was carried out to investigate what determined responsiveness of fishes to environmental variations.

square (EGLS) method, and computed the bootstrapped (1000 times) 95% confidence limits to perform hypothesis tests (Ives & Zhu, 2006).

Analysis of environmental effects on fishes

We examined climate effects on the geographic distribution of fish at interannual and decadal scales, as outlined in the procedures of statistical methods (Fig. 2). We defined the cold (1951–1976) and the warm (1977–1998) periods following the definition of the PDO (Mantua et al., 1997). To examine interannual variability, regression analysis was used to investigate the relationship between the median (mean) latitudes and environmental variables for each taxon. We investigated also 1-year time-lagged values representing delayed environmental effects, as observed in coastal and neritic species in the southern California region (Hsieh et al., 2008) and the North Sea (Perry et al., 2005). When analyzing the correlation between environmental variables and geographic distribution of a fish species, we used only the data corresponding to the principal seasons of that species. To account for serial dependence in time series data, the EGLS method was used (Ives & Zhu, 2006). We also examined species' southern and northern boundaries in relation to the environmental variables. For species where the median (mean) latitudes (or boundaries) were significantly correlated with abundances, we controlled for abundance and tested for the partial correlation between the median latitudes (or

boundaries) and the environmental variables, because the geographic extent of marine populations may be correlated with the population size (MacCall, 1990; Hsieh *et al.*, 2008). (The results are qualitatively the same when abundance was included as a covariate for each of the 34 taxa.)

In order to examine the change in distribution of each taxon from the cold to the warm period, we estimated the centroid of distribution for each period from the time series of the distribution-centers. The centroid of each period was estimated by the method of 50% convex hull peeling (Zani *et al.*, 1998) with all distribution-centers equally weighted. This method is robust to the bias caused by outliers. We tracked the direction and magnitude of the movement for each taxon. To test whether the change in larval distribution from the cold to warm period was statistically significant, we used the randomization test of shift in distribution (Hsieh *et al.*, 2008).

We then considered whether geographically shifting and nonshifting species have significantly different ecological traits and phylogeny. Here, 'geographically shifting species' are defined as species showing either a significant distributional (including median latitude and boundaries) relationship with environmental variables or a significant change in distribution domain from the cold to the warm period. The ecological traits include geographic distribution (warm water species, temperate species, and transitional species), vertical migratory or deep-dwelling, and spawning duration (number of months per year that a species spawns); the phylogeny is referred to species taxonomic order that potentially exhibit evolutionary constraints (Hsieh *et al.*, 2008). A logistic regression was applied to determine the factor(s) that caused the significant change in geographic distribution. We used median latitudes here because it is robust against outliers. Nevertheless, substituting median with mean values resulted in qualitatively similar conclusions.

We also examined environmental effects on fish abundance (Fig. 2). Again, when analyzing the correlation between environmental variables and abundance of a fish species, we used only the data corresponding to the principal seasons of that species. For the interannual scale, regression analysis based on EGLS was used to examine the relationship between fish abundance and environmental variables. For the decadal scale, we applied a permutation test (Manly, 1997) to determine whether abundance changed significantly from the cold to the warm period for each taxon. For this test, the null distribution was generated by randomly shuffling the time series in a manner that retained the autocorrelation structure (Politis *et al.*, 1999) as follows. First, we connected head to tail of a time series to form a circle.

Second, we randomly drew X_1 from the circular series. Third, with probability p, X_2 was drawn randomly, and with probability $(1-p)$, X_2 was chosen as the 'next available' observation from the circular series following X_1. The probability p is determined based on the autocorrelation structure of the original time series (detailed in Politis & White, 2004). This procedure was carried out 1000 times to generate the null distribution. Again, species with a significant correlation with the environmental variables or a significant change in abundance from the cold to warm period are defined as 'abundance shifting species.' A logistic regression was applied to examine whether abundance shifting and nonshifting species have significantly different ecological traits and phylogeny.

Results

Environmental variations

The CalCOFI, SST, and SST-PC1 exhibited strong interannual and decadal variability (Fig. 3a and b). The interannual variations of CalCOFI SST were correlated with the SOI (Fig. 3f and Table 1) and NPI (Fig. 3h and Table 1), and its decadal variations were associated with the PDO (Fig. 3e and Table 1). Particularly, the significant warming between 1976 and 1998 strongly affected the water column properties. For example, the stratification of the water column intensified during the warm period, as evidenced by the increased buoyancy frequency at the pycnocline depth (Fig. 3c). To further show the spatial variation of temperature change in the CalCOFI region, we examined the upper-layer heat content for CalCOFI lines 80 and 90 for spring cruises when the CalCOFI region is most productive. The Hovmoller diagrams showed that the area occupied by warm water expanded and the contour line of $8 \times 10^9 \, \mathrm{J \, m^{-2}}$ heat content approached shoreward through time (Fig. 4). Along with these physical changes, the zooplankton biovolume declined in the warm period, albeit with strong interannual variations corresponding to ENSO events (Fig. 3d). In fact, all environmental variables examined here were correlated (Table 1), except the NPGO (Fig. 3g).

