Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes

Chih-hao Hsieh, Christian S. Reiss, Roger P. Hewitt, and George Sugihara

Abstract: We compare the changes in geographic distribution of exploited fish species versus unexploited ones living in the same environment. For this comparative study, we use the 50-year larval fish time series from the California Cooperative Oceanic Fisheries Investigations, which allows us to view fishing as a treatment effect in a long-term ecological experiment. Our results indicate that exploited species show a clearer distributional shift in response to environmental change than unexploited species, even after accounting for life history and ecological traits and phylogeny. The enhanced response (improved signal–noise ratio) to environmental change in exploited species may be a consequence of reduced spatial heterogeneity caused by fishery-induced age (size) truncation and the constriction of geographic distribution that accompanies fishing pressure. We suggest that reduced spatial heterogeneity can cause exploited populations to be more vulnerable to climate variability, an effect that could have considerable importance in the management of fish stocks. This is the first study to compare the geographic distributions of a large suite of exploited and unexploited fish species from the northeastern Pacific in response to climate variability.

Résumé : Nous comparons les changements dans la répartition géographique chez des espèces de poissons exploitées par comparaison à ceux des espèces non exploitées qui vivent dans le même milieu. Dans cette étude comparative, nous utilisons des données chronologiques sur les larves de poissons accumulées pendant 50 ans par « California Cooperative Oceanic Fisheries Investigations », ce qui permet de considérer la pêche comme un effet du traitement expérimental dans une expérience écologique de longue durée. Nos résultats indiquent que les espèces exploitées montrent un changement plus marqué dans leur répartition en réaction aux modifications de l'environnement, même une fois prises en compte les caractéristiques de leur cycle biologique et de leur écologie, ainsi que leur phylogénie. La réponse plus marquée (rapport signal–bruit amélioré) aux changements de l'environnement chez les espèces exploitées peut être une conséquence de la réduction de l'hétérogénéité spatiale causée par un plafonnement dans les âges (tailles) dû à la pêche et au rétrécissement de la répartition géographique qui accompagne la pression de la pêche. Nous pensons que l'hétérogénéité spatiale réduite peut rendre les populations exploitées plus vulnérables à la variabilité climatique, un effet qui pourrait avoir des répercussions considérables sur la gestion des stocks de poissons. La nôtre est la première étude à comparer les répartitions géographiques d'un grand ensemble d'espèces de poissons exploitées et non exploitées dans le Pacifique nord en fonction de la variabilité du climat.

[Traduit par la Rédaction]

Introduction

Understanding synergistic effects of anthropogenic and climatic impacts on biological populations is important for ecosystem conservation and management (Walther et al. 2002; Harley et al. 2006). Climatic fluctuations have had impacts on the abundance, geographic distribution, and phenology of species (Stenseth et al. 2002; Walther et al. 2002; Parmesan and Yohe 2003). At the extreme, climate change may increase the probability of extinction of species by reducing suitable habitats (Thomas et al. 2004). In addition, differential responses of different trophic levels to climate may cause trophic mismatch in space or time (Beaugrand et al. 2003; Edwards and Richardson 2004). Although biological responses to environmental variations have been extensively studied, how anthropogenic effects may alter the sensitivity of biological populations to environmental variations is not well known and is the focus of this investigation.

For marine fishes, one of the most serious anthropogenic impacts is fishing, although water pollution and habitat destruction may be important. Because fishing pressure may

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reduce the resilience of exploited populations facing climate variability, climatic effects may have more severe impacts on commercially exploited species (Murphy 1967; Hsieh et al. 2005*a*; Harley et al. 2006). Therefore, an important improvement to the management of fisheries is to account for how fishing affects the ability of fish populations to respond to climate change (Pikitch et al. 2004). By comparing exploited with unexploited fish species living in the same environment, Hsieh et al. (2006) showed that fishing elevated the variability of exploited populations, presumably by truncating their age structure. Here, we extend this comparative approach to examine how fishing affects the geographic distribution of fish populations in response to climate variability.

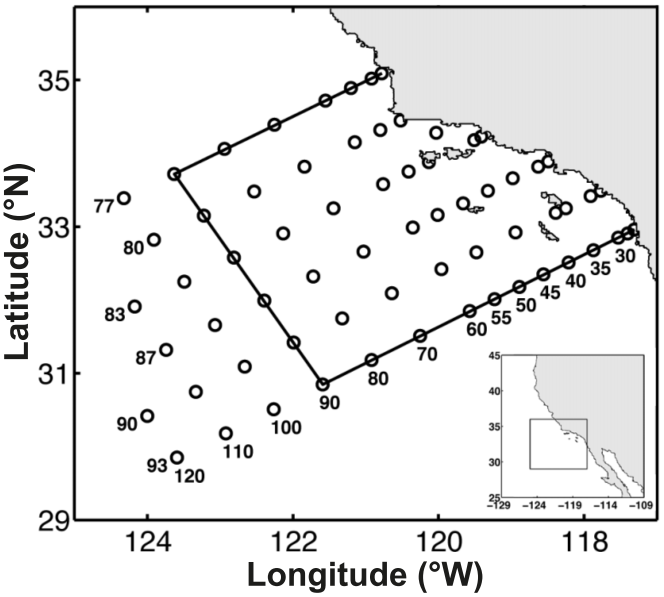
In the northeastern Pacific, climatic effects on fish abundance have been extensively studied (Hare and Mantua 2000; Benson and Trites 2002; Smith and Moser 2003), and effects on fish assemblages have been observed (Holbrook et al. 1997). The effects of climate variability on the geographic distributions of fishes in the northeastern Pacific were also examined (Benson et al. 2002; Rodriguez-Sanchez et al. 2002; Brodeur et al. 2003). Here, we study the geographic distributions of a large suite of fish species in response to climate in the southern California region.

In this study, we examine climatic effects on the geographic distributions of fish populations using the larval fish data collected from the California Cooperative Oceanic Fisheries Investigations (CalCOFI, www.calcofi.org) (Fig. 1) in the southern sector of the California Current system (Hsieh et al. 2005*b*). We assume that the spatial distribution of larvae is indicative of the spatial distribution of spawning population that produced them in the CalCOFI region, as most larvae taken in plankton nets are in a very early stage of development. However, effects of physical advection and diffusion on eggs and larvae may partially obscure this relationship. These effects may be species-specific and depend on ecological characteristics of species such as spawning behaviors and living habitats. These ecological factors will also be considered in analyses.

We focus on ocean temperature regimes as the most biologically relevant indicator of climatic state. More specifically, we use sea surface temperatures (SSTs) from the CalCOFI region as a proxy for climate. The CalCOFI SSTs have been shown to reflect both interannual and decadal climatic variations in the northeastern Pacific (Di Lorenzo et al. 2005; Schneider et al. 2005), as well as the global warming trend (Di Lorenzo et al. 2005). To investigate potential basin-wide climatic effects, we also use large-scale climatic indices, such as the Southern Oscillation Index (Trenberth 1984) and the Pacific Decadal Oscillation Index (Mantua et al. 1997).

The most important question addressed in this study is whether fishing has an added effect on the geographic distributions of exploited species as they respond to climate variability. To examine this question, we compare distributional responses of exploited and unexploited species to our climate proxies. Because fishing is a selective process, the exploited and unexploited groups might not be formed randomly. To perform a reasonable comparison of the exploited with the unexploited species, we account for possible intrinsic biases associated with fishing. These potential biases include life history traits, ecological traits, and phylogeny. We show that exploited species are more responsive to climate in their geographical distribution than unexploited species, after accounting for the potential biases. To explain the differential responses of exploited and unexploited species, we investigate potential fishing effects on changes in spatial area of occupancy and spatial heterogeneity of fishes.

Fig. 1. Map showing the spatial pattern of CalCOFI 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. The inset map shows the west coast of the United States, with the study area indicated as the rectangle.



Materials and methods

Spatial data

To examine how climate affects geographic distributions of fish populations, we study the larval fish time series (1951–2002) developed by the CalCOFI from the southern sector of the California Current system. We examine 29 coastal or neritic species that are abundant and consistently enumerated in the CalCOFI surveys (Hsieh et al. 2005*b*), including 13 exploited and 16 unexploited species (Table 1). Among the unexploited species, seven are taken as fisheries bycatch; however, mortality due to bycatch is not known. The CalCOFI surveys have collected comprehensive oceanographic and biological data since 1949 (consistent larval fish data are only available since 1951), with at least four quarterly cruises per year (except for triennial sampling from 1967 to 1984) (Hsieh et al. 2005*b*). We use only data landward of station 90 of the standard CalCOFI grid in this study (54 stations within the inner box illustrated in Fig. 1) in order to avoid statistical bias due to missing data (because occasionally offshore stations were not sampled during some cruises) in examining the spatial distribution of fish. Principal distributions of the species examined here are landward of station 90 (Moser et al. 2001), except for *Tetragonurus cuvieri*, which has a distribution that sometimes expands beyond station 90. Therefore, using data of the 54 stations will, in general, limit bias. The CalCOFI sampling domain lies in

Table 1. Results of regressions of the effects of interannual changes in sea surface temperature (SST), Pacific Decadal Oscillation Index (PDO), and Southern Oscillation Index (SOI) on mean latitude and southern and northern boundaries for 29 fish species off southern California, after correcting the effect in change of abundance.

