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Long-term shifts in the species composition of a coastal fish community

Jeremy S. Collie, Anthony D. Wood, and H. Perry Jeffries

Abstract: To study decadal shifts in a coastal nekton community, we analyzed data on 25 fish and invertebrate species collected from 1959 to 2005 by the University of Rhode Island, Graduate School of Oceanography (Narragansett, Rhode Island, USA). This weekly trawl survey samples two locations: inside Narragansett Bay and in Rhode Island Sound. Over four decades, the community has shifted progressively from vertebrates to invertebrates and, especially since 1980, from benthic to pelagic species. Demersal species that declined include winter flounder (*Pseudopleuronectes americanus*), silver hake (*Merluccius bilinearis*), and red hake (*Urophycis chuss*); meanwhile warm-water fish (butterfish, *Peprilus triacanthus*; scup, *Stenotomus chrysops*) and invertebrates (lobster, crab, squid) increased with time. Total numbers reached a maximum in the 1990s, while mean body size decreased. Taxonomic diversity increased over time, as the community shifted from fish to invertebrates of several phyla. The shifts in species composition correlate most strongly with spring–summer sea surface temperature, which increased 1.6 °C over the 47-year time series. Species composition was also correlated with the winter North Atlantic Oscillation index and chlorophyll concentration, which has declined since the 1970s. Triggered primarily by rising temperatures, these decadal changes have altered the trophic structure of the nekton community, resulting in a shift from benthic to pelagic consumers.

Résumé : Afin d'étudier les changements dans la communauté du nekton côtier à l'échelle des décennies, nous analysons les données sur 25 espèces de poissons et d'invertébrés récoltées de 1959 à 2005 par le Graduate School of Oceanography de l'University of Rhode Island (Narragansett Bay, Rhode Island, USA). Cet inventaire hebdomadaire au chalut échantillonne deux sites, l'intérieur de la baie de Narragansett et le détroit du Rhode Island. Au cours des quatre décennies, la communauté s'est modifiée graduellement d'une dominance de vertébrés à une d'invertébrés et, particulièrement depuis 1980, d'espèces benthiques à pélagiques. Les espèces démersales qui ont connu un déclin incluent la plie rouge (*Pseudopleuronectes americanus*), le merlu argenté (*Merluccius bilinearis*) et la merluche rouge (*Urophycis chuss*); en revanche, les poissons d'eau chaude (le stromatée à fossettes, *Peprilus triacanthus*; le spare doré, *Stenotomus chrysops*) et les invertébrés (homards, crabes, calmars) se sont accrus dans le temps. Les nombres totaux ont atteint un maximum durant les années 1990, alors que la taille corporelle moyenne diminuait. La diversité taxonomique a augmenté avec le temps, à mesure que la communauté changeait des poissons aux invertébrés appartenant à plusieurs phylums. La corrélation la plus forte s'observe entre les changements de composition spécifique et la température de la surface de la mer au printemps et en été qui s'est accrue de 1,6 °C au cours de la période de 47 années. Il y a aussi une corrélation entre la composition spécifique et l'indice de l'oscillation de l'Atlantique Nord en hiver et la concentration de chlorophylle, en déclin depuis les années 1970. Occasionnés principalement par l'augmentation des températures, ces changements à l'échelle des décennies ont modifié la structure trophique de la communauté du nekton, ce qui a entraîné le remplacement des consommateurs benthiques par des consommateurs pélagiques.

[Traduit par la Rédaction]

Introduction

Fish populations vary on temporal scales ranging from interannual to millennial (Hilborn and Walters 1992; Baumgartner et al. 1992). In most biotic time series with durations in the range of 30–50 years, variability increases with the number of years included in the calculation, resulting in “reddened” power spectra (Pimm and Redfern 1988). This decadal variability manifests itself as strings of years with high and low abundances, with important implications for population persistence, human governance, and decision-

making. Interannual recruitment variability can be filtered or damped by the adult biomass of iteroparous fish species with long life spans (Spencer and Collie 1997). In contrast, decadal-scale variability squarely fits the life spans of many fish species and human planning horizons (Steele 1996).

Decadal variability can arise from a number of processes: species interactions, delayed density dependence, and spatially explicit or age-structured population dynamics (Akçaya et al. 2003). Decadal-scale population variability can also be inherited from environmental variations, which may be quasi-cyclic (Chavez et al. 2003) or secular trends. Non-

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linear species interactions can amplify decadal variability in climatic forcing, resulting in abrupt and large-amplitude shifts in the biota (Collie et al. 2004). Such regime shifts in community composition create additional challenges to understanding population variability and for informing human decisions (Scheffer et al. 2001).

The long-term data that exist for freshwater and marine communities reflect the interplay of these population processes. Eutrophication has shifted many lakes from clear-water states to persistent turbid-water states with concomitant effects on the food web (Carpenter 2003). Dramatic changes in community structure of the Laurentian Great Lakes have been driven by phosphorous loading and trophic interactions among a succession of introduced species (Bunnell et al. 2006).

The best time series of marine fish abundance come from trawl surveys on the continental shelves. In the northwest Atlantic, North Sea, and Gulf of Thailand, dramatic shifts in species composition have occurred, in response primarily to fishing pressure and secondarily to changes in the marine climate (Hall 1999). On the eastern Scotian Shelf, commercial fishing and decadal variability in water temperature appear to have shifted the fish community from a demersal to a pelagic-dominated state (Choi et al. 2004). The existing examples of species replacements on decadal time scales suggest some form of compensation mediated by competition and predator–prey interactions (Hall 1999). For example, the depletion of cod stocks in the North Atlantic over the past 40 years has been correlated with increased abundance of shrimp, crab, and lobster (Worm and Myers 2003).

Changes in community composition have also been observed in estuarine fish assemblages, although the existing data are often discontinuous and nonstandardized (Attrill and Power 2002; Genner et al. 2004). Compared with those on the continental shelf, estuarine fish communities may have greater exposure to anthropogenic stresses. They are more accessible to fisheries and may also suffer greater levels of pollution, habitat loss, and the presence of more introduced species. For example, estuarine species are exposed to endocrine disruptors that can alter sex ratios (Beresford et al. 2004). With shallower water columns, estuaries may respond more quickly to climate change than deeper waters offshore.

The University of Rhode Island, Graduate School of Oceanography (GSO; Narragansett, Rhode Island, USA), fish trawl is one of the few long-term, standardized fish surveys. Conducted weekly since 1959, the fish trawl has documented decadal shifts in the fish community of a temperate estuary (Jeffries and Johnson 1974). Several hypotheses have been advanced to explain the replacement of resident demersal fish species with seasonal migrants and invertebrate species (Jeffries and Terceiro 1985). One hypothesis is the sequential fishing of resident bay species favoring the offshore migrant species as local resources were depleted (Oviatt et al. 2003). The expected consequences of fishing are the removal of predator species (Jackson et al. 2001) followed by shifts in size structure to smaller forage species as a result of predator release (Myers et al. 2007). A shift from demersal to pelagic species is expected in eutrophied estuaries, as has been observed in European semi-enclosed seas (de Leiva Moreno et al. 2000). Finally, rising water temper-

atures (Oviatt 2004) should favor southern over boreal species. This study documents the long-term patterns in the GSO fish trawl and examines the utility of several community metrics for tracking the large shifts in species composition. We examine which forcing variables (fishing, chlorophyll, temperature, and other climate variables) are related to the shifts in species composition and the derived community metrics. The choice of forcing variables is limited to those with time series of sufficiently long duration. Finally, we examine the support for the various hypotheses that have been advanced to explain the shifts in species composition.