The surface temperature variations also were reflected in the water column heat content (Fig. 5), as revealed by a significant correlation between the heat contents and SST (Table 1). To investigate environmental variations of the living habitats of the two fish groups, two depth intervals were chosen for the integral: HC1 is the heat content between 20 and 200 m where migrating species occur at night, while HC2 is between 300 and 500 m where nonmigrating mesopelagic fishes typically reside. Linear regression analy-
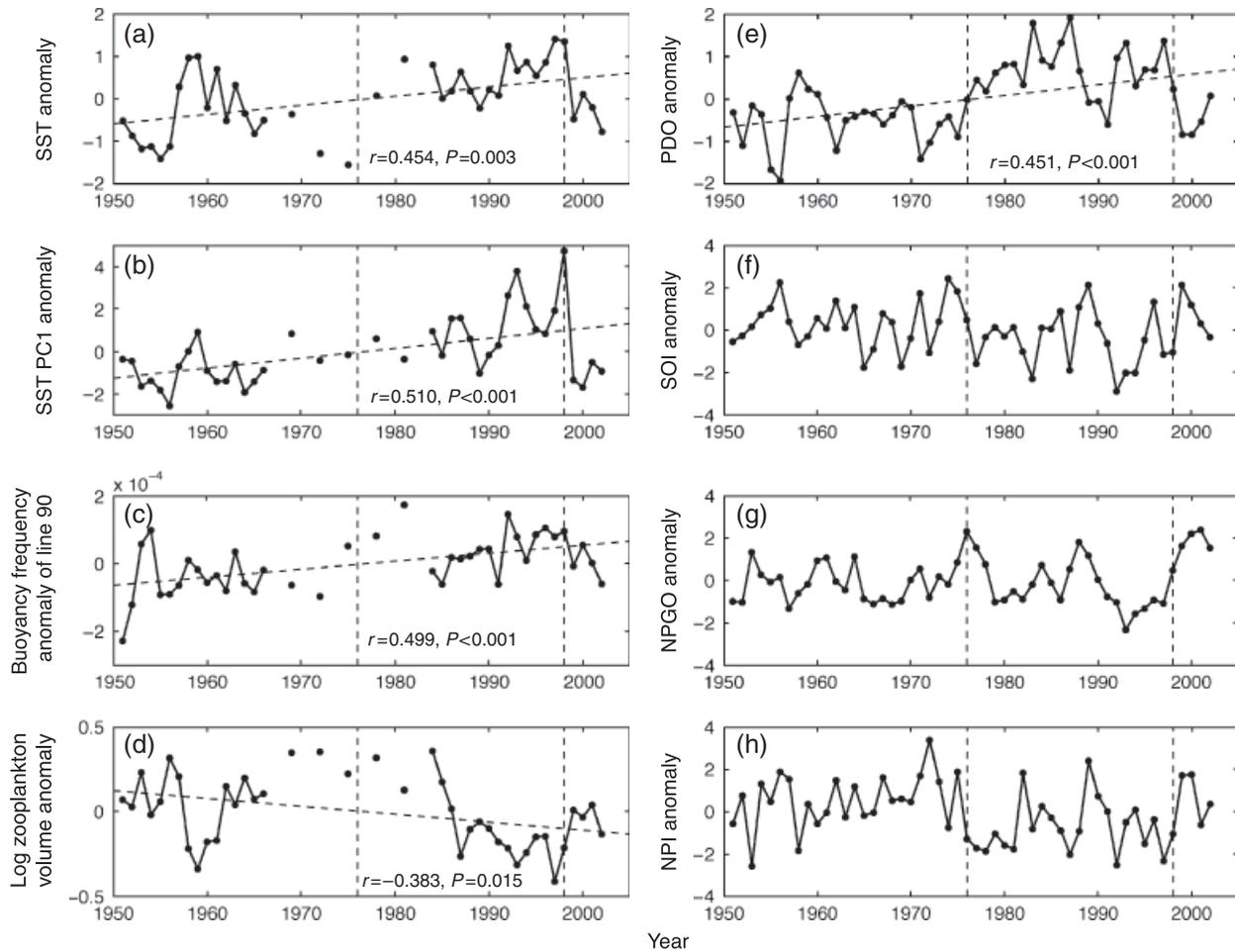
Fig. 3 Time series anomalies of local environmental variables: (a) sea surface temperature (SST), (b) first principal component of spatial SST, (c) average buoyancy frequency at the pycnocline depth for the line 90, and (d) zooplankton displacement volume for the studied area (sensu Fig. 1), and large-scale climate indices: (e) Pacific Decadal Oscillation, (f) Southern Oscillation Index, (g) North Pacific Gyre Oscillation, and (h) North Pacific Index. Note that for the local variables, sampling was triennial from 1966 to 1984. If a time series exhibited a significant long-term trend, a trend line (the dashed line) is shown along with the coefficient of correlation and *P*-value. The two vertical dashed lines indicate years of change of climate regimes. PC1, first principal component.

sis showed that the HC1 increased with time roughly 10 times more than the HC2 (Fig. 5). Thus, although the upper-ocean warming signal appeared as deep as 500 m, significant warming mainly affected the upper 200 m of the water column (Fig. 5) that the migrating species utilize at night.

Changes in geographic distribution

Climate change had less clear effects on the geographic distribution of oceanic fish. At the annual scale, 14 of the 34 taxa significantly shifted their median latitudes in relation to the environmental variables (Table 2). We discuss only the results based on the median latitudes here because it is more robust than the mean latitudes. The results based on the mean latitudes are also pre-

sented (Table 2), and, in fact, the mean and median latitudes are highly correlated for every species ($P <$ 0.01). In addition to the median latitude, nine species significantly shifted their northern boundaries and five species significantly shifted their southern boundaries in relation to the environmental variables (Table 2). Note that for the species showing a significant correlation with environmental variables, only the single best-fit environmental variable was selected in the multivariate regression analysis (Table 2); this is due to high collinearity among environmental variables (Table 1).

Because warming is an important physical change in the CalCOFI region (Fig. 3a), we are interested in how those fish species responded to changes in SST. We found that, among the shifting species, eight showed a significant positive correlation with the SSTs in their median

Table 1 Correlation matrix of environmental variables

	SST	SST-PC1	Buoyancy frequency	Upper layer heat content	Lower layer heat content	Zooplankton volume	PDO	SOI	NPGO
SST									
SST-PC1	0.652*								
Buoyancy frequency	0.561*	0.468*							
Upper layer heat content	0.799*	0.764*	0.444*						
Lower layer heat content	0.536*	0.443*	0.402*	0.522*					
Zooplankton volume	−0.411*	−0.273	−0.189	−0.348*	−0.154				
PDO	0.637*	0.539*	0.383*	0.518*	0.195	−0.426*			
SOI	−0.586*	−0.615*	−0.080	−0.489*	−0.557*	0.416*	−0.562*		
NPGO	−0.199	−0.296	0.087	−0.209	−0.139	0.318	−0.200	0.322*	
NPI	−0.546*	−0.479*	−0.442*	−0.484*	−0.370*	0.396*	−0.655*	0.515*	0.135