		SST			PDO			SOI			
Species (geographic affinity)	Common name	Mean latitude	Southern boundary	Northern boundary	Mean latitude	Southern boundary	Northern boundary	Mean latitude	Southern boundary	Northern boundary	Shift in domain
Exploited*											
Engraulis mordax (1)	Northern anchovy				0.017			0.005			0.021
Merluccius productus (1)	Pacific hake or whiting	0.002			<0.001						0.001
Microstomus pacificus (2)	Dover sole										
Paralabrax clathratus (3)	Kelp bass	0.003		0.045							0.009
Paralichthys californicus (3)	California halibut	0.006			0.002			0.003†			0.043
Parophrys vetulus (2)	English sole										0.035
Sardinops sagax (3)	Pacific sardine	0.014		0.007	0.009						0.005
Scomber japonicus (3)	Pacific chub mackerel			0.005			0.006†				0.020
Scorpaenichthys marmoratus (2)	Cabezon		0.022[†]								
Sebastes aurora (2)	Aurora rockfish					0.036					
Sebastes paucispinis (2)	Bocaccio										
Sphyraena argentea (3)	Pacific barracuda	0.014		0.019							0.003
Trachurus symmetricus (1)	Jack mackerel										
Bycatch*											
Chromis punctipinnis (3)	Blacksmith			0.012							
Hippoglossina stomata (2)	Bigmouth sole										
Lyopsetta exilis (2)	Slender sole										
Pleuronichthys verticalis (3)	Hornyhead turbot										
Sebastes jordani (2)	Shortbelly rockfish										
Symphurus atricaudus (3)	California tonguefish										
Zaniolepis frenata (2)	Shortspine combfish	0.003[‡]						0.045[‡]			
Unexploited*											
Argentina sialis (1)	Pacific argentine										0.003
Cololabis saira (1)	Pacific saury										
Hypsoblennius jenkins (2)	Mussel blenny										
Icichthys lockingtoni (1)	Medusafish										
Leuroglossus stilbius (1)	California smoothtongue				0.032						
Ophidion scrippsae (3)	Basketweave cusk-eel										
Oxylebius pictus (2)	Painted greenling										
Tetragonurus cuvieri (2)	Smalleye squaretail										
Trachipterus altivelis (2)	King-of-the-salmon										

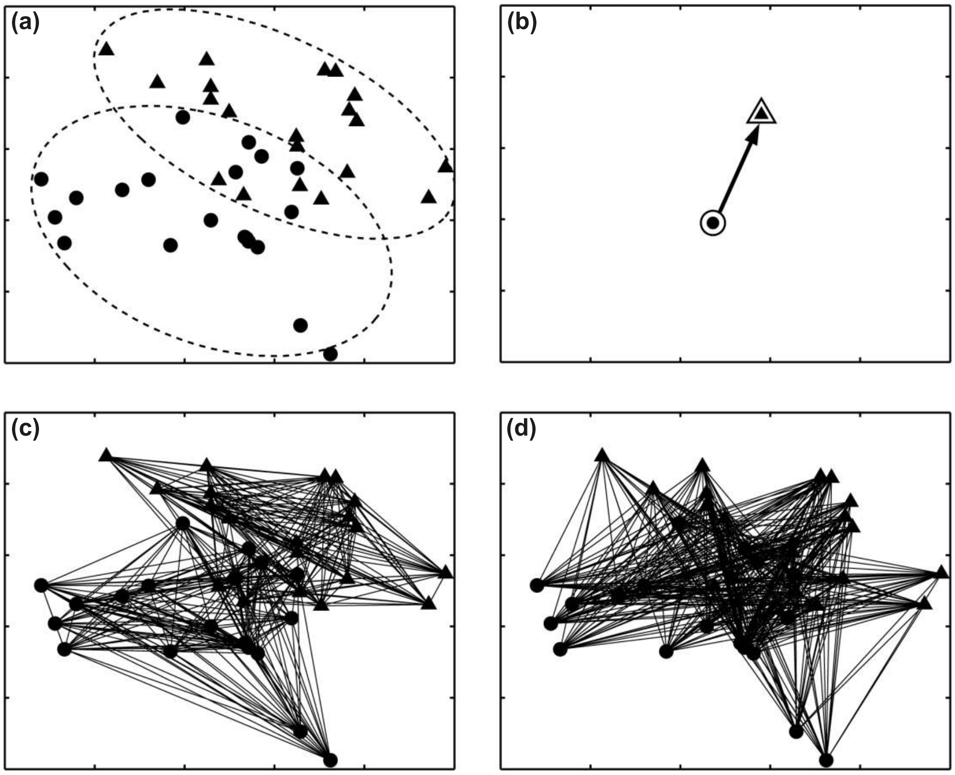
Note: Geographic affinity of each fish species is determined based on its principal geographic distribution in the Northeast Pacific: 1, widely distributed species; 2, cool-water species; 3, warm-water species) (Hsieh et al. 2005*a*). The southern boundaries are analyzed for only cool-water species, and northern boundaries for only warm-water species. The results remain qualitatively the same when abundances are not included in the analysis as a covariate. The final column indicates the results of a test of difference in geographic domain between the cold (1951–1976) and warm (1977–1998) periods. Only significant results ($p < 0.05$) are listed.

*Exploitation status of each species is determined according to Hsieh et al. (2005*b*). Information on fishing mortality of bycatch species is not known. Data sources of fishing mortality and history of exploitation for exploited species where available are provided in Appendices A and B.

[†] The significant regression with 1-year lag.

[‡] *Zaniolepis frenata* shows a negative relationship with temperature and SOI. The reason for this negative relationship is unknown.

Fig. 2. Schematic illustrating spatial analyses of change in distribution domain of fishes. (*a*) Circles and triangles represent hypothetical distribution center in individual year in the cold and warm periods, respectively. (*b*) The circle and triangle represent the centroid of the spatial distribution domain for the cold and warm periods, respectively, and the arrow indicates the magnitude and direction of the change between the two periods. To test whether the change in distribution between the two periods is significant, we computed all pairwise distances of distribution centers (*c*) within and (*d*) between the two periods. The change in distribution is significant if the ratio of the average pairwise distances within and between are statistically smaller than the null ratio generated from a randomization procedure.



a latitudinal transitional region where subarctic and subtropical fishes meet (Horn and Allen 1978), which provides a good opportunity to investigate distributional responses of fishes to climate. Although the CalCOFI plankton sampling equipment and protocols have changed over time, these changes will not bias the spatial statistics used here (Hsieh et al. 2005*b*). In addition, although the sampling frequency is higher than quarterly from 1951 to 1984, we use only the quarterly data in this study so that the variance associated with the spatial data is not biased because of the difference in sampling effort of each year.

We determine the center of geographic distribution (mean latitude and longitude) in each year for each species by first averaging the station values across the principal season in which the larvae occur (i.e., spawning season of the species, Hsieh et al. 2006) and then calculating the distribution center as the abundance-weighted average of the annual map. Thus, a time series of the distribution center is obtained for each species. In addition, the southern (northern) boundary is calculated as the minimum (maximum) latitude in which a species occurs for each year.

We use average sea surface temperature (SST) within our study region (Fig. 1, the inner box of inset) as a proxy for climatic signals. The SST data are from the CalCOFI stations (calcofi.org/newhome/data/data.htm). When analyzing the correlation between SST and the geographic distribution of a fish species, we use only the SST data corresponding to the spawning season of that species. The annual average SST is calculated by averaging the spatial and temporal data (quarterly data within the spawning seasons). Hereafter, we use SST to refer to the annual average SST. We also examine large-scale climatic indices (the Southern Oscillation Index (SOI; cgd.ucar.edu/cas/catalog/climind/soi.html) and the Pacific Decadal Oscillation Index (PDO; jisao.washington.edu/pdo/PDO.latest)) following the same analytical framework.

Data analyses

For each species, regression analysis is used to investigate the relationship between the mean latitude and SST and 1-year time-lagged SST. We also examine the southern boundaries for cool-water species and northern boundaries for warm-water species (Table 1) in relation to the SSTs. Because the geographic extent of marine populations may be correlated with population size (Swain and Sinclair 1994; Marshall and Frank 1995; Blanchard et al. 2005), we control for abundance and test for the partial correlation between the mean latitude (or boundaries) and SSTs. We analyze the effects of SOI and PDO following the same manner.

We also examine the bidecadal scale variation in fish distributions because climatic variability is important at this time scale in the North Pacific (Mantua et al. 1997; Biondi et al. 2001). We define the cold (1951–1976) and the warm (1977–

Fig. 3. Examples illustrating the calculation of the spatial heterogeneity index based on Pacific hake (*Merluccius productus*). The spatial heterogeneity index was calculated as the area under the standardized rank abundance curve. The examples indicate (*a*) high spatial heterogeneity in 1960 and (*b*) low heterogeneity in 1992.