Materials and methods

Field

Every week since 1959, the demersal community at two stations in Narragansett Bay, Rhode Island, has been sampled by the GSO fish trawl. One station is located mid-bay in the West Passage, east of Fox Island, at a depth of 7.3 m; the second is located in Rhode Island Sound running south of Whale Rock at a depth of 20 m (Fig. 1). In this paper, we use “bay” to refer to the Fox Island station and “sound” to refer to the Whale Rock station. In the history of the GSO fish trawl, four vessels have been used: F/V *Billie II* (13 January 1959 – 28 June 1977), F/V *Dulcinea* (28 June 1977 – 16 July 1982), F/V *Gail Ann* (16 July 1982 – 8 September 1987), and R/V *Cap'n Bert* (8 September 1987 – present). Surface and bottom water temperatures were recorded at each station with a standard Niskin bottle and bucket thermometer.

The trawl nets, deployment, and towing speed have been standardized throughout the time series. The otter trawl has a bottom sweep of 15.2 m, an effective opening of 6.5 m, and cod-end mesh size of 5.1 cm (Captain Tom Puckett, University of Rhode Island, Kingston, RI 02882, USA, personal communication). The trawl doors, attached 18.2 m from the net mouth, are 1.52 × 0.76 m. Winches let out a marked amount of cable adjusted to the depths of each station: 36.5 m of cable at Fox Island and 82 m at Whale Rock. Tow duration at each station is 30 min at a speed of 2 knots (3.7 km·h⁻¹) over bottom. Following each tow, the net is retrieved and the contents are emptied into a checker box, sorted to the lowest taxon possible, counted, and weighed. The weight data began in 1994 and therefore are not used in this study.

Analyses

Of 130 species recorded in the GSO trawl-survey database, the most numerous 25 species from the years 1959–2005 were selected for this analysis (Table 1). This subset was selected to ensure that all 25 species were sufficiently numerous at both stations to have been identified consistently since the start of the fish trawl. Though the abundance of particular species has changed markedly, their frequency of occurrence has been consistent over time. These top 25 species accounted for 96% of a total of over 1.8 million animals recorded; therefore their dynamics will adequately capture the main shifts in community composition. Sampling was missed in occasional weeks because of poor weather or boat maintenance. Of 564 months, all but one had two or

Fig. 1. Map of Narragansett Bay (Rhode Island, USA) showing the two bottom-trawl stations. The bay station is north of Fox Island and the sound station is south of Whale Rock. Inset shows location in the northeastern USA. Arrows indicate the direction and distance of each tow.



more surveys; 91% of the months had three or more surveys. To minimize the potential effect of missing data, we first calculated monthly means and then averaged the monthly means to obtain the annual mean catch per 30-min tow of each species.

Ordination of the species abundances by year was based on the Bray–Curtis similarity index (S) calculated from square-root-transformed annual mean abundance. The Bray–Curtis measure is widely used and has properties that are desirable for ecological studies, including coincidence, complementarity, relative invariance, independence of joint absence, localization, and dependence on totals (Clarke et al. 2006). Nonmetric multidimensional scaling (MDS; Field

et al. 1982) was applied to the similarity matrices to ordinate the years in two dimensions. Similarity matrices were compared with the Spearman rank correlation coefficient (ρ). We tested for serial shifts in species composition by correlating the similarity matrix of the samples with a similarity matrix constructed from the rank-ordered years (Clarke et al. 1993).

A stepwise algorithm was used to identify sets of species that accounted for most of the temporal pattern of the community composition. Starting with a random subset of species, the BVSTEP routine sequentially adds and subtracts species (Clarke and Warwick 1998). The test statistic is the rank correlation between the similarity matrices for the sub-

Table 1. Top 25 species in the University of Rhode Island, Graduate School of Oceanography, trawl survey from 1959–2005.

Common name	Scientific name	Habitat	Maximum size (cm)	Preferred temperature (°C)	Mean catch per tow
Scup	<i>Stenotomus chrysops</i>	Demersal	40.0	14.5	71.25
Winter flounder	<i>Pseudopleuronectes americanus</i>	Demersal	46.0	8.8	65.62
Cancer crab (Atlantic rock and Jonah)	<i>Cancer irroratus</i> and <i>Cancer borealis</i>	Demersal	14.0 ^a	14.5	60.61
Butterfish	<i>Peprilus triacanthus</i>	Pelagic	30.5	13.0	49.06
Silver hake	<i>Merluccius bilinearis</i>	Demersal	76.0	10.0	33.88
Longfin squid	<i>Loligo pealeii</i>	Pelagic	40.0	12.0	28.97
American lobster	<i>Homarus americanus</i>	Demersal	80.0	11.0	12.73
Little skate	<i>Leucoraja erinacea</i>	Demersal	54.0	8.5	11.32
Windowpane	<i>Scophthalmus aquosus</i>	Demersal	51.0	13.4	11.02
Red hake	<i>Urophycis chuss</i>	Demersal	50.0	8.5	9.53
Spider crab	<i>Libinia emarginata</i>	Demersal	10.0 ^a	11.5	5.78
Atlantic herring	<i>Clupea harengus</i>	Pelagic	43.0	7.0	4.99
Northern searobin	<i>Prionotus carolinus</i>	Demersal	45.0	16.0	4.98
Sea star	<i>Asterias forbesi</i>	Demersal	12.5 ^b	22.5	4.94
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i>	Demersal	45.7	9.3	4.80
Fourspot flounder	<i>Paralichthys oblongus</i>	Demersal	45.0	11.4	3.70
River herring (alewife and blueback herring)	<i>Alosa pseudoharengus</i> and <i>Alosa aestivalis</i>	Pelagic	37.0	9.0	3.09
Cunner	<i>Tautoglabrus adspersus</i>	Demersal	43.2	14.5	1.87
Summer flounder	<i>Paralichthys dentatus</i>	Demersal	61.0	15.5	1.82
Lady crab	<i>Ovalipes ocellatus</i>	Demersal	7.5 ^a	13.0	1.38
Horseshoe crab	<i>Limulus polyphemus</i>	Demersal	60.0	30.0	1.29
Bluefish	<i>Pomatomus saltatrix</i>	Pelagic	115.0	13.5	1.10
Striped searobin	<i>Prionotus evolans</i>	Demersal	48.5	14.7	0.87
Tautog	<i>Tautoga onitis</i>	Demersal	90.0	13.5	0.81
Weakfish	<i>Cynoscion regalis</i>	Pelagic	100.0	21.8	0.79

Note: Maximum size is total length, unless otherwise indicated. Mean catch per tow was calculated over both stations and all years.

^aCarapace width.

^bArm length.

set of species and the similarity matrix of the full community. Though different subsets may give the same correlation (redundant species), by repeated runs, a set of species was identified that was consistently correlated with the full community.

Trends in the abundance of individual species were measured by regressing the logarithm of abundance against time ($\ln N_t = \ln N_0 + m \cdot t$). Years with zero catches for particular species were replaced with one-half the minimum catch for that species. Across all species, the incidence of zero catches was 7.1% at the bay station and 8.9% at the sound station. The slopes of these semilogarithmic regressions (m) and their associated confidence intervals were used to indicate the temporal trends in species abundance.