*Indicates a significant correlation ($\alpha = 0.05$) after accounting for the autocorrelation structure in the time series.
SST, sea surface temperature; SST-PC1, first principal component of spatial-explicit SST distribution; buoyancy frequency, buoyancy frequency at the pycnocline depth; upper layer heat content, heat content of depth 20–200 m for line 80 and 90 averaged; lower layer heat content, heat content of depth 300–500 m for line 80 and 90 averaged; zooplankton volume, small zooplankton biovolume; PDO, Pacific Decadal Oscillation Index; SOI, Southern Oscillation Index; NPGO, North Pacific Gyre Oscillation index; NPI, North Pacific Index.
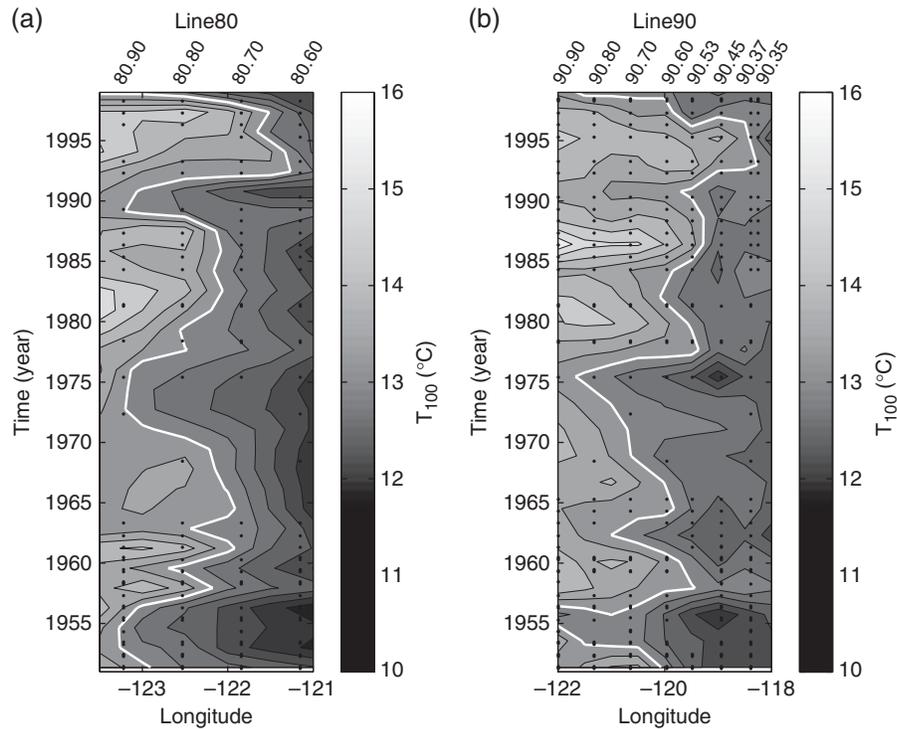

Fig. 4 Hovmoller diagrams show the warming of upper-ocean (heat content from 20 to 200 m) in spring (April–June, when the studied area is most productive) along Line 80 (a) and Line 90 (b). Contour interval is 0.4×10^9 J/m^{-2}. Black dots represent *in situ* temperature observations. The white contour represents the 8×10^9 J m^{-2} line. Notice that there is a significant gap of observations in the 1970's. CalCOFI station numbers are marked above the top axis.
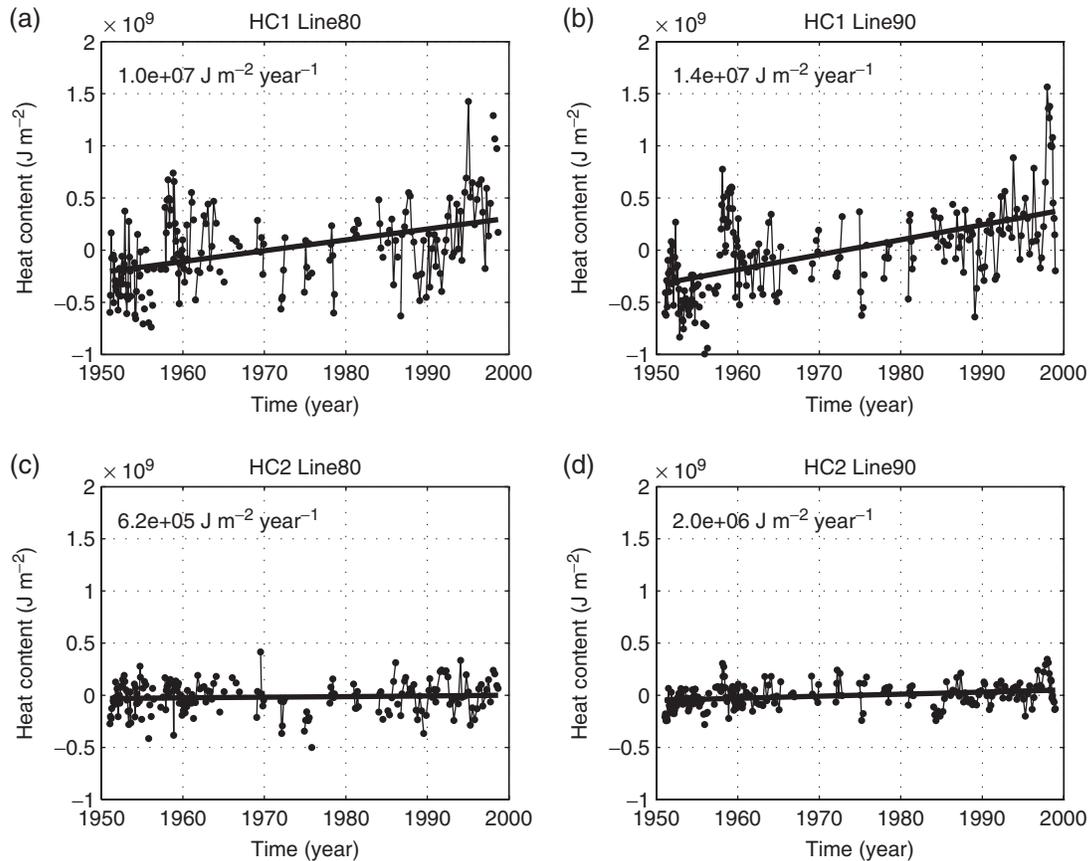
Fig. 5 Heat content anomalies for Line 80 (a, c) and Line 90 (b, d) in the upper layer (20–200 m, a, b) and lower layer (300–500 m, c, d). Upper-ocean heat content was defined as the vertical integral of $\rho C_p T(z)$, where ρ is the average seawater density (1025 kg m^{-3}), C_p is the heat capacity of seawater (3985 J kg^{-1} K^{-1}), and T(z) is vertical temperature profile obtained by interpolating the temperature into 1 m vertical resolution. The upper layer has a stronger warming trend than the lower layer. HC1, heat content between 20 and 200 m; HC2, heat content between 300 and 500 m. Regression in (c) is not significant.