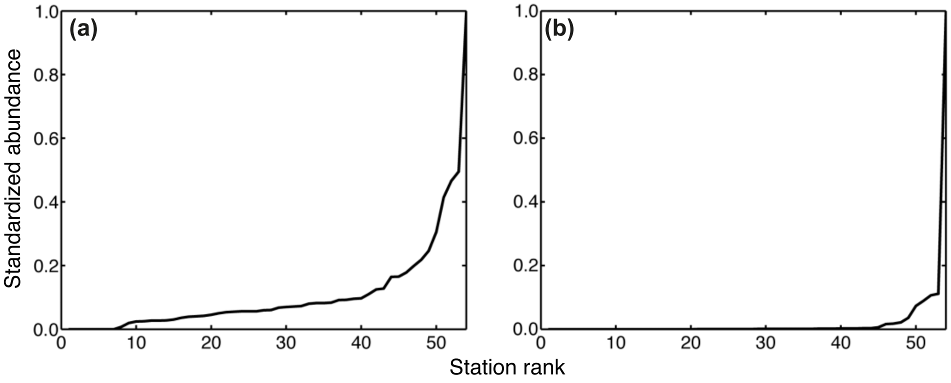
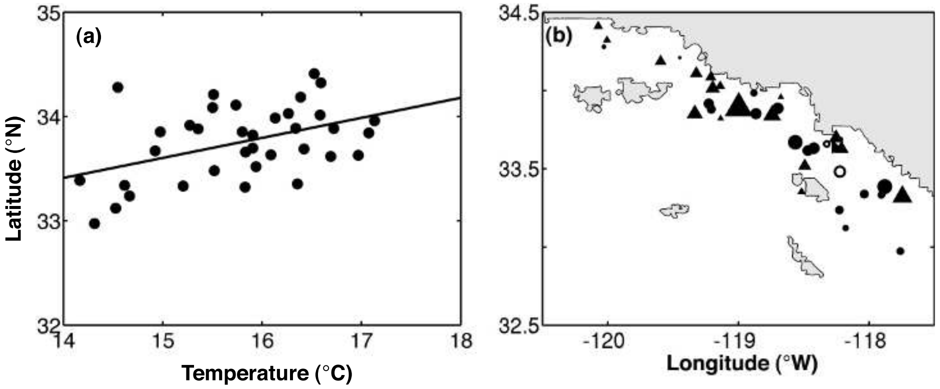


Fig. 4. An example showing (*a*) the relationship between mean latitude and mean sea surface temperature (SST) and (*b*) distribution centers (1951–1976, solid circles; 1977–1998, solid triangles; 1999–2002, open circles) for California halibut. In (*b*), the size of the symbol is proportional to the mean abundance for a given year.



1998) period following the definition of the PDO (Mantua et al. 1997). A transition back to another cold period may have occurred in 1999 (Ohman and Venrick 2003; Peterson and Schwing 2003), but the post-1998 time series is too short to confirm; therefore, data beyond 1998 are omitted in the analyses at the bidecadal scale. For each species, the centroids of the cold and warm periods are calculated from the time series of the distribution center using the method of 50% convex hull peeling, with all data equally weighted (Zani et al. 1998). This method is robust to the bias caused by outliers. We track the direction and magnitude of the movement from the cold to the warm period for each species. To test whether the change in larval distribution domain from the cold to the warm period is statistically significant, we use an ANOVA-like nonparametric test by comparing all pairwise distances of distribution centers within and between the two periods (illustrated in Fig. 2). The statistic is computed as follows:

(1) We compute the sum of all pairwise distances between distribution centers within period 1,

$$\Omega_1 = \sum \left\| x_{i1} - x_{j1} \right\|, \quad i \neq j, i > j$$

and within period 2,

$$\Omega_2 = \sum \left\| x_{i2} - x_{j2} \right\| \quad i \neq j, i > j$$

where x_{i1} and x_{i2} represent points in two-dimensional Euclidean space in periods 1 and 2, respectively, and i and j are indices for years (Fig. 2*c*).

(2) We then compute the average of pairwise distances within periods,

$$W = \frac{1}{N(N-1)/2 + M(M-1)/2}(\Omega_1 + \Omega_2)$$

where there are N and M points in periods 1 and 2, respectively.

(3) We compute the average of pairwise distances between periods,

$$B = \frac{1}{NM}\sum \left\| x_{k1} - x_{l2} \right\|$$

where k = 1 to N and l = 1 to M (Fig. 2*d*).

(4) The statistic $T = W/B$ is used to determine whether there is a significant change in distribution domain.

Fig. 5. Magnitudes and direction of changes in distribution from the cold (1951–1976) to the warm (1977–1998) period for different fish species.

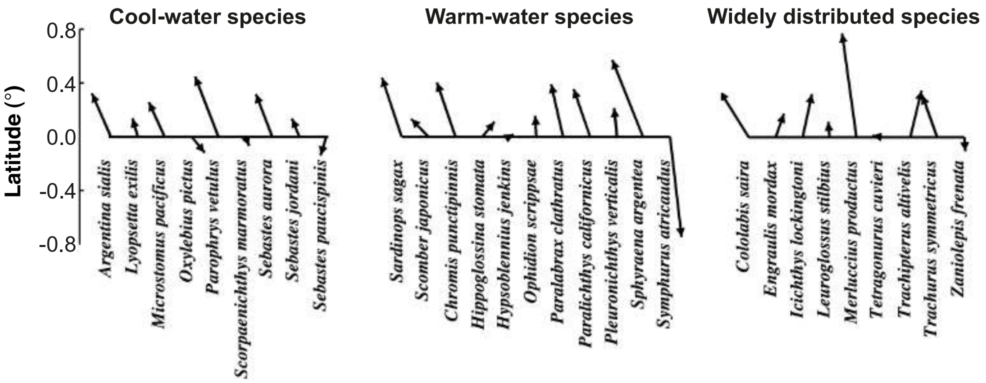


Fig. 6. Comparison of life history traits of shifting and nonshifting species. Means are shown with 95% bootstrapped confidence limits with bias correction. No significant difference is found between the shifting and nonshifting species ($p > 0.05$), although the shifting species have, on average, higher average maximum length, length-at-maturation, age-at-maturation, and fecundity. Statistical power associated with the bootstrapped *t* test is also shown.

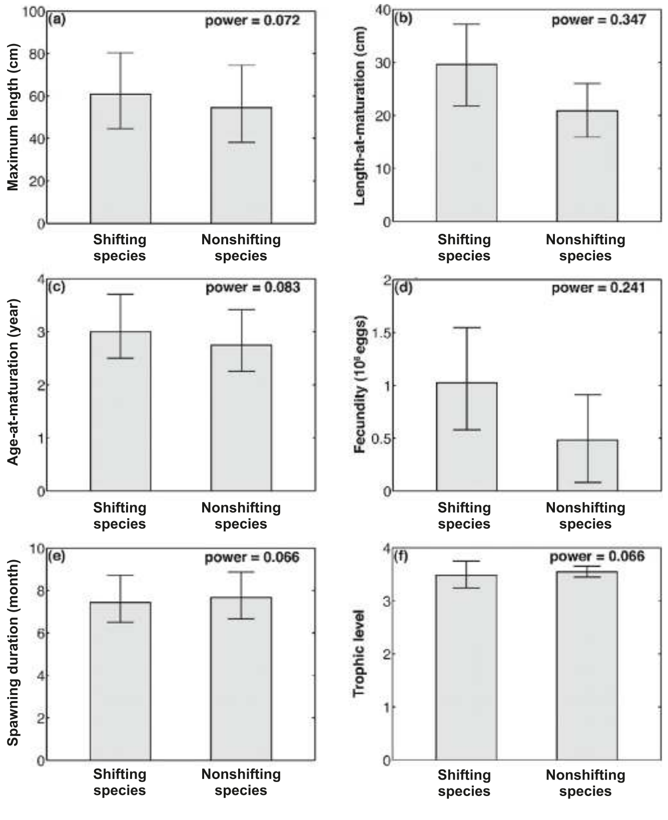


Table 2. Contingency table showing numbers of shifting and nonshifting species in each taxonomic order.

Order	Shifting	Nonshifting
Clupeiformes	2	0
Gadiformes	1	0
Perciformes	4	4
Beloniformes	0	1
Osmeriformes	2	0
Lampriformes	0	1
Pleuronectiformes	2	5
Scorpaeniformes	3	3
Ophidiiformes	1	0

Note: Results of the Monte Carlo two-way contingency table analysis indicate that phylogeny does not determine whether or not a fish species shows a distributional response to temperature ($p = 0.982$).

A significant change in larval distribution domain between the two periods corresponds to a small T. We randomize the data 1000 times and obtain the null ratios T^*. The change is deemed significant if T falls in the 5% lower tail.