We calculated the standard species diversity indices (Simpson, Shannon–Weiner, Pielou) and a diversity index that accounts for the taxonomic relatedness of the species, which were classified by species, genus, family, order, class, and phylum (Supplemental Table S1, available online from the NRC Data Depository).²

Taxonomic distinctness (Δ^*) is an extension of the Simp-

son index, which accounts for the taxonomic distance (ω_{ij}) between species i and j , while removing the dominating effect of the species abundance distribution ($x_i x_j$):

$$\Delta^* = \frac{\sum \sum_{i < j} \omega_{ij} x_i x_j}{\sum \sum_{i < j} x_i x_j}$$

Taxonomic diversity measures have been found to be more sensitive to environmental change and less sensitive to sample size than traditional diversity indices (Warwick and Clarke 1995). Taxonomic distinctness is expected to decrease with increasing disturbance. A spatial analysis of trawl-survey data in the North Sea found that areas with low taxonomic distinctness corresponded with low abundance of elasmobranchs, a taxonomic group the life-history characteristics of which make it particularly sensitive to fishing (Rogers et al. 1999).

The pelagic–demersal ratio was calculated simply as the sum of individuals of pelagic species divided by the sum of individuals of demersal species (de Leiva Moreno et al. 2000). Each species was assigned a maximum size, L_{\max} ,

²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3756. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

from the literature (Table 1). Mean L_{\max} across species, weighted by the yearly mean abundance of each species, was used as a proxy for mean size in the community because length and weight measurements were not made in all years. We also defined a preferred temperature (T_{pref}) for each species as the midpoint of the preferred temperature range taken from the literature (Table 1). Mean T_{pref} , weighted by the annual mean abundance of each species, was used to index the temperature preference of the fish community over time.

A set of environmental data was selected to correlate with the species abundance data summarized by the diagonal matrix of Bray–Curtis dissimilarity (D), which is the complement of similarity ($D = 1 - S$). This set was limited to variables with sufficiently long time series to permit meaningful tests. We used the sea surface temperatures (SST) measured on the fish trawl because of a gap in bottom temperatures between 1964 and 1977. Monthly mean temperatures were calculated, again to minimize potential effects of missing weeks. The monthly means were then averaged to obtain seasonal and annual means. Chlorophyll a concentration was measured from 1973–1990 and 1999–2005 in Narragansett Bay near our Fox Island station (Fulweiler et al. 2007). The chlorophyll concentrations are annual means of weekly samples from the surface and bottom of the water column. Trawl fishing effort data from the fishing area that includes Rhode Island Sound (Northeast Fisheries Science Center (NEFSC) statistical area 529) were used as an index of fishing pressure. These nominal effort data are in units of days fished per year for the period 1965–2005.

In addition to these local variables, we examined potential correlations with basin-scale climate indices. Calculated from the difference in normalized sea-level pressure between the Azores and Iceland, the North Atlantic Oscillation (NAO) is an index of wind patterns over the North Atlantic (Hurrell 1995). The winter NAO index (December through March) is the dominant climate signal in the North Atlantic (Hurrell 1995) and has been widely related to biotic indices (e.g., Stenseth et al. 2003), including estuarine fish populations (Attrill and Power 2002). The Atlantic Multidecadal Oscillation (AMO) is the area-weighted average SST in the North Atlantic (Enfield et al. 2001).

The fish trawl catches individuals starting at about 10 cm long and 1 year old. Hypothesizing that fish abundance may be related to past environmental conditions, we calculated correlations with the environmental variables at lags of 0, 1, and 2 years. We used the BIOENV procedure, which performs a nonparametric Mantel test (Clarke and Ainsworth 1993). Rank correlation coefficients were calculated between the matrix of environmental variables (Euclidean distance) and the matrix of community data (Bray–Curtis dissimilarity). Randomization tests were used to test the significance of the correlations. Recognizing that autocorrelation in the time series and multiple testing increase the chance of spurious correlations, we used $p = 0.01$ as a critical level.

In addition to the multivariate correlations, we conducted univariate linear regressions of the biotic (dependent) variables against potential explanatory (independent) variables. The biotic variables included the grouped species abundances (squids, pelagic fish, benthic invertebrates, and demersal

fish) and several community metrics (taxonomic distinctness, pelagic–demersal ratio, and mean L_{\max}). Three of the environmental variables (annual SST, winter NAO, and the AMO) were available for all 47 years. These three variables were entered into a stepwise regression, with minimum Akaike information criterion (AIC) as the criterion for inclusion. For the two variables that were not available for the full time series, days fished and chlorophyll a , we used simple linear regression with the probability of a nonzero slope as the measure of significance.