latitudes, namely, *Aristostomias scintillans*, *Chauliodus macouni*, *Nannobrachium* spp., *Notoscopelus resplendens*, *Protomyctophum crockeri*, *Stenobrachius leucopsarus*, *Symbolophorus californiensis*, and *Tarletonbeania crenularis*. For these species, the rate of shift in median latitude ranged from 14 to 68 km °C^{-1} (average = 29 ± 11 km °C^{-1}).

Changes in geographic distributions of fishes at the bi-decadal scale also were observed. Except for *Bathylagus pacificus*, *Ceratoscopelus townsendi*, *Chiasmodon niger*, *Poromitra* spp., *Sternoptychidae*, *Scopelogadus bispinosus*, *Tactostoma macropus*, and *Triphoturus mexicanus*, the distribution centers of all 26 other taxa moved poleward from the cold period to the warm period. This is highly significant as a meta-analysis (binomial test, $P = 0.002$), suggesting that most oceanic species in the southern California ocean ecosystem move poleward in response to warming. The movements ranged from 1 to 128 km (average = 42 ± 12 km). The average direction of movements from the cold to warm period was northwestward along the coast (Fig. 6). No pattern

was found related to taxonomic position or ecological traits (logistic regression, $P = 0.342$).

Although most species moved northward from the cold to warm period, upon investigating their distribution-centers closely, only eight species significantly shifted their geographic distribution (Table 2). We show an example of a species (*S. leucopsarus*) exhibiting a significant change in distribution (Fig. 7a and b) and a counter example, *C. macouni* (Fig. 7c and d). Although both species moved poleward from the cold to the warm period (Fig. 7b and d), the separation was statistically distinct for *S. leucopsarus* (Fig. 7a) but not for *C. macouni* (Fig. 7c).

Results of logistic regression indicated that habitat (mesopelagic vs. vertical-migrating) was the main factor affecting whether oceanic fishes responded to climate in their geographic distribution (logistic regression, $P = 0.027$). The habitat effect remained significant if analyses were done separately on the datasets of annual and decadal scales ($P = 0.012$ and 0.036, respectively).

Table 2 Results of regressions of the effects of interannual changes in environmental variables on median and mean latitude, and southern and northern boundaries for 34 fish taxa off southern California

Species*	Geographic affinity	Habitat	Median latitude	Mean latitude	Southern boundary	Northern boundary	Shift in domain
Aristostomias scintillans	Cold	Mesopelagic	+ Buoyancy	+ Buoyancy		+ Buoyancy	
Bathylagoides wesethi	Cold	Mesopelagic					
Bathylagus pacificus	Cold	Mesopelagic					
Ceratoscopelus townsendi	Broad	Migrator					
Chauliodus macouni	Cold	Mesopelagic	+ SST				
Chiasmodon niger	Warm	Bathypelagic					
Cyclothone spp. (*signata*)	Warm	Migrator	+ Buoyancy				
Diaphus theta	Cold	Migrator	+ Zooplankton	−NPGO		+ HC1‡	
Diogenichthys atlanticus	Warm	Mesopelagic					
Hygophum reinhardtii	Warm	Migrator					
Idiacanthus antrostomus	Broad	Mesopelagic					
Lipolagus ochotensis	Cold	Mesopelagic	+ HC1	+ HC1			
Melamphaes spp. (*lugubris, parvus*)	Warm	Mesopelagic	+ HC1	+ SST-PC1			
Microstoma sp.	Cold	Mesopelagic					
Myctophidae	NA†	NA†					+
Myctophum nitidulum	Warm	Migrator		+ Buoyancy	+ SOI	+ SOI	
Nannobrachium spp. (*ritteri*)	Broad	Migrator	+ HC1	+ HC1	+ SOI	+ SOI	+
Nansenia candida	Cold	Mesopelagic					
Notolychnus valdiviae	Broad	Migrator					
Notoscopelus resplendens	Broad	Migrator	+ SST	+ PDO	+ PDO‡	+ PDO‡	+
Paralepididae (*Lestidiops ringens*)	Broad	Mesopelagic					
Poromitra spp. (*crassiceps*)	Broad	Mesopelagic					
Protomyctophum crockeri	cold	Migrator	−NPGO	+ SST		+ PDO‡	+
Scopelarchidae	Broad	Mesopelagic					
Scopelogadus bispinosus	warm	Mesopelagic	+ SST	−NPGO		−NPGO	
Scopelosaurus spp.	Broad	Mesopelagic					
Stenobrachius leucopsarus	Cold	Migrator	+ Buoyancy‡	+ Buoyancy‡	+ SST‡		+
Sternoptychidae (*Argyropelecus* spp.)	Broad	Mesopelagic					+
Stomias atriventer	Warm	Mesopelagic					
Symbolophorus californiensis	Cold	Mesopelagic	+ HC1	+ HC1		+ HC1	
Tactostoma macropus	Cold	Mesopelagic	+ Buoyancy	+ Buoyancy			
Tarletonbeania crenularis	Cold	Migrator	+ PDO	+ PDO	+ SST‡		+
Triphoturus mexicanus	Warm	Migrator				+ SST‡	
Vinciguerria lucetia	Warm	Migrator					+

A significant positive/negative correlation ($P < 0.05$) is indicated by a $+/-$ sign along with the environmental variable. See legends of Table 1 for the definition of environmental variables. The final column indicates the results of a test of difference in geographic domain between the cold (1951–1976) and warm period (1977–1998). Ecologic characteristics of each species are included.
*Species in parenthesis is/are the predominant species within the taxonomic complex. *Microstoma* sp. is a valid species (Moser, 1996).
†NA indicates that classification of geographic affinity and habitat is not possible for the taxonomic complex.
‡When abundance is found significantly related to latitudes, we remove the abundance effects and test its partial correlation.
PDO, Pacific Decadal Oscillation; SOI, Southern Oscillation Index.; NPGO, North Pacific Gyre Oscillation index; SST, sea surface temperature.