We then consider whether shifting and nonshifting species have significantly different life history traits (Perry et al. 2005). Here, "shifting species" are defined as species showing a significant distributional (including mean latitude and boundaries) relationship with SST or climate index or a significant change in distribution domain from the cold to the warm period. We examine six life history traits: maximum length, length-at-maturation, age-at-maturation, fecundity, spawning duration, and trophic level (Hsieh et al. 2006). For each trait, we use bootstrapped *t* tests to examine whether or not a significant difference in the mean value of life history trait exists between shifting and nonshifting species and compute the associated statistical power (Beran 1986). Bootstraps are carried out 1000 times, and 95% confidence limits of the mean are calculated with accelerated bias correction (Efron and Tibshirani 1986). We then use a Monte Carlo two-way contingency table analysis (Romesburg and Marshall 1985) to test whether fish species showing a significant distributional response to climate have a particular phylogenetic relationship (based on fish species orders). In addition, a logistic regression is applied to determine whether the shifting species are associated with specific ecological traits (geographic affinity, habitat, and spawning mode (Hsieh et al. 2006)) and exploitation (exploited or not).

Two indices are developed to investigate potential fishing effects on spatial pattern of fish: spatial area of occupancy and spatial heterogeneity of abundance distribution. These two aspects of spatial distribution are selected because it has been suggested that fishing may reduce spatial area of occupancy and spatial heterogeneity of exploited populations (Berkeley et al. 2004). The spatial area of occupancy of each

Fig. 7. Time series of spatial area of occupancy (blue) and index of spatial heterogeneity (green) for (*a*–*m*) exploited, (*n*–*t*) bycatch, and (*u*–*ac*) unexploited groups. Plotted are raw indices (solid circles) along with the smoothed curve based on locally weighted scatterplot smoother (LOWESS). Time series of exploitation fraction of certain species (*a*–*g*) are plotted (red lines with solid circles) with a scale from 0 to 1. Values of exploited fraction were extracted from stock assessment reports (Appendix B). A moratorium was applied to (*d*) *Sardinops sagax* and (*e*) *Scomber japonicus*. Figure 7 is continued on pages 954 and 955.

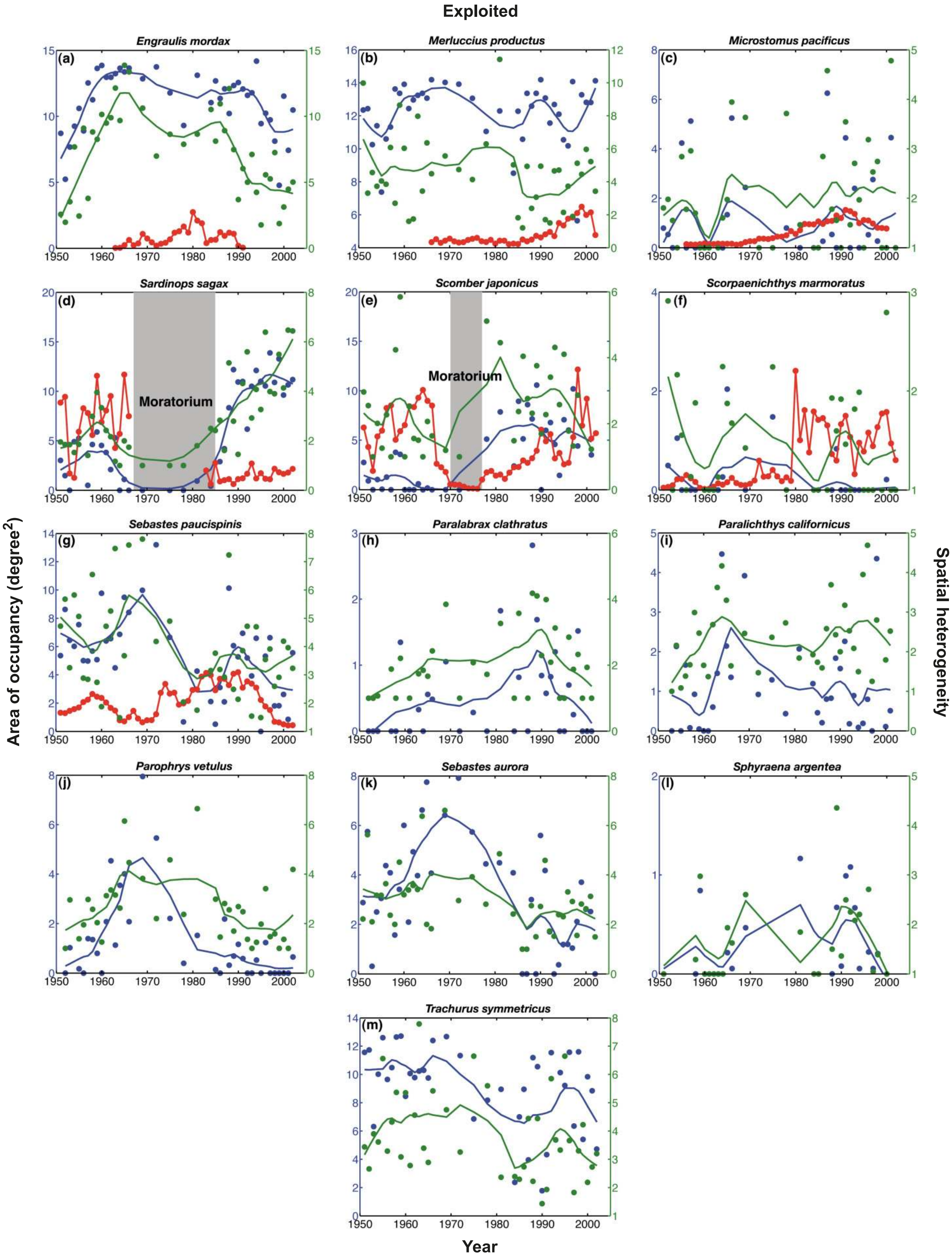


Fig. 7 (*continued*).

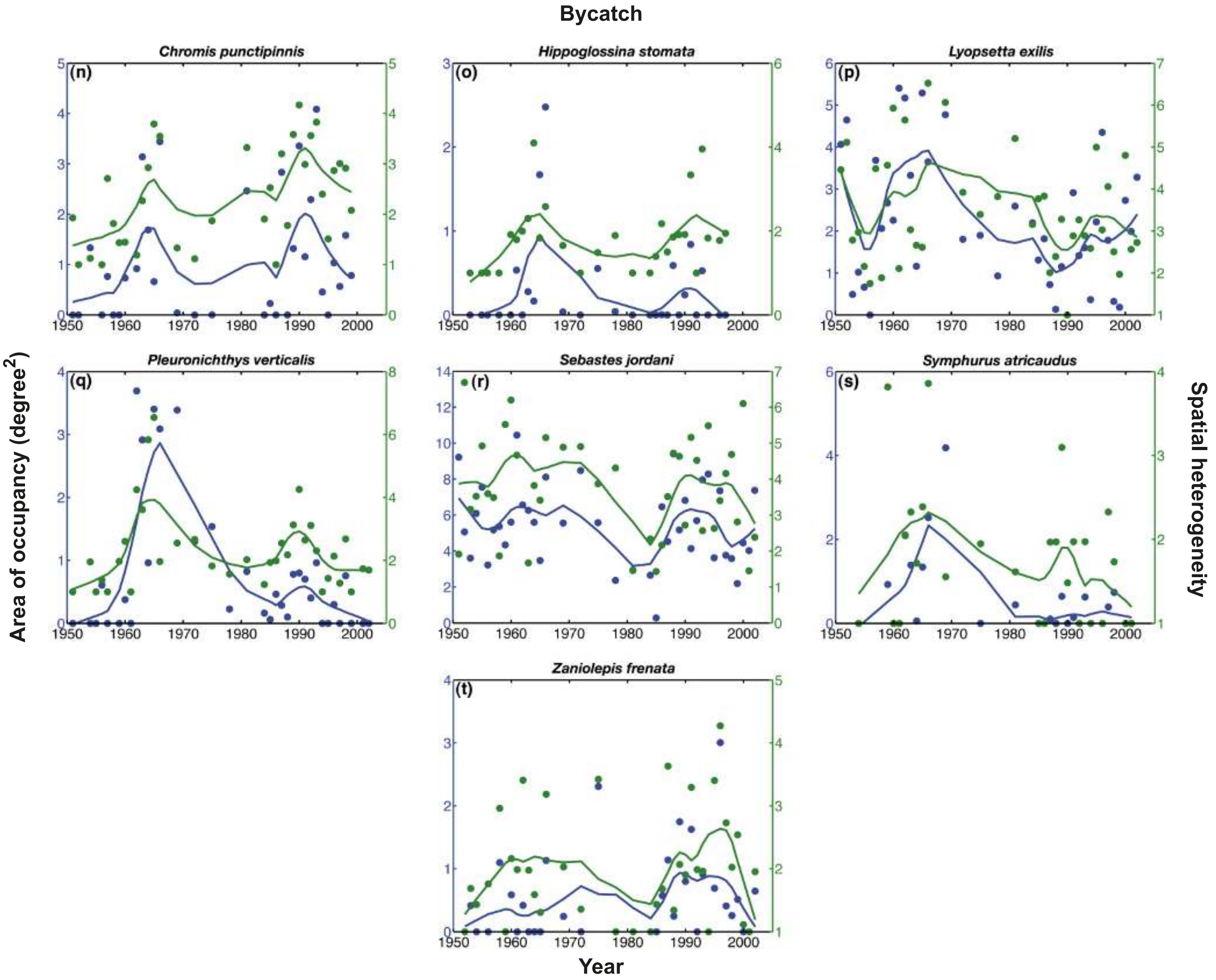


Table 3. Results of logistic regressions showing effects of ecological traits and fishing on fish species' responsiveness to climate variations.