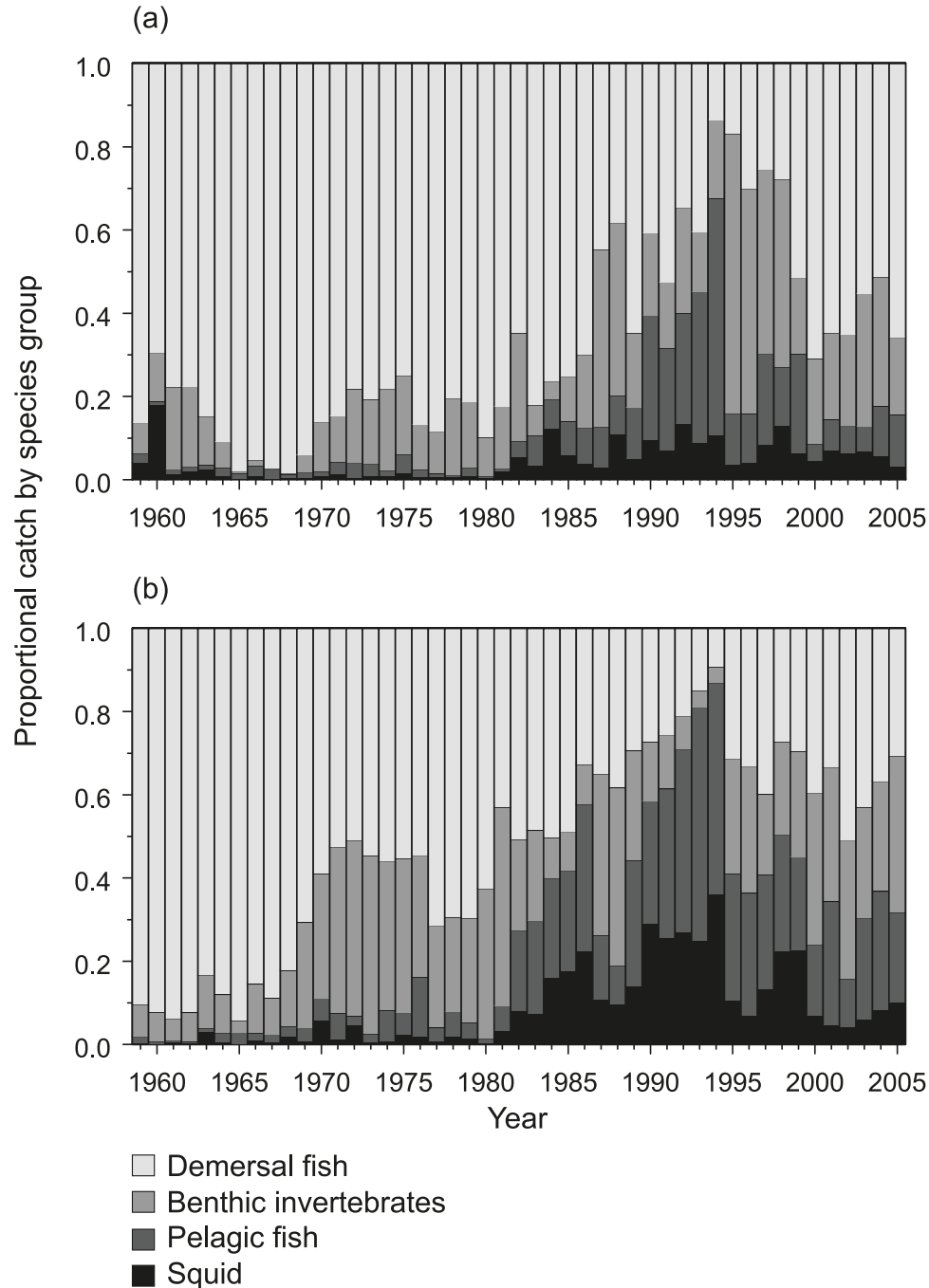
Results

The species composition of the fish and invertebrate community has changed dramatically since 1959 (Fig. 2). Following a decade of dominance by demersal fish in the 1960s, benthic invertebrates became more abundant in the 1970s, especially at the sound station (Fig. 2b). The main shift was in the rise of the pelagic fish and squid in the 1980s, such that pelagic species accounted for more than half of the numbers in 1994. This shift to pelagic species has persisted since 1995, though demersal fish have regained dominance at the bay station (Fig. 2a).

Ordination of the community data by nonmetric, multidimensional scaling (MDS) revealed significant serial shifts in species composition at both stations (Fig. 3). The points cluster by decade, especially at the sound station (Fig. 3b). There was a significant correlation between the similarity matrices at each site ($\rho = 0.79$, $p = 0.001$), indicating a shared temporal pattern, though the species composition and community trajectories differed somewhat between stations. The major shifts occurred between 1984 and 1985 at the bay station and between 1980 and 1981 at the sound station (Fig. 3). There is no indication that species composition in the 2000s is returning to the community that characterized the start of the time series in 1959. Between 2002 and 2003, there was a suggestion at the bay station that the community might be shifting toward the species composition that prevailed in the 1970s (Fig. 3a). On the other hand, the tight clustering of the points since 1995 suggests that the community at the sound station has shifted to a persistent configuration.

Most of the 25 species had significant trends in abundance during the 47-year period (Fig. 4). To put these trends in perspective, an instantaneous rate of -0.1-year^{-1} sustained for 47 years would leave approximately 1% of the initial population. Cunner, longhorn sculpin, northern searobin, silver hake, and winter flounder had similar rates of decline at both stations. On the other hand, striped searobin, four-spot flounder, river herring, bluefish, butterfly, scup, little skate, *Cancer* crab, lady crab, American lobster, and longfin squid all had significant rates of increase at both stations (see Table 1 for species names). Atlantic herring was the only species with no significant temporal trend at either station (Fig. 4). The instantaneous rate of increase or decrease (m) is a useful way to summarize the time trends, but the actual trajectories are irregular, not smooth exponential curves, as shown below.

At each station, BVSTEP was used to identify a subset of species that accounted for most of the temporal pattern in community composition that was illustrated by the ordina-

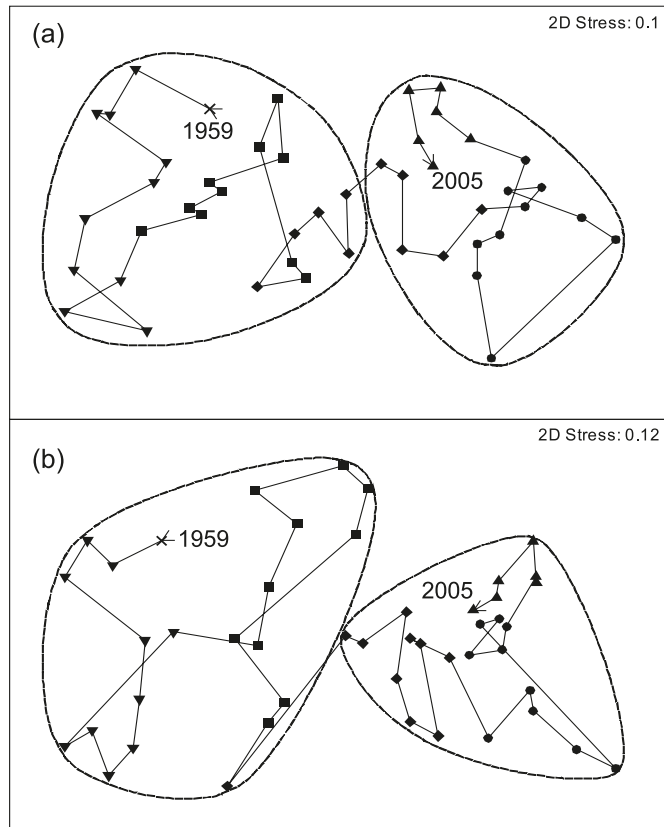
Fig. 2. Shifts in the relative abundance of species groups at (a) Bay Station and (b) Sound Station.

tion of the similarity matrices for all 25 species (Fig. 3). The similarity matrix of the abundances of these species over years had a rank correlation (ρ) of 0.95 with the corresponding similarity matrix for all 25 species. At the bay station, this subset comprised nine species: three demersal fish that decreased over time (winter flounder and silver and red hake), two fish (butterfish and scup), one elasmobranch (little skate), and three invertebrates (*Cancer* crab, American lobster, and longfin squid), which all increased (Fig. 5). Together, these nine species accounted for 58% of the dissimilarity between the two clusters of years in Fig. 3a, as calculated with the similarity percentages procedure

(SIMPER; Clarke 1993). SIMPER determines which species contribute the most to the similarity and dissimilarity of groups of samples (in our case, years). At the sound station, six of the same nine species (minus winter flounder, scup, and American lobster) had a correlation of 0.96 with the similarity matrix for all 25 species (Fig. 5). These six species accounted for 57% of the dissimilarity between the two clusters of years in Fig. 3b.

Total abundance of the 25 species increased over time at both stations (Fig. 6a). Abundance peaked between 1993 and 1995 and declined during the past 10 years. The species diversity indices all increased somewhat over time, but for