Changes in abundance

Climate variations have significant effects on the abundance of oceanic fishes. At the interannual scale, abundance of 24 of the 34 species exhibited a significant relationship with the environmental variables (Table 3). Among those species, *Cyclothone* spp., *Diaphus theta*, and Myctophidae were positively correlated with zooplankton biovolume. For the other 21 taxa, except for *Poromitra* spp., *S. leucopsarus* and *T. crenularis*, all

exhibited a positive relationship with temperature or temperature-related variables (Table 3). At the decadal scale, 25 among 34 species showed a significant increase, and only *T. crenularis* showed a significant
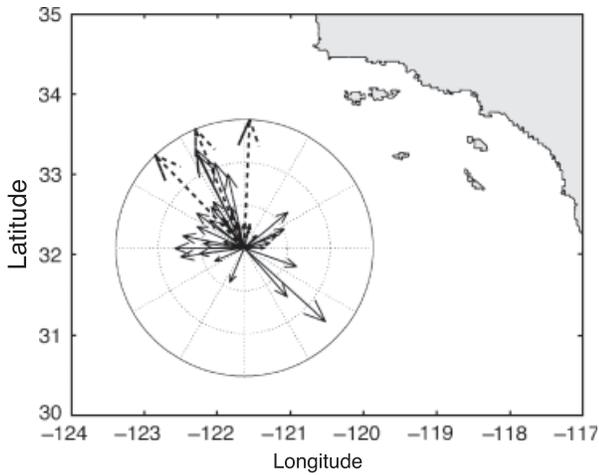
decrease, in abundance from the cold to warm period (Table 3). These results indicate an overall increase in the abundances of oceanic fish in responding to the warming trend in the southern California area. Among species showing a significant response to climate in their annual abundances, the change was not associated with their ecological traits or phylogeny (logistic regression, $P = 0.315$). Similar conclusions were reached for the decadal changes in abundance between the cold and warm period (logistic regression, $P = 0.274$) and for both annual and decadal scales combined ($P = 0.552$).

Fig. 6 Summaries of moving directions (solid arrows) from the cold to warm period for the oceanic species. The average direction and associated 95% bootstrapped confidence limits are represented by dashed arrows.

Discussion

Environmental variations

The CalCOFI water temperature pattern is driven by climate variations at the interannual scale, as reflected in the SOI (Fig. 3f) and NPI (Fig. 3h), and at the decadal scale, such as PDO (Fig. 3e) (Bograd & Lynn, 2003; Di Lorenzo *et al.*, 2005), as shown by the significant correlations in our analyses (Table 1). Our analyses further corroborate those conclusions by showing that the spatial pattern of SST and water column heat content are highly correlated with those climate indices
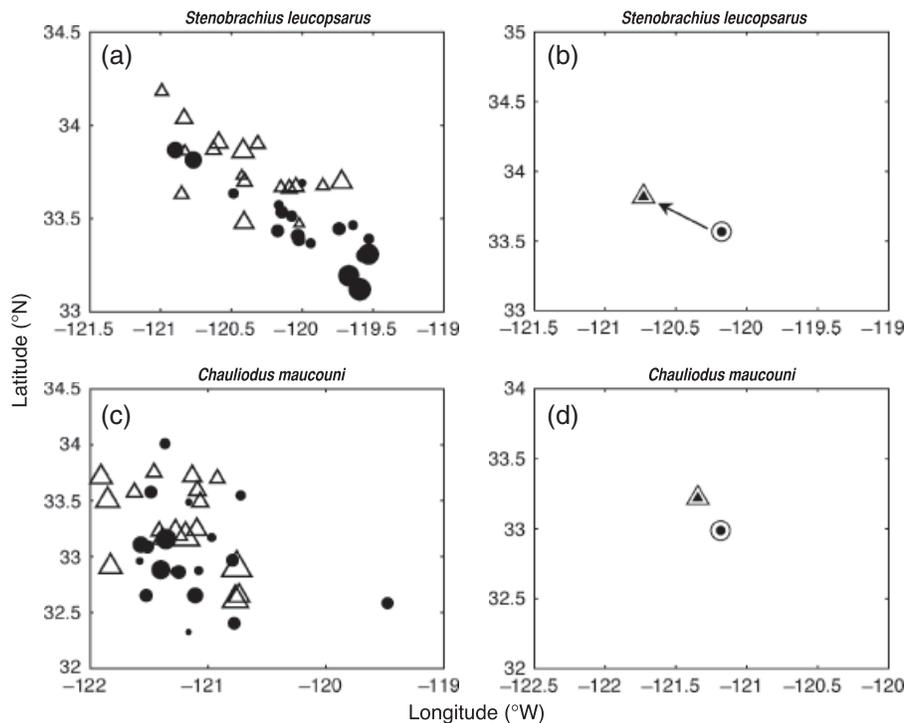

Fig. 7 Examples showing the spatial distributions of species that passed the randomization test for shift in geographic distribution (a, b) and that did not pass the test (c, d). Solid circles and open triangles represent distribution-centers for the cold and warm periods (a, c), and sizes of the circles (a, c) represent relative average abundances of the year; the double circle and triangle indicate the change in centroid from the cold to warm period (b, d). Note that the spatial scales are different for these two species but comparable between (b) and (d).