Model	Variable	p value
Shifting = fishing	Fishing	0.006
+ geographic affinity	Geographic affinity	0.319
+ habitat	Habitat	0.852
+ spawning mode	Spawning mode	0.601

Note: Ecological traits of fish species are described in Hsieh et al. (2006). Geographic affinity: cold water, warm water, or widely distributed. Habitat: free-living in water column, living on soft bottom, or associated with kelp. Spawning mode: pelagic spawners, demersal spawners, or live-bearers.

species is calculated as the area of the minimal polygon that encloses stations with positive abundance for each year. Thus, changes in the spatial area of occupancy are indicative of constriction or expansion of spatial distribution. The index of spatial heterogeneity is calculated as follows. For each year, we first standardize the abundances in all stations to be between 0 and 1, i.e., dividing abundances by the maximal abundance value. We then plot the abundance rank curve (Fig. 3) and calculate the area under the curve as the index of spatial heterogeneity. If fish abundances are more evenly distributed in stations, the abundance rank curve tends to be more evenly distributed (e.g., Fig. 3*a*). By contrast, if fish abundances are concentrated in only a few stations, then the abundance rank curve is highly skewed (e.g., Fig. 3*b*). Because we standardize abundances by the maximal value, a highly skewed abundance rank curve results in a smaller area under the curve (Fig. 3*b*) and thus a lower index of spatial heterogeneity. Time series of spatial indices are obtained for each species. To show the temporal trend of each species, we plot a smoothed curve using a locally weighted scatterplot smoother (LOWESS) with a span of 5 years (Cleveland and Devlin 1988). We then normalize each smooth curve to unit mean and variance and summarize the overall trend of spatial indices for the fish assemblage by plotting all curves together and calculating the average.

Results

Climate variability significantly influences the geographic distributions of some fish populations, and this influence depends on temporal scale. Again, shifting species are defined

Fig. 7 (*concluded*).

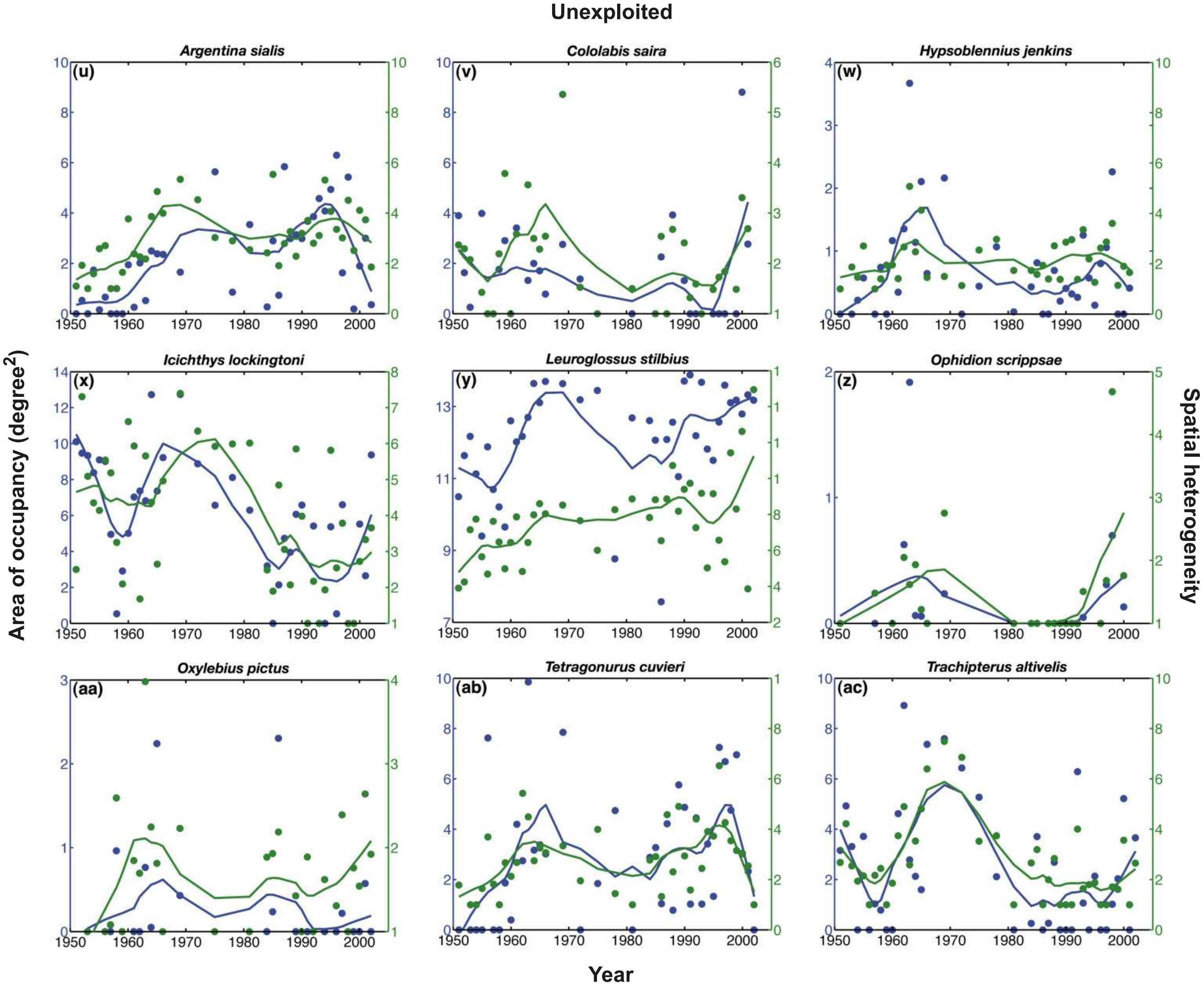


Fig. 8. Smoothed curves (broken lines) representing normalized indices of (*a*) spatial area of occupancy and (*b*) spatial heterogeneity, with the average (solid line) for all species except *Sardinops sagax* and *Scomber japonicus*, which are excluded because a moratorium was applied in the 1970s, which has strongly influenced the trend of the spatial indices. In general, the indices increased from 1950s to late 1960s and decreased afterward.

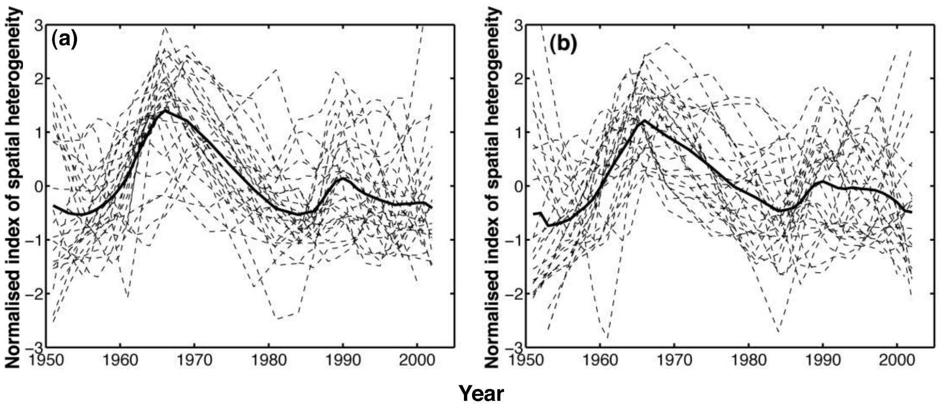
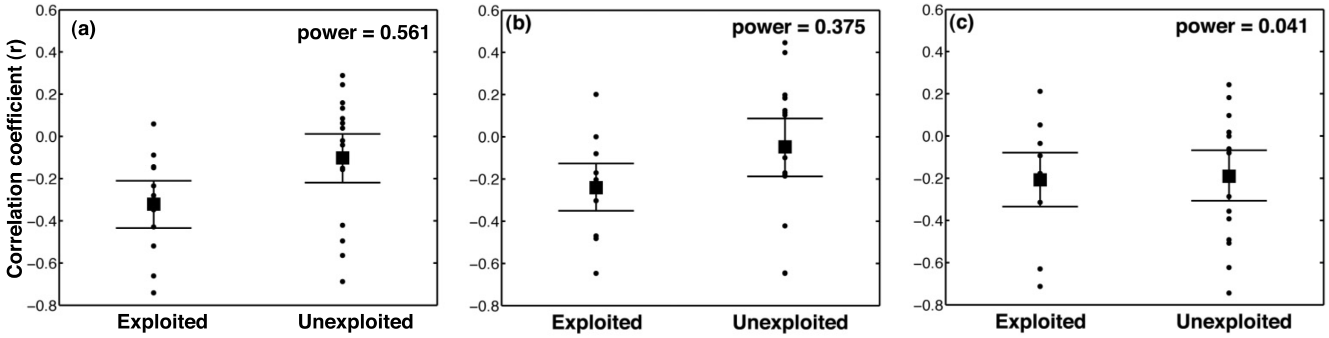


Table 4. Results of correlation analysis between spatial indices and time and between spatial indices and abundance.