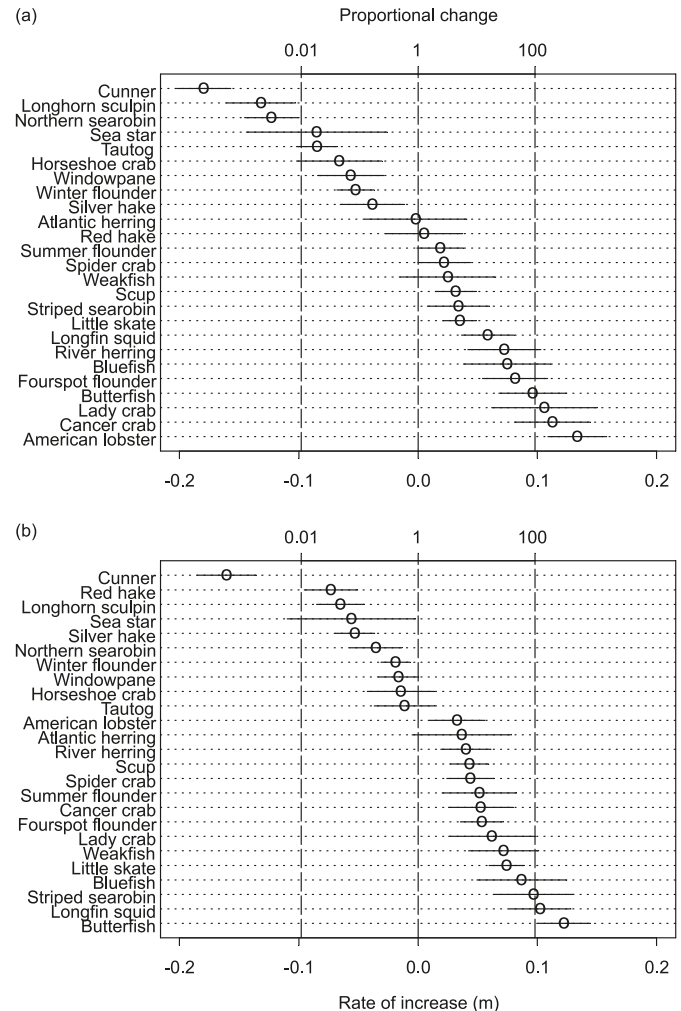
Fig. 3. Ordination of the abundances of 25 species in 47 years: (a) bay station (Fox Island); (b) sound station (Whale Rock). The non-metric multidimensional scaling (MDS) was based on the Bray–Curtis similarity of square-root-transformed data. Each point represents one year; points that are closer together have more similar species composition than distant points. Symbols indicate the decades: inverted triangles, 1960s; squares, 1970s; diamonds, 1980s; circles, 1990s; upright triangles, 2000s. The contours enclose clusters with $\geq 60\%$ similarity. 2D, two dimensional.



most of the standard indices, the temporal trends were insignificant. Temporal patterns were much more apparent in diversity indices that incorporate the taxonomic relatedness of the species. Average taxonomic distinctness was lowest in the 1960s when the community was dominated by demersal fish species, which are related at the class and order levels (Fig. 6b). Taxonomic distinctness increased significantly with time ($p < 0.001$) at both stations as species from different phyla and classes became abundant, especially Crustacea and Cephalopoda.

In addition to the increase in invertebrates, there was a shift to pelagic species in the 1980s (Fig. 6c). Even though the bottom trawl primarily targets demersal species, by 1994, the pelagic–demersal ratio exceeded 1 at both stations and has remained above 0.1 since then. Although mean numbers per tow increased at both stations, the species that became more abundant tended to be ones with smaller body size (Fig. 6d). A decline in weighted mean L_{\max} is apparent at both stations and was especially pronounced in the sound where mean L_{\max} declined by about one-third or 20 cm. Over time, the community shifted toward species with higher temperature preferences (Figs. 6e, 6f). Mean T_{pref}

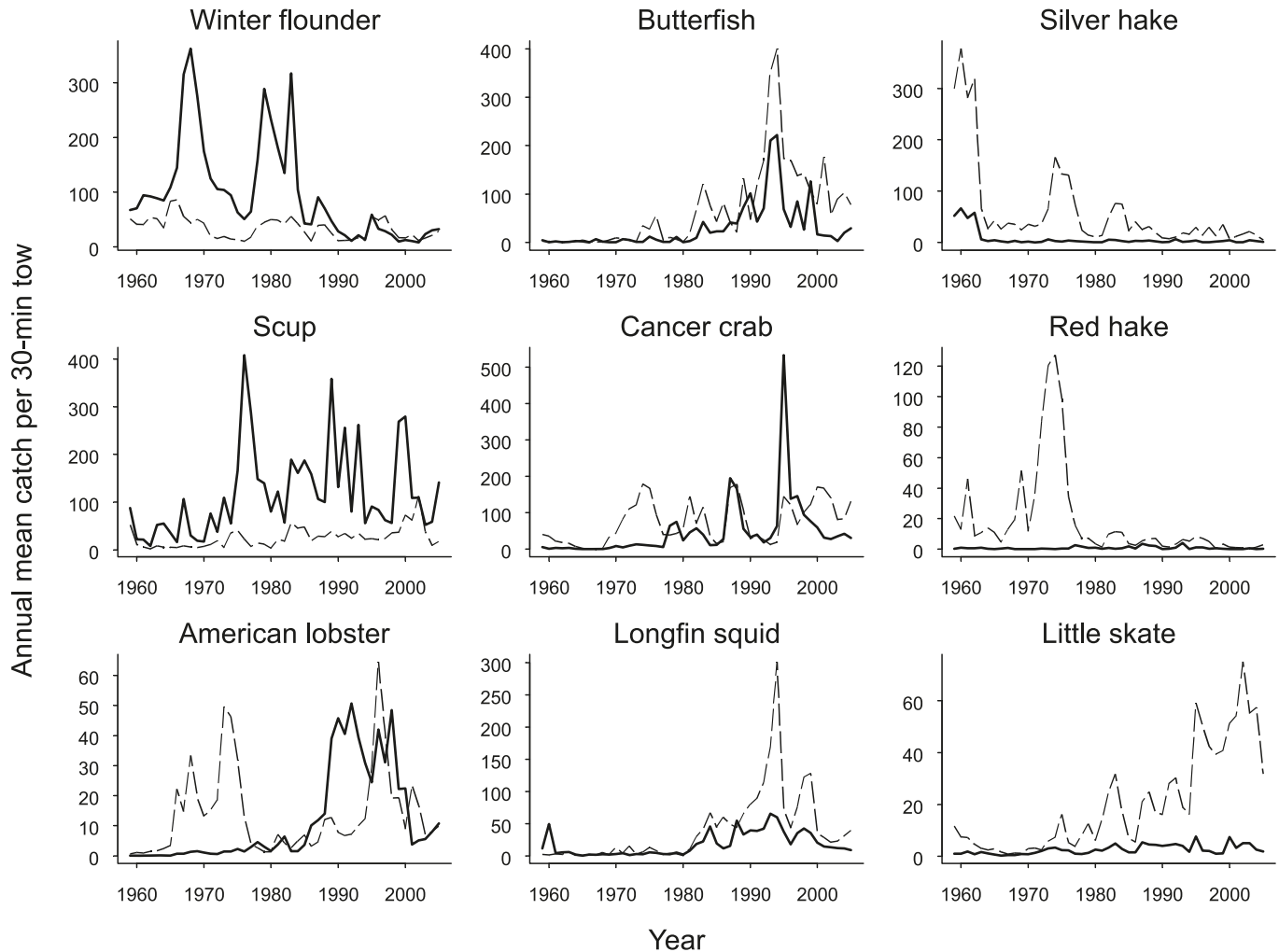
Fig. 4. Rates of increase or decrease of 25 species: (a) bay station; (b) sound station. The open circles represent the slopes (m) from regression of log-transformed abundance against time; the horizontal solid lines are the 95% confidence intervals of the slopes. The broken vertical lines indicate a 100-fold decrease (0.01), no change (1), and 100-fold increase (100) over 47 years.



increased by 2°C over the 47-year time series according to analysis of covariance ($p(\text{equal slopes}) = 0.43$, $p(\text{zero slope}) < 0.001$). At the bay station, T_{pref} increased with a sinusoidal pattern that was driven by the alternating abundances of winter flounder (cool) and scup (warm) (Fig. 6e); the increase in T_{pref} was more linear at the sound station (Fig. 6f).