Table 3 Average larval abundances in the cold (1951–1976) and warm (1977–1998) periods and results of regressions of the effects of interannual changes in environmental variables on the abundance for 34 fish taxa

Species	Abundance* (1951–1976)	Abundance* (1977–1998)	Regression analysis†
Aristostomias scintillans	**0.006**	**0.032**	+ SST
Bathylagoides wesethi	2.819	4.222	+ HC1
Bathylagus pacificus	**0.131**	**0.461**	
Ceratoscopelus townsendi	**0.297**	**1.555**	+ HC1
Chauliodus macouni	**0.362**	**0.702**	
Chiasmodon niger	**0.012**	**0.108**	+ HC1
Cyclothone spp. (*signata*)	0.858	0.546	+ Zooplankton
Diaphus theta	1.761	2.269	+ Zooplankton
Diogenichthys atlanticus	**0.616**	**2.050**	+ SSTPC1
Hygophum reinhardtii	**0.009**	**0.082**	+ HC1
Idiacanthus antrostomus	**0.221**	**0.510**	+ SST-PC1
Lipolagus ochotensis	**2.936**	**7.683**	
Melamphaes spp. (*lugubris, parvus*)	0.934	0.805	
Microstoma sp.	**0.142**	**0.335**	
Myctophidae	0.429	0.615	+ Zooplankton
Myctophum nitidulum	**0.017**	**0.074**	+ HC1
Nannobrachium spp. (*ritteri*)	**2.726**	**4.543**	+ SST-PC1
Nansenia candida	0.147	0.200	
Notolychnus valdiviae	**0.012**	**0.033**	
Notoscopelus resplendens	**0.023**	**0.080**	
Paralepididae (*Lestidiops ringens*)	**0.431**	**0.694**	
Poromitra spp. (*crassiceps*)	0.069	0.108	−NPI
Protomyctophum crockeri	**1.684**	**4.173**	
Scopelarchidae	**0.048**	**0.174**	+ SST-PC1
Scopelogadus bispinosus	**0.044**	**0.101**	+ Buoyancy
Scopelosaurus spp.	**0.040**	**0.097**	+ PDO
Stenobrachius leucopsarus	44.900	38.803	−Buoyancy
Sternoptychidae (*Argyropelecus* spp.)	**0.281**	**1.213**	+ SST-PC1
Stomias atriventer	**0.138**	**0.324**	+ HC1
Symbolophorus californiensis	**1.023**	**1.804**	+ SST-PC1
Tactostoma macropus	**0.017**	**0.047**	+ PDO
Tarletonbeania crenularis	**3.134**	**1.168**	−PDO
Triphoturus mexicanus	**3.339**	**5.405**	+ HC1
Vinciguerria lucetia	**2.546**	**19.547**	+ SST-PC1

A randomization test was applied to determine whether there was a significant difference in abundance between the warm and cold periods.

*Bold indicates a significant difference ($\alpha = 0.05$) in abundance between the warm and cold periods in the randomization test.

†Only significant regressions ($P < 0.05$) are presented. Plus signs and minus signs indicate positive and negative correlations along with the environmental variable, respectively. See legends of Table 1 for the definition of environmental variables.

PDO, Pacific Decadal Oscillation; SOI, Southern Oscillation Index; NPI North Pacific Index; SST, sea surface temperature; PC1, first principal component.

(Table 1 and Fig. 3). Recent studies indicated that another dominant mode of climate variation known as NPGO strongly affected the upwelling and advection pattern in the southern California region (Di Lorenzo *et al.*, 2008). Because NPGO is by definition orthogonal to temperature pattern in the North Pacific, it shows no significant correlation with the SST-related variables that we investigated here (Table 1).

Importantly, the warming of the CalCOFI region during 1976–1998 intensified the stratification of the water column. Maximum buoyancy frequency showed that the density difference across the pycnocline significantly increased in the warm period (Fig. 3c) (see also Kim & Miller, 2007), which might cause less vertical mixing in the upper ocean and bring less nutrient from the bottom layer. The intensified stratification was speculated to be the main factor driving the long-term decline of the CalCOFI zooplankton biovolume (Roemmich & McGowan, 1995a, b), which is also seen in our analysis (Fig. 3d). The pattern of our zooplankton

biovolume time series is consistent with that shown by Lavaniegos & Ohman (2007), though they used a smaller geographic domain (based on data landward of station 70, sensu Fig. 1) and only spring cruises. Lavaniegos & Ohman (2007) further analyzed the zooplankton carbon biomass and found significant reductions in response to ENSO events but no declining trend from 1951 to 2005. They concluded that the total zooplankton biomass for the past half century was rather stable, and the declining trend found in the zooplankton biovolume was driven by the significant decline of gelatinous zooplankton that contributed minimally to the total zooplankton biomass. We think this conclusion would hold when annual data were considered; however, we do not have zooplankton carbon biomass data for our quarterly cruises and cannot test this assertion. Nevertheless, one should note that total zooplankton carbon biomass might not be a suitable indicator of food condition for fish. Even though the biomass remained the same, the species composition or size structure of zooplankton might have changed, which would influence the feeding habitat of fishes. In fact, it has been shown that size structure of zooplankton changed in different upwelling and mixing regimes in the CalCOFI region (Rykaczewski & Checkley, 2008).

Certainly, the climate variations have affected not only the temperature and temperature-mediated ecosystem conditions but also other properties of the CalCOFI region, for instance circulation patterns (Bograd & Lynn, 2003; Di Lorenzo *et al.*, 2005, 2008) (see also discussion in the section 'Changes in abundance'). Unfortunately, those variables (both local variables and climate indices) were significantly correlated (Table 1), and it is difficult to separate temperature effects from others using multivariate regression analyses. Thus we avoided over-interpreting our regression results; rather, we focused on temperature and temperature-related changes. Indeed, such difficulty was recognized before the end of the 20th century (McGowan *et al.*, 1998) but remains challenging today.