		Spatial heterogeneity				Area of occupancy			
		vs. time		vs. abundance		vs. time		vs. abundance	
Exploitation status	Species	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Exploited	*Engraulis mordax*	–0.223	0.166	0.556	<0.001	–0.109	0.505	0.508	0.001
	Merluccius productus	–0.230	0.154	–0.393	0.012	–0.008	0.960	0.027	0.867
	Microstomus pacificus	0.144	0.381	0.736	<0.001	0.011	0.948	0.630	<0.001
	Paralabrax clathratus	0.249	0.162	0.633	<0.001	0.227	0.203	0.685	<0.001
	Paralichthys californicus	0.216	0.206	0.189	0.271	–0.024	0.891	0.330	0.049
	Parophrys vetulus	–0.212	0.207	0.605	<0.001	–0.339	0.040	0.455	0.005
	Sardinops sagax	0.651	<0.001	0.595	<0.001	0.715	<0.001	0.706	<0.001
	Scomber japonicus	0.182	0.289	0.409	0.013	0.667	<0.001	0.581	<0.001
	Scorpaenichthys marmoratus	–0.147	0.407	0.408	0.017	–0.216	0.220	0.499	0.003
	Sebastes aurora	–0.334	0.038	0.230	0.159	–0.418	0.008	0.389	0.014
	Sebastes paucispinis	–0.306	0.055	0.189	0.243	–0.445	0.004	0.569	<0.001
	Sphyraena argentea	0.245	0.238	0.155	0.461	0.233	0.263	0.333	0.104
	Trachurus symmetricus	–0.269	0.093	–0.048	0.769	–0.430	0.006	0.248	0.123
Bycatch	*Chromis punctipinnis*	0.455	0.008	0.282	0.111	0.215	0.230	0.502	0.003
	Hippoglossina stomata	0.192	0.319	0.377	0.044	–0.120	0.537	0.295	0.120
	Lyopsetta exilis	–0.209	0.196	0.312	0.050	–0.300	0.060	0.362	0.022
	Pleuronichthys verticalis	–0.108	0.531	0.315	0.061	–0.298	0.078	0.263	0.121
	Sebastes jordani	–0.183	0.259	–0.011	0.949	–0.175	0.281	0.329	0.038
	Symphurus atricaudus	–0.277	0.161	0.171	0.395	–0.383	0.049	0.383	0.049
	Zaniolepis frenata	0.125	0.461	0.555	<0.001	0.235	0.162	0.744	<0.001
Unexploited	*Argentina sialis*	0.410	0.009	0.212	0.188	0.534	<0.001	0.444	0.004
	Cololabis saira	–0.128	0.484	0.253	0.162	–0.059	0.747	0.541	0.001
	Hypsoblennius jenkins	0.080	0.640	0.207	0.218	–0.098	0.564	0.262	0.118
	Icichthys lockingtoni	–0.435	0.005	0.547	<0.001	–0.538	<0.001	0.755	<0.001
	Leuroglossus stilbius	0.496	0.001	–0.077	0.636	0.333	0.036	0.274	0.087
	Ophidion scrippsae	0.096	0.665	0.614	0.002	–0.174	0.427	0.791	<0.001
	Oxylebius pictus	0.009	0.963	0.224	0.242	–0.124	0.521	0.174	0.367
	Tetragonurus cuvieri	0.287	0.076	0.469	0.003	0.221	0.177	0.712	<0.001
	Trachipterus altivelis	–0.311	0.051	0.515	0.001	–0.226	0.162	0.594	<0.001

Note: Only data after 1969 were used because fishing effort has increased since then for many exploited species (Leet et al. 2001).

Fig. 9. Comparison of correlation coefficients (r) between (a) time and spatial area of occupancy, (b) time and the indices of spatial heterogeneity, and (c) time and abundance for exploited and unexploited groups. The patterns of bycatch and unexploited groups are similar; therefore, data of these two groups are combined as the unexploited. Only data after 1969 were used because fishing effort has increased since then for many exploited species (Leet et al. 2001). *Sardinops sagax* and *Scomber japonicus* are excluded because a moratorium was applied in the 1970s. On average, the decreasing trend of spatial indices of exploited species are stronger than that of unexploited species (a and b), although this difference is not statistically significant (bootstrapped t test, $p > 0.05$). By contrast, the decreasing trend of abundance of exploited species are identical to that of unexploited species (c). Each solid circle represents r of each species; the square represents the mean value; and horizontal bars represent 95% bootstrapped confidence limits. Statistical power associated with the bootstrapped t test is also shown.



as species showing a significant interannual spatial relationship with SST or climate index or a significant bidecadal scale change in distribution from the cold to the warm period.

At the annual scale, seven of the 29 species significantly shift their mean latitude in relation to SST (Table 1; see Fig. 4*a* for an example). In addition, five warm-water species significantly shift their northern boundaries interannually in relation to SSTs, and one cool-water species, *Scorpaenichthys marmoratus* (cabezon), significantly shifts its southern boundary in relation to the 1-year lagged SSTs (Table 1). All shifting species show a positive correlation with the SSTs, except for *Zaniolepis frenata* (shortspine combfish). For the shifting species, the rate of shift in mean latitude ranged from 17 to 37 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$ (average = 25 ± 5 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$, seven species). The only shifting cool-water species moved 49 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$ in its southern boundary. The rate of shift in the northern boundary of warm-water species ranged from 21 to 43 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$ (average = 31 ± 7 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$, five species).

Fewer species (eight) show a significant relationship to the climate indices (PDO or SOI) in their latitudinal distribution (Table 1) compared with their relationships to the SST. Most of the species that show a significant relationship to the climate indices also exhibit a significant relationship to the SST. The only exceptions are *Sebastes aurora* and *Leuroglossus stilbius*, which show significant relationships to the PDO in its southern boundary and mean latitude, respectively (Table 1), and *Engraulis mordax*, which shows a significant relationship to both the PDO and SOI in its mean latitude (Table 1).

At the bidecadal scale, broad distributional shifts are observed for the assemblage as a whole (see Fig. 4*b* for an example). A total of 24 species (cool-water species, 6 out of 9; warm-water species, 10 out of 11; widely distributed species, 8 out of 9) shifted their distribution poleward from the cold period to the warm period (Fig. 5). This is a highly significant ensemble result (binomial test, $p < 0.001$), suggesting that most species move poleward in response to the warming in the southern California Current ecosystem. The movements range from 1 to 86 km (average = 31 ± 7 km). However, upon closely investigating their distribution centers, only nine of the species show a significant shift in their geographic distribution (Table 1). Thus, although most species show a tendency to move poleward in response to decadal-scale warming regimes, the signal is clear in only nine out of 29 species.

Additionally, regardless of the time scale examined, the tendency for a species to exhibit a clear response to temperature is significantly associated with fishing (Table 1). Considering the annual and bidecadal scales together, 14 species show a clear distributional shift in response to climate, and among them, 10 are exploited species and only four are unexploited species (Table 1). We find no significant differences in life history traits between shifting and nonshifting species ($p > 0.05$; Fig. 6), although the statistical power is low (< 0.35) because of a small sample size. Furthermore, whether or not a species exhibits a significant response to temperature changes or climate index is not associated with their phylogeny (Table 2), geographic affinity, habitat, or spawning mode (Table 3).

The reason that exploited species showing a stronger association with climate may be related to fishing effects on spatial distribution of fish, as suggested by the analyses on spatial area of occupancy or spatial heterogeneity of fish (Fig. 7). This can be seen in several exploited species by comparing the trend of spatial index and the trend of exploitation fraction (i.e., the fraction of fish population removed by fisheries) (Figs. 7*a*–7*g*). For example, fishing mortality for *Merluccius productus* increased from late 1960s and spatial indices declined since then, although with significant variation (Fig. 7*b*). Fishing effects on spatial indices can be seen in *Sardinops sagax* and *Scomber japonicus* by comparing spatial indices before and after a moratorium (Figs. 7*d* and 7*e*). The spatial indices were relatively low and fishing mortality was relatively high before the moratorium, and the spatial indices bounced back after a moratorium. For *S. japonicus*, the spatial heterogeneity again decreased when fishing mortality increased (Fig. 7*e*).

Overall (excluding *S. sagax* and *S. japonicus*), the average spatial indices increased from the 1950s to the late 1960s and then decreased thereafter (Fig. 8), albeit with significant variations. *Sardinops sagax* and *S. japonicus* are excluded in this calculation because a moratorium was applied in the 1970s, which strongly influenced the trend of spatial indices. The existence of such a common trend suggests climatic effects on spatial distribution of the fish assemblage. Coincidently, fishing effects also increased around the late 1960s and early 1970s for many exploited species (MacCall et al. 1976; Leet et al. 2001). Such fishing effects can be seen from the temporal trend of fishing mortality for some species (Figs. 7*a*–7*h*) and can be inferred from the history of fisheries for the species for which fishing mortality estimates are not available (Appendix A). Thus, climatic and fishing effects are confounded here.