The environmental time series that correlated most strongly with the species dissimilarity matrix were SST and chlorophyll a concentration (Table 2). High correlations were found with annual mean SST at all three lags. The highest correlations with temperature were for spring–summer SST with a 2-year lag. Many of the species recruit to the trawl survey at ages 1 and 2; therefore, the lagged SST indices correspond to conditions experienced during spawning and the early life stages. Sea surface temperature had an increasing trend during this period (Fig. 7a). Spring–summer SST increased 1.61°C over the 47-year time series according to analysis of covariance ($p(\text{equal slopes}) = 0.89$,

Fig. 5. Annual mean abundances of the nine species that are primarily responsible for the ordinations in Fig. 3: bay station, solid line; sound station, broken line. These nine species account for most of the pattern at the bay station. The six species in the middle and right columns explain the pattern seen at the sound station. Abundances of the other 16 species are plotted in Fig. S1 (see Supplemental data)².



$p(\text{zero slope}) < 0.001$). Annual mean SST increased by 1.3°C over the same time period.

Community composition, as measured by the species dissimilarity matrix, was significantly correlated with chlorophyll *a* concentration (Table 2). The correlation was higher at the bay station than at the sound station, possibly because chlorophyll was measured at a midbay station close to Fox Island. Chlorophyll had a declining trend during this period (Fig. 7b). Correlations with chlorophyll were not calculated for lags other than 0 because of the limited number of years and the data gap within the time series. Low and insignificant correlations were found between the species dissimilarity matrix and the number of days fished (Table 2). Fishing effort varied during this time period (Fig. 7b), but the pattern did not match the species abundance trends.

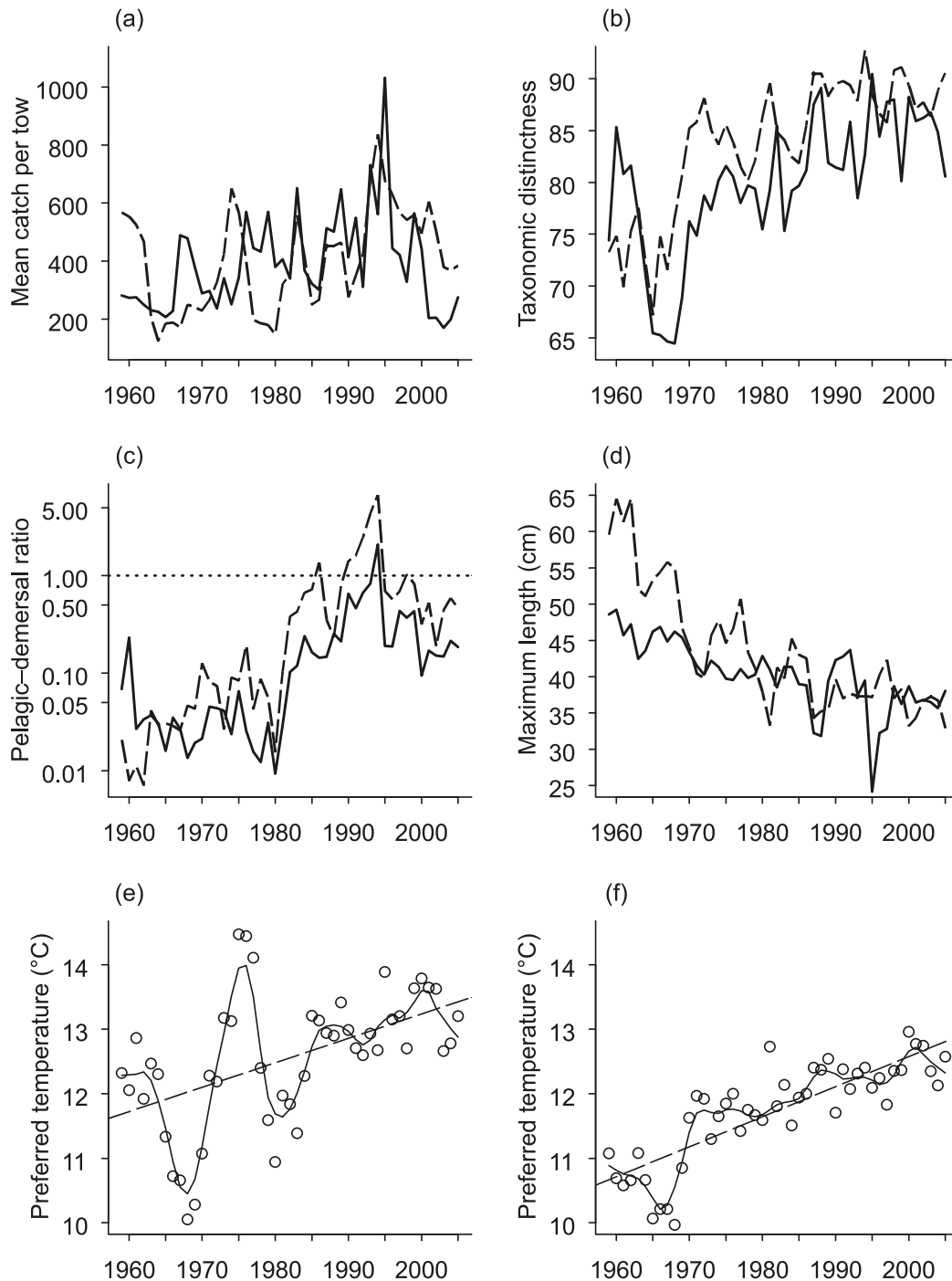
The species dissimilarity matrix had intermediate level, but nominally significant correlations with winter NAO at all lags (Table 2). Winter NAO had a generally increasing trend since the 1960s (Fig. 7c), which matches some of the trends in species abundance. Winter NAO is correlated with SST, especially winter SST (bay $\rho = 0.56$; sound $\rho = 0.50$), which may explain why both are correlated with the fish

species composition. Low and insignificant correlations were found between the species dissimilarity matrix and the Atlantic Multidecadal Oscillation (AMO). The decadal pattern of the AMO (Fig. 7c) is quasi-cyclic and does not match the temporal shift in species composition.

We also tested for correlations between community composition and sets of environmental variables (in analogy with multiple regression). However, the differing lengths of the environmental time series limited the combinations of variables we could test (Table 2). For indices with the same number of years, the rank correlations with several variables (e.g., SST, NAO, AMO) were no higher than those for a single variable (SST alone). Therefore we report only the correlation coefficients for single environmental variables in Table 2.

Univariate regressions were performed to identify how individual components of the fish and invertebrate community responded to the environmental factors (Table 3). All of the biotic variables except taxonomic distinctness and mean L_{max} were log-transformed for the linear regressions. Therefore, the magnitudes of the slopes in each column indicate the relative importance of that factor on each biotic variable.

Fig. 6. Community metrics calculated for the bay station (solid lines) and sound station (broken lines): (a) total mean catch per 30-min tow; (b) taxonomic distinctness (Δ^*); (c) pelagic–demersal ratio; (d) weighted mean maximum length, L_{\max} ; (e and f) weighted mean preferred temperature, T_{pref} , at (e) the bay station and (f) the sound station. The solid lines in (e) and (f) are lowess smoothers and the broken lines are the linear time trends.