Changes in geographic distribution

Climate change has affected geographic distributions of oceanic fish populations off southern California, although the signal is not very strong (Fig. 6). Among the 34 taxa examined, only 16 showed a statistically significant annual distributional shift (median latitude or boundaries) in relation to the environmental variables (Table 2). This may be because the latitudinal range of the study area (30–35°N, Fig. 1) is small and none of the studied taxa is bounded by this range. However, our results are consistent with other studies (Murawski, 1993; Brander *et al.*, 2003; Perry *et al.*, 2005)

in showing poleward shifts of most fishes in response to warmer average SST. The average shift rate in median latitude (29 km °C^{-1}) of southern California oceanic fishes is similar with the average shift rate (25 km °C^{-1}) found in southern California coastal and coastal–neritic species (Hsieh *et al.*, 2008) but smaller than that of North Sea fishes (average 87 km °C^{-1} calculated from Perry *et al.*, 2005) and North Atlantic fishes (ranges from 56 to 89 km °C^{-1} reported by Murawski, 1993). The smaller shift rate may reflect the smaller latitudinal range of this study (30–35°N) in comparison with the North Sea (51–62°N) and north Atlantic (36–45°N) studies because estimates of distribution-centers may be less reliable when the true population center moves beyond the study boundary. Alternatively, species living at lower latitudes might be less sensitive to warming (Root *et al.*, 2003); that is, the environmental variation of the CalCOFI region is smaller than that of the North Sea or North Atlantic Ocean. The temperature gradient of the CalCOFI region is on average 91 km °C^{-1} (ranging from 55 to 204 km °C^{-1} from 1951 to 2002), compared with $\sim$ 400 km °C^{-1} for the North Sea and North Atlantic Ocean.

The changes of latitudinal distributions of fishes may likely be caused by changes in the water temperature, as many significant correlations were found between the shifting species and temperature-related variables (Table 2). The significant correlations between fish distributions and the climate indices (Table 2) may also operate through climatic effects on temperature. While NPGO was found to be an important mode driving upwelling and nutrient dynamics in the southern California region (Di Lorenzo *et al.*, 2008), it did not appear to be a strong factor affecting the latitudinal distribution of oceanic fishes (Table 2). At this stage, it is difficult to separate temperature effects from others, because all environmental variables examined here are correlated (Table 1). Interestingly, however, among the 16 species that showed a significant relationship with environmental variables, 63% are vertical-migrators and 37% are nonmigrators (Table 2).

We found that 76% of the species' distribution centroids moved poleward in response to warmer temperature, when comparing the cold and warm periods (Fig. 6). However, only eight species passed the randomization test for a significant shift in distribution centroid (Table 2), again suggesting that the signal is not very strong. Given the geographic limit of our study area and noisiness of the data, our results indicate that most species have responded to warming, but some species show a stronger response than others. Interestingly, vertical-migrating species showed a clearer distributional shift than nonmigrators, with 43% responding to the increase in temperature compared with 5% of the nonmigrators (Table 2).

Why would vertical-migrating species show a clearer distributional shift than deep-dwelling nonmigratory species? This may be explained by uneven warming of the water column in the CalCOFI domain. When examining heat content anomalies in the CalCOFI region for the different depth intervals, we found that the upper layer of the water column warmed more significantly than the deeper layer (Fig. 5). It is possible that the migrating species sensed this climate warming (when they migrate to the surface layer) and moved poleward, while mesopelagic species did not feel strong effects of the warming because they live in the deep layer (300–600 m) where temperature change was relatively small.

Changes in abundance

In addition to poleward movements in response to the warming, many species (74%) showed an increase in abundance from the cold to warm period (Table 3). Regression analyses at the interannual scale also showed a positive correlation between fish abundances and temperature-related variables for 18 species (Table 3). One might suspect that only warm water species would increase their abundance due to climate warming. Surprisingly, cold water and broadly distributed taxa also increased in abundance (Table 3). The increase in abundance of oceanic taxa cannot be explained by the ecological traits we examined, or by phylogeny. Three taxa exhibited a positive correlation with the zooplankton biovolume (Table 3). However, because the zooplankton biovolume cannot be used as a good indicator to food availability (Lavaniegos & Ohman, 2007), this correlation should be treated with caution.

What might cause the overall increase in the abundance of oceanic fish responding to warming in the CalCOFI region? We again seek answers to this question by examining changes in water column physics. We suspected that increased stratification of the water column due to warming would create a more suitable living condition for oceanic species. Intensified stratification of the CalCOFI area indeed happened in the warm period (Fig. 3c). Moreover, the intensified stratification in the warm period may have created an unfavorable condition (e.g. changes in food conditions) for coastal–neritic species (see discussion in the section 'Environmental variations'). As a consequence, coastal–neritic species retreated shoreward. By contrast, oceanic fish that are preadapted to this kind of environment have no difficulty living in this more Gyre-like condition. As the coastal–neritic fish retreated shoreward, more oceanic fish extended shoreward, perhaps due to competitive release. To examine the competitive release hypothesis, we calculated the average abun-

dance maps of the cold and warm period for oceanic and coastal–neritic fish, respectively. The data of coastal–neritic species (including Pacific sardine, northern anchovy, Pacific chub mackerel, Pacific hake, etc.) collected in CalCOFI surveys were defined and described by Hsieh *et al.* (2005). For the oceanic fish, we used only the taxa with a significant increase in abundance from the cold to warm period (Table 3) to calculate the bidecadal average abundance map. We summed over the abundance of these species for each year and calculated the bidecadal average for the cold and warm period. The bidecadal averages of the coastal–neritic fish were calculated using the same method.

From the comparison of bi-decadal average abundance maps of oceanic vs. coastal–neritic species, the spatial distribution of oceanic fish indeed extended shoreward from the cold (Fig. 8a) to warm (Fig. 8c) period, while the spatial distribution of the coastal–neritic fish retreated shoreward (Fig. 8b and d). This contrast in spatial distribution became clearer when the difference of the warm and cold period (warm–cold) for the oceanic (Fig. 8e) and coastal–neritic (Fig. 8f) fish was calculated. The opened environment due to the retreat of the coastal–neritic fish may be then occupied by the oceanic fish during the warm period (Fig. 8e and f, correlation analysis, $r = -0.306$, $P = 0.024$). Our results suggest the possibility of competitive release; however, we cannot rule out the possibility that the shoreward movement of oceanic species was caused by changes in circulation pattern.