To separate fishing and climatic effects, we calculate the correlation between the spatial indices and time using data after 1969 (Table 4) and compare the trends (correlation coefficients) between exploited and unexploited species using bootstrapped t tests. When the raw spatial indices are used for the comparison, the declining trends in spatial index are on average stronger in the exploited group than unexploited group; however, this difference is not statistically significant ($p > 0.05$; Figs. 9*a* and 9*b*). We notice that the temporal trends of spatial indices are not independent of changes in abundance for several species (Table 4). Reduction in spatial area of occupancy and heterogeneity is associated with reduction in abundance. However, when the same correlation analysis is carried out for the abundance data, we find that the declining trends in abundance are almost identical for the exploited and unexploited groups (Fig. 9*c*). These findings suggest that fishing has impacts on population spatial structures and that such effects may be overlooked if we investigate abundance trends alone.

Discussion

Climate variability affects geographic distributions of fish populations within the California Current ecosystem, although the signal is not very strong. Among the 29 species examined, only 12 species show a significant interannual distributional shift (mean latitude or boundaries) in relation to SST or climate indices. This may be because the latitudinal range of the current study (30–35°N) is small and none of the studied species is bounded by this range. Our results are consistent with those of other studies (Murawski 1993; Brander et al. 2003; Perry et al. 2005) reporting poleward shifts of most fishes in response to warmer average SST. The mean latitudinal shift rate of 25 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$ reported here is smaller than that reported for either North Sea fishes (average 87 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$ calculated from Perry et al. 2005) or North Atlantic fishes (ranges from 56 to 89 $\text{km}\cdot{}^{\circ}\text{C}^{-1}$ reported by Murawski 1993). The smaller shift rate may be due to the smaller latitudinal range of this study (30–35°N) compared with those of the North Sea study (51–62°N) and North Atlantic study (36–45°N), because estimates of distribution centers may be biased when the true population moves beyond the study boundary. Thus, the shifting rates may be underestimated in this study. Alternatively, species living at lower latitudes might be less sensitive to warming (Root et al. 2003).

When comparing the fish distribution centroid in the cold period with that of the warm period, we find that 83% of species move poleward in response to warmer average SST. The average shifting distance of the distribution centroid is 31 km. Again, this value may be underestimated owing to the limitation of our sampling range. Whether such a distributional shift may have impacts on the living habitat, food source, and thus survival of fish populations warrants further investigation.

Among the 29 species, only nine species pass the randomization test for a shift in their distribution centroids, further indicating that the signal is not very strong. Given the geographic limit of our study area and noisiness of the data, our results show that most species have responded to temperature, but some species show a stronger response than others.

Which factor determines whether or not a species shows a significant response in the distribution (i.e., high signal–noise ratio)? More often than not, the shifting species are those that are commercially exploited, i.e., exploited species exhibit a higher signal–noise ratio. Other factors such as life history traits, phylogeny, and ecological traits are not as important. In addition, no significant difference in mean abundance exists between the shifting and nonshifting species (bootstrap t test, $p > 0.05$, power = 0.303).

We hypothesize that the higher signal–noise ratio may be explained by fishery-induced constriction of geographic distribution combined with size (age) truncation of a fish population. Consider an unexploited population that normally has a relatively large number of spawners, larger geographic area with complex spatial margins, and higher spatial heterogeneity (MacCall 1990; Berkeley et al. 2004). The larvae produced by these spawners, along with effects caused by advection and diffusion, might be expected to show higher spatial heterogeneity. Under this condition, with complex spatial margins, the center of distribution that we calculated from unexploited species may not accurately reflect the true spatial location of the natural population. Therefore, although the spatial domain of an unexploited population might have changed from one environmental condition to another, this signal might not be clearly represented by a shift in the center of distribution. In contrast, when a fish population is under fishing pressure, its distribution area may shrink, spatial heterogeneity may be diminished, and the number of spawning individuals may decline (MacCall 1990). Thus, the distribution center of an exploited population represents more precisely the spatial location of the natural population as spatial heterogeneity is greatly reduced. In addition, such effect may be further reinforced by fishery-induced size (age) truncation. Poorly managed fisheries tend to truncate the age–size structure of fish populations by removing large and old individuals through size- or age-selective fishing mortality (Conover and Munch 2002; Berkeley et al. 2004; Hutchings and Reynolds 2004). Recent studies have shown that such effects would have evolutionary consequences (Conover and Munch 2002; Swain et al. 2007). Evidence of size (age) truncation has been found in several exploited species examined in this study (Hsieh et al. 2006). Because large and old individuals tend to produce higher quantity eggs and because spawning locations may be age-dependent (Hutchings and Myers 1993; Marteinsdottir and Steinarsson 1998; Berkeley et al. 2004), fishery-induced size (age) truncation can potentially reduce the heterogeneity in the spatial structure of populations.

Our hypotheses are partially supported by our analyses on spatial area of occupancy and spatial heterogeneity of fish distribution. The declining trends of spatial indices after 1969 are stronger in the exploited group, although the difference is not statistically significant. This suggests that fishing effects may have reduced the spatial coverage or altered the spatial structure of fish populations. This mechanism sometimes can operate without revealing a clear declining trend in abundance. Such kinds of fishing effects on population spatial structures may happen, even when fishing mortality is at a level thought to be moderate (Berkeley et al. 2004).

A significant shift in larval distribution in response to climate is more likely to be observed for an exploited population that has a more local (thus environmentally homogeneous) spatial distribution. This may operate if fishing reduces the heterogeneity in the spatial structure of exploited populations, in other words, if fishing forces exploited populations to “put all their eggs in a smaller spatial basket”. As a consequence, exploited populations may become more vulnerable to environmental stochasticity and more sensitive to climate effects (Berkeley et al. 2004). This may explain why exploited species show higher temporal variability in population size than unexploited species, as shown in Hsieh et al. (2006).

Our results indicate that the geographic distribution of exploited populations shows a stronger signal in response to climate variations. This enhanced signal may be a consequence of reduced spatial heterogeneity of fish populations caused by fishery-induced age truncation or constriction of their spatial distribution. It is worth pointing out that fishing may not directly increase sensitivity in geographic distribution of exploited populations in response to climate; rather, fishing enhances their distributional signals by reducing spatial heterogeneity. The reduced spatial heterogeneity may make exploited species more vulnerable to climatic effects, for example, the impacts of climate-induced trophic mismatch or reduction in suitable habitat. The effects of fishing, climate, and the interactions of these two factors on the dynamics of fish populations should be borne in mind for sound fisheries management. Conservation measures designed to maintain the age and spatial structures of fish populations should contribute to their sustainability (Berkeley et al. 2004).

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References

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., and Reid, P.C. 2003. Plankton effect on cod recruitment in the North Sea. Nature (London), **426**: 661–664.

Benson, A.J., and Trites, A.W. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish Fish. **3**: 95–113.

Benson, A.J., McFarlane, G.A., Allen, S.E., and Dower, J.F. 2002. Changes in Pacific hake (*Merluccius productus*) migration patterns and juvenile growth related to the 1989 regime shift. Can. J. Fish. Aquat. Sci. **59**: 1969–1979.

Beran, R. 1986. Simulated power functions. Ann. Stat. **14**: 151–173.

Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries, **29**: 23–32.

Biondi, F., Gershunov, A., and Cayan, D.R. 2001. North Pacific decadal climate variability since AD 1661. J. Clim. **14**: 5–10.

Blanchard, J.L., Mills, C., Jennings, S., Fox, C.J., Packham, B.D., Eastwood, P.D., and O’Brien, C.M. 2005. Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. Can. J. Fish. Aquat. Sci. **62**: 2001–2009.

Brander, K., Blom, G., Borges, M.F., Erzini, K., Henderson, G., MacKenzie, B.R., Mendes, H., Ribeiro, J., Santos, A.M.P., and Toresen, R. 2003. Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? ICES Mar. Sci. Symp. **219**: 261–270.

Brodeur, R., Pearcy, W., and Ralston, S. 2003. Abundance and distribution patterns of nekton and micronekton in the Northern California Current transition zone. J. Oceanogr. **59**: 515–535.

Cleveland, W.S., and Devlin, S.J. 1988. Locally weighted regression: an approach to regression analysis by local fitting. J. Am. Stat. Assoc. **83**: 596–610.

Conover, D.O., and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. Science (Washington, D.C.), **297**: 94–96.

Di Lorenzo, E., Miller, A.J., Schneider, N., and McWilliams, J.C. 2005. The warming of the California Current system: dynamics and ecosystem implications. J. Phys. Oceanogr. **35**: 336–362.

Edwards, M., and Richardson, A.J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature (London), **430**: 881–884.

Efron, B., and Tibshirani, R. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Stat. Sci. **1**: 54–75.

Hare, S.R., and Mantua, N.J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. **47**: 103–145.

Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., and Williams, S.L. 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. **9**: 228–241.

Holbrook, S.J., Schmitt, R.J., and Stepnens, J.J.S. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecol. Appl. **7**: 1299–1310.