Year

Squid abundance at both stations was positively related to annual SST and winter NAO and negatively correlated with chlorophyll concentration (Table 3). At the bay station, squid abundance was also positively related to the AMO. The abundance of pelagic fish was also positively related to SST and winter NAO at both stations. At the sound station, pelagic fish were also positively related to fishing effort and

negatively related to chlorophyll concentration. Benthic invertebrate abundance was strongly related to annual SST, especially at the bay station. Demersal fish abundance at the bay station was negatively related to the AMO and positively related to chlorophyll concentration; at the sound station, there were no significant regressions for demersal fish.

Table 2. Rank correlations between environmental variables and fish species composition.

Lag (year)	Annual SST (°C)	Spring–summer SST (°C)	Chlorophyll <i>a</i> concentration (mg·m ⁻²)	Days fished	Winter NAO	AMO
Bay Station (Fox Island)						
0	0.26	0.27	0.40	0.03	0.19	0.02
1	0.23	0.38	NA	0.04	0.18	0.01
2	0.27	0.39	NA	0.07	0.17	0.03
Sound Station (Whale Rock)						
0	0.29	0.28	0.33	0.03	0.16	0.05
1	0.28	0.33	NA	0.07	0.18	0.05
2	0.30	0.37	NA	0.09	0.15	0.02
No. of years	47	47	25	42	47	47

Note: The BIOENV procedure was used to calculate the rank correlation between the distance matrix of the environmental variables and the dissimilarity matrix of abundance data. Significance levels were determined with 999 replicates of a randomization test; bold type indicates $p < 1\%$. SST, sea surface temperature; NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation; NA, not available.

Taxonomic distinctness increased with SST (Table 3). It was also positively related to the AMO at the bay station and with winter NAO at the sound station. The pelagic–demersal ratio ($P:D$) increased with SST, winter NAO, and the number of days fished. At the sound station, the $P:D$ was also positively related to chlorophyll concentration. There was a strong negative relationship between the mean L_{\max} and annual SST. At the bay station, there was also a negative relationship between mean size and days fished. In summary, the signs of the regression coefficients were consistent between the two stations. There were consistent effects of SST on all of the biotic variables except demersal fish. Winter NAO was consistently related to the pelagic component of the community. Chlorophyll concentration was generally negatively related to the pelagic component of the community except the $P:D$ at the sound station.

Discussion

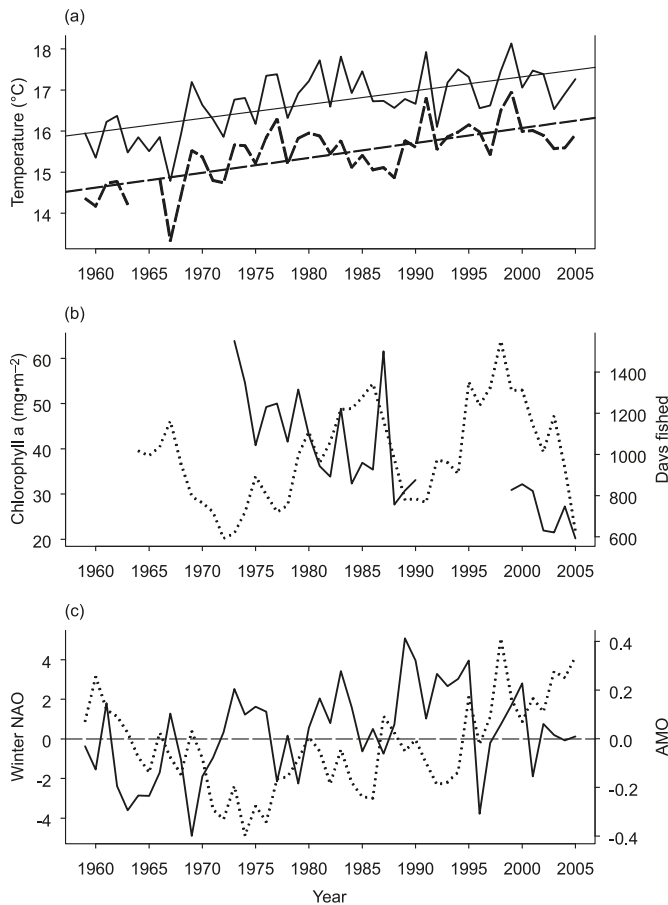
The species composition of the fish and invertebrate community in Narragansett Bay and adjacent Rhode Island Sound shifted dramatically between 1959 and 2005. A gradual transition from fish to invertebrate species was punctuated by an abrupt shift from a benthic to a pelagic regime between 1980 and 1981. Given the abruptness of this transition, it could be considered a regime shift (Collie et al. 2004). Although efforts have been made to standardize the operation of the fish trawl, the timing of species shifts could be confounded with necessary changes in fishing boats over the years. Species-specific catchability could alter in response to changing temperature or predator abundance. We believe that any potential vessel or catchability effects would be minor compared with large shifts in species composition observed. Our results are consistent with those of the Rhode Island Department of Environmental Management trawl survey, which started in 1979 and overlapped half of our time series. Though data are missing for the first two decades, demersal fish species have become less numerous, relative to pelagic species, since 1979 (Oviatt 2004). We conclude that the shift in species composition is real and not a sampling artifact.

Several of the community metrics calculated in this study capture the major shifts in species composition. Taxonomic distinctness increased at both sites as the dominant benthic fish were replaced with a mixture of fish and invertebrate species. The $P:D$ is a sensitive indicator that has been related to nutrient enrichment of inland seas (de Leiva Moreno et al. 2000). However, increases in $P:D$ have also been observed in continental-shelf communities (Fogarty and Murawski 1998; Choi et al. 2004) where anthropogenic eutrophication has not occurred. If fisheries target demersal species, the $P:D$ is expected to increase with fishing (Rochet and Trenkel 2003).

The mean L_{\max} index was also very sensitive to the shift in community structure. It can be a useful proxy for the actual mean size in the community for situations in which not every individual is measured. The decline in mean size is consistent with the prediction that fishing will shift the size composition of a community toward small species with shorter life spans (Rochet and Trenkel 2003). Fishing also truncates the age structure, reducing mean size within species and, in extreme cases, selecting for genotypes with smaller size at age (Law 2000). To the extent that fishing caused the shifts in Narragansett Bay, the observed declines in mean L_{\max} are a conservative measure of the decline in mean size. A shift toward smaller body size is also predicted as a physiological response to global warming. The increase in mean T_{pref} paralleled the increase in SST, supporting the hypothesis that southern species are replacing northern ones.

In summary, these community metrics capture the dominant patterns in the multivariate data, particularly the long-term shifts. These metrics are very useful for making comparisons with other communities, which may have similar dynamics but different species identities. For example, de Leiva Moreno et al. (2000) compared the $P:D$ among 14 semi-enclosed seas around Europe. Geographic comparisons of community metrics may help to elucidate the cause of long-term shifts in species composition. Temporal changes in the community metrics are consistent with several hypotheses, but none of them can be considered exclusive. Likewise, there is no reference or baseline level for an unimpacted community. Notwithstanding the long time series and the fact that the most rapid changes in Narragan-

Fig. 7. Environmental indices. (a) Average spring–summer sea surface temperature and corresponding linear regression lines (bay station, solid lines; sound station, broken lines). (b) Annual mean chlorophyll *a* concentration (solid line). The 1973–1990 chlorophyll data are from Li and Smayda (1998); the 1999–2005 data are from <http://www.gso.uri.edu/phytoplankton>. Nominal trawl fishing effort in Northeast Fisheries Science Center (NEFSC) statistical area 539, which includes Rhode Island Sound, at the mouth of Narragansett Bay (dotted line). Days fished were normalized by Marc Terceiro (NEFSC, 166 Water Street, Woods Hole, MA 02543, USA, personal communication, 2006) as hours fished/24. (c) Winter North Atlantic Oscillation index (NAO, solid line) from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>. Atlantic Multidecadal Oscillation (AMO, dotted line) from <http://www.cdc.noaa.gov/Timeseries/AMO>.



sett Bay have probably occurred in the period since 1960, the Bay has been continuously fished for over 100 years and numerous changes to the habitat and fauna occurred during that time (Oviatt et al. 2003). Therefore, the species that were present in the 1960s may already have constituted a “shifted baseline.”