In addition to the warming of the southern CCE, changes of circulation patterns might also contribute to the increased abundance of oceanic fishes. For example, Di Lorenzo *et al.* (2005) used CalCOFI hydrographic data to calculate the geostrophic current and suggested that the California Current intensified during the warm period. This potentially could bring more cold water fishes from the transitional region into the CCE, but does not explain the increases in warm water fishes. It is possible that the counter current (from south to north) also intensified during the warm period, which would potentially bring in more warm water fishes. Furthermore, Di Lorenzo *et al.* (2005) showed that the center of the equatorward alongshore geostrophic current appeared closer to the coastline during 1980–2000 than during 1950–1970. This suggests that oceanic fishes had more opportunities to reach the CalCOFI domain during the warm period. However, these suggestions remain uncertain due to the paucity of vertical profile data of the CalCOFI region in the early period. Data assimilated models may be useful to further examine those physical changes. A more detailed analysis of the low – frequency changes in the ocean circulation patterns in the SCCS is needed to
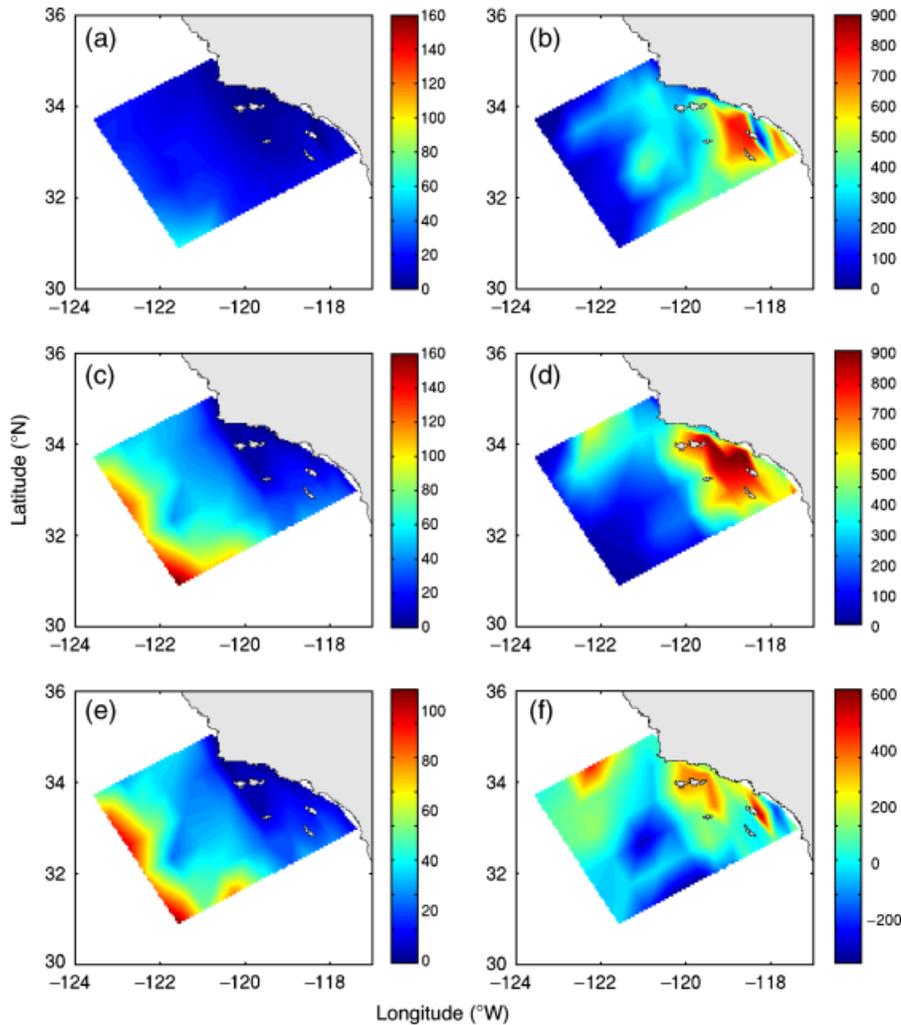
Fig. 8 Average abundance (individuals/10 m²) maps of the oceanic and coastal–neritic species in the cold (a, b) and warm (c, d) period respectively, and the difference of the average abundances between the warm and cold period (warm – cold) for oceanic (e) and coastal–neritic group (f). For the oceanic group, only taxa with significantly higher abundance in the warm period were used, while for the coastal–neritic group, all taxa were used for calculation.

clarify the relative role played by advection dynamics, surface fluxes of heat and momentum, and remote coastally trapped waves.

Conclusion

Climate change has had significant effects on the abundances of oceanic fishes, and to a lesser extent on their geographic distributions. Our ability to investigate the geographic distributions is limited by the range of the CalCOFI surveys (CalCOFI surveys originally covered the area from roughly 22–42°N, but since 1985 have been largely limited to southern California), because estimates of distribution-centers may be biased when the true population center moves beyond the study boundary. In addition, the temperature gradient is not

very large (compared with the North Sea and North Atlantic Ocean). Nevertheless, we found that ecologic traits (mesopelagic vs. vertical-migrating) played an important role in determining the sensitivity of fish in response to climate variations. Improving our knowledge of life history and ecological traits of fish species will enhance our ability to investigate climatic and anthropogenic effects on fish populations (Hsieh et al., 2006; Anderson et al., 2008). The most interesting finding of this study is the overall increase in the abundance and the shoreward expansion of spatial distribution of the oceanic taxa. Our analyses suggest that this phenomenon may be due to the changed ocean environment and possibly competitive release of coastal–neritic fish as a consequence of intensified stratification during the warm climate period, although changes in circulation

may also play a role. Apparently, climate change has effects on not only population but also ecosystem level properties. Gaining a mechanistic understanding of our ecosystems is warranted and cannot be done without long-term ecological studies.

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