Horn, M., and Allen, L.G. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. **5**: 23–42.

Hsieh, C.H., Glaser, S.M., Lucas, A.J., and Sugihara, G. 2005*a*. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature (London), **435**: 336–340.

Hsieh, C.H., Reiss, C., Watson, W., Allen, M.J., Hunter, J.R., Lea, R.N., Rosenblatt, R.H., Smith, P.E., and Sugihara, G. 2005*b*. A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: a community approach. Prog. Oceanogr. **67**: 160–185.

Hsieh, C.H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. Nature (London), **443**: 859–862.

Hutchings, J.A., and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2468–2474.

Hutchings, J.A., and Reynolds, J.D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. Bioscience, **13**: 297–309.

Leet, W.S., Dewees, C.M., Klingbeil, R., and Larson, E.J. 2001. California's living marine resources: a status report. California Department of Fish and Game, Oakland, California.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Washington.

MacCall, A.D., Stauffer, G.D., and Troadec, J.-P. 1976. Southern California recreational and commercial marine fisheries. Mar. Fish. Rev. **38**: 1–32.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meterol. Soc. **78**: 1069–1079.

Marshall, C.T., and Frank, K.T. 1995. Density-dependent habitat selection by juvenile haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. **52**: 1007–1017.

Marteinsdottir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod (*Gadus morhua*) eggs and larvae. J. Fish Biol. **52**: 1241–1258.

Moser, H.G., Charter, R.L., Smith, P.E., Ambrose, D.A., Watson, W., Charter, S.R., and Sandknop, E.M. 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951–1998. CalCOFI Atlas, **34**: 1–166.

Murawski, S.A. 1993. Climate change and marine fish distributions: forecasting from historical analogy. Trans. Am. Fish. Soc. **122**: 647–658.

Murphy, G.I. 1967. Vital statistics of the Pacific sardine (*Sardinops caerulea*) and the population consequences. Ecology, **48**: 731–736.

Ohman, M.D., and Venrick, E.L. 2003. CalCOFI in a changing ocean. Oceanography, **16**: 76–85.

Parmesan, C., and Yohe, G. 2003. A global coherent fingerprint of climate change impacts across natural systems. Nature (London), **421**: 37–42.

Perry, A.L., Low, P.J., Ellis, J.R., and Reynolds, J.D. 2005. Climate change and distribution shifts in marine fishes. Science (Washington, D.C.), **308**: 1912–1915.

Peterson, W.T., and Schwing, F.B. 2003. A new climate regime in Northeast Pacific ecosystems. Geophys. Res. Let. **30**: 1896.

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K.J. 2004. Ecosystem-based fishery management. Science (Washington, D.C.), **305**: 346–347.

Rodriguez-Sanchez, R., Lluch-belda, D., Villalobos, H., and Ortega-Garcia, S. 2002. Dynamic geography of small pelagic fish populations in the California Current system on the regime time scale (1931–1997). Can. J. Fish. Aquat. Sci. **59**: 1980–1988.

Romesburg, H.C., and Marshall, K. 1985. CHITEST: a Monte-Carlo computer program for contingency table tests. Comput. Geosci. **11**: 69–78.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. Nature (London), **421**: 57–60.

Schneider, N., Di Lorenzo, E., and Niiler, P.P. 2005. Salinity variations in the Southern California Current. J. Phys. Oceanogr. **35**: 1421–1436.

Smith, P.E., and Moser, H.G. 2003. Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region. Deep-Sea Res. Part II, **50**: 2519–2536.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S., and Lima, M. 2002. Ecological effects of climate fluctuations. Science (Washington, D.C.), **297**: 1292–1296.

Swain, D.P., and Sinclair, A.F. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? Can. J. Fish. Aquat. Sci. **51**: 1046–1054.

Swain, D.P., Sinclair, A., and Mark Hanson, J. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proc. R. Soc. B, **274**: 1015–1022.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., and Williams, S.E. 2004. Extinction risk from climate change. Nature (London), **427**: 145–148.

Trenberth, K.E. 1984. Signal versus noise in the Southern Oscillation. Mon. Weather Rev. **112**: 326–332.

Walther, G., Post, E., Convey, P., Menzel, A., OParmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological response to recent climate change. Nature (London), **416**: 389–395.

Zani, S., Riani, M., and Corbellini, A. 1998. Robust bivariate boxplots and multiple outlier detection. Comput. Stat. Data Anal. **28**: 257–270.

Appendices A and B follow.

Appendix A

Table A1. Exploitation history of the commercial species in the California area.

Species	Common name	Exploitation history
*Engraulis mordax**	Northern anchovy	Low exploitation from 1958 to 1964, slight exploitation from 1965 to 1982, essentially no exploitation after 1982
*Merluccius productus**	Pacific hake	Only incidental catch prior to 1966, large-scale harvesting of Pacific hake in the US zone began in 1966
*Sardinops sagax**	Pacific sardine	High exploitation before 1967, moratorium from 1967 to1985, regulated exploitation after 1985
*Scomber japonicus**	Pacific mackerel	High exploitation before 1970, moratorium from 1970 to 1977, restricted exploitation from 1977 to 1985, increased exploitation after 1985
Trachurus symmetricus	Jack mackerel	High exploitation from 1947 to 1979, low exploitation after 1979
*Microstomus pacificus**	Dover sole	High exploitation after 1970
Paralabrax clathratus	Kelp bass	High exploitation after 1970
Paralichthys californicus	California halibut	High exploitation
Parophrys vetulus	English sole	Exploitation
*Scorpaenichthys marmoratus**	Cabezon	High exploitation due to recreational fishing, particularly since 1980
Sebastes aurora	Aurora rockfish	Exploitation, particular after 1970
*Sebastes paucispinis**	Bocaccio	High exploitation after 1970
Sphyraena argentea	Pacific barracuda	Exploitation

Note: The exploitation history is based on Leet et al. (2001), MacCall et al. (1976), and Ralston (1998).
*Time series of exploitation fraction for species with stock assessment available to us are plotted in Fig. 7.

References

Leet, W.S., Dewees, C.M., Klingbeil, R., and Larson, E.J. 2001. California's living marine resources: a status report. California Department of Fish and Game, Oakland, California.

MacCall, A.D., Stauffer, G.D., and Troadec, J.-P. 1976. Southern California recreational and commercial marine fisheries. Mar. Fish. Rev. **38**: 1–32.

Ralston, S. 1998. The status of federally managed rockfish on the US West Coast. Marine harvest refugia for West Coast rockfish: a workshop, NOAA Tech. Memo. No. NMFS-SWFSC-255.

Appendix B

Table B1. Data sources for fishing mortality (exploitation fraction) extracted from stock assessment reports for six exploited species.

Species	Common name	Domain of assessment	Source
Engraulis mordax	Northern anchovy	California	Jacobson et al. 1994
Merluccius productus	Pacific hake	US west coast	Helser et al. 2003
Sardinops sagax	Pacific sardine	California	MacCall 1979; Conser et al. 2004
Scomber japonicus	Pacific chub mackerel	US west coast	Hill and Crone 2005
Microstomus pacificus	Dover sole	US west coast	Sampson 2005
Scorpaenichthys marmoratus	Cabezon	Southern California	Cope and Punt 2005
Sebastes paucispinis	Bocaccio	California	MacCall 2003

References

Conser, R., Hill, K.T., Crone, P.R., Lo, N.C.H., and Felix-Uraga, R. 2004. Assessment of the Pacific sardine stock for U.S. management in 2005. Pacific Fishery Management Council, 7700 NE Ambassador Place Suite 101, Portland, OR 97220-1384, USA.

Cope, M.J., and Punt, A.E. 2005. Status of cabezon (*Scorpaenichthy marmoratus*) in California waters as assessed in 2005. Pacific Fishery Management Council, 7700 NE Ambassador Place Suite 101, Portland, OR 97220-1384, USA.

Helser, T.E., Methot, R.D., and Fleischer, G.W. 2003. Stock assessment of Pacific hake (whiting) in U.S. and Canadian waters in 2003. Pacific Fishery Management Council, 7700 NE Ambassador Place Suite 101, Portland, OR 97220-1384, USA.

Hill, K.T., and Crone, P.R. 2005. Assessment of the Pacific mackerel (*Scomber japonicus*) stock for U.S. management in the 2005–2006 season. Pacific Fishery Management Council, 7700 NE Ambassador Place Suite 101, Portland, OR 97220-1384, USA.

Jacobson, L.D., Lo, N.C.H., and Barnes, J.T. 1994. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. Fish. Bull. U.S. **92**: 711–124.

MacCall, A.D. 1979. Population estimate for the waning years of the Pacific sardine fishery. CalCOFI Rep. **20**: 72–82.

MacCall, A.D. 2003. Status of bocaccio off California in 2003. Pacific Fishery Management Council, 7700 NE Ambassador Place Suite 101, Portland, OR 97220-1384, USA.

Sampson, D.B. 2005. The status of Dover sole off the U.S. West Coast in 2005. Pacific Fishery Management Council, 7700 NE Ambassador Place Suite 101, Portland, OR 97220-1384, USA.