Mounting evidence has revealed that even small increases in water temperature over extended periods of time can directly influence the species composition, distribution, and abundances of surrounding fish communities (Murawski 1993; Genner et al. 2004; Perry et al. 2005). Sea surface temperature in the English Channel and Bristol Channel, UK, increased by over 1 °C from 1905 to 2005 (Genner et al. 2004). Compositional changes resulting from SST warm-

ing were observed in both locations; various opportunistic species, already present in the community, flourished in the warmer conditions and quickly became the dominant species. Temperature-driven changes in species distributions have been observed elsewhere in the northwest Atlantic. Variations in water temperature were significant in explaining changes in mean latitude of occurrence of 12 of 36 species (Murawski 1993). Weighted mean catches of these species shifted poleward by 0.5°–0.8° latitude (55–89 km) for each 1 °C increase in water temperature. Even larger distributional shifts have been observed in the North Sea in response to a 1 °C increase in sea temperature from 1977 to 2001 (Perry et al. 2005). The average shift for 15 fish species was 1.6° latitude (172 km); 13 of these 15 shifts were poleward.

A similar mechanism may be acting in Narragansett Bay, with temperature increases influencing species distributions and resident species being replaced by opportunistic seasonal migrants. In situ SST data had the highest and most consistent correlations with species composition and abundance in both the univariate and multivariate tests. Temperature increases correlated with the increased abundance of squids, pelagic fish, benthic invertebrates, taxonomic distinctness, and the *P:D*; mean L_{\max} was negatively correlated with SST. The 1.6 °C increase in winter temperature is correlated with the decline of various species that reside in Narragansett Bay during the cold winter months (e.g., winter flounder, silver hake, and red hake). These sub-boreal species have been replaced by seasonal migrants that are more abundant during the summer months (e.g., butterfish and scup). Estuarine species with discrete subpopulations (e.g., winter flounder, tautog, cunner) may not be able to shift their distribution rapidly as temperature increases, and their decline may therefore be an early indicator of global warming.

In addition to in situ SST, there were weaker, but still significant, correlations with basin-scale climate indices. Winter NAO was positively correlated with the pelagic component of the community and the *P:D*. These correlations suggest that the shift from a benthic- to pelagic-dominated community may have been triggered by the winter NAO, which has switched to predominantly positive values since 1980 (Hurrell 1995). The NAO has previously been correlated with the abundance, growth, and migration phenology of estuarine fish (Attrill and Power 2002; Sims et al. 2004). Finally, the increase in the AMO was correlated with the decline in demersal fish at the bay station. The basin-scale indices may reflect environmental conditions in the broader region occupied by migratory species.

There were no strong correlations between species composition and fishing effort, which varied by a factor of two since 1964. The number of days fished was positively correlated with the pelagic component of the community and negatively correlated with L_{\max} at the bay station, as would be predicted from fishing effects. Admittedly, a single index of fishing effort does not permit a strong test of fishing effects. For fished species, one would expect a negative relationship between abundance and fishing effort, but that this relationship would occur with time dynamics and lags. Fishing is implicated in the decline of some of the commercially important fish species (e.g., winter flounder, tautog).

Table 3. Linear regressions of biotic variables against potential explanatory variables.

Variables	Annual SST		Winter NAO		Annual AMO		Days fished		Chlorophyll <i>a</i>	
	Slope	<i>p</i>	Slope	<i>p</i>	Slope	<i>p</i>	Slope	<i>p</i>	Slope	<i>p</i>
Bay Station (Fox Island)										
Squid	0.783	0.007	0.207	0.006	0.807	0.020			−0.044	0.006
Pelagic fish	0.921	0.004	0.246	0.004						
Benthic invertebrates	1.264	<0.001								
Demersal fish					−1.053	0.005			0.021	0.005
Taxonomic distinctness	3.507	0.032			10.355	0.030				
Pelagic–demersal ratio	0.693	0.026	0.202	0.013			0.002	0.043		
Mean L_{\max} (total length)	−3.142	0.008					−0.008	0.009		
Sound Station (Whale Rock)										
Squid	1.028	0.014	0.324	0.004					−0.062	0.007
Pelagic fish	1.322	<0.001	0.246	0.007			0.002	0.030	−0.048	0.012
Benthic invertebrates	0.662	0.002								
Demersal fish										
Taxonomic distinctness	5.678	<0.001	0.759	0.033						
Pelagic–demersal ratio	1.236	0.002	0.247	0.015			0.002	0.048	0.002	0.034
Mean L_{\max} (total length)	−9.044	<0.001								

Note: Only slopes with associated probability ($p < 0.05$) are reported. SST, sea surface temperature; NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation.

However, fishing mortality rates are not available for all of the dominant species, which makes it difficult to quantify the impacts of fishing at the community level. Some unfished species (e.g., cunner, northern searobin) have declined dramatically, whereas some of the species that have increased are now the targets of commercial fisheries (e.g., butterfish, scup, longfin squid). Although fishing may have partly triggered the shift, the fisheries also responded opportunistically to the more recent species composition.

Some of the changes in species composition can be interpreted as releases from competition or predation. The decline of several fish species that feed primarily on crustaceans (red hake, northern searobin, longhorn sculpin) and corresponding increase in *Cancer* crab and American lobster is consistent with a release from predation (Worm and Myers 2003). The increase in little skate abundance at the sound station mirrors coastwide increases in skate abundance during the same period and may be attributed to less competition or predation release (Myers et al. 2007). The reduction in silver hake, a dominant piscivore, may have contributed to the increase in forage fish species (butterfish, longfin squid). However, other piscivore species (e.g., bluefish and striped bass) increased during the same period.

A significant correlation was found between the fish species composition and chlorophyll *a* concentration in Narragansett Bay. The decline in chlorophyll *a* was correlated with increases in squid and pelagic fish and declines in demersal fish. The two-thirds decline in chlorophyll *a* is surprising given that nutrient inputs to Narragansett Bay have changed little during this period (Nixon et al. 2007). One explanation for the reduction in chlorophyll is a reduction in the magnitude of the spring bloom in response to increased water temperatures (Oviatt 2004). According to this explanation, warmer temperatures have increased zooplankton grazing rates such that more of the primary productivity is grazed in the water column, with less accumulating

and sinking to the benthos. The coincident decrease in chlorophyll *a* and increase in the *P:D* in Narragansett Bay is opposite to the positive relationship between $\log(P:D)$ and $\log(\text{Chl } a)$ observed among European semi-enclosed seas (de Leiva Moreno et al. 2000).

A shift from benthic to pelagic consumers is also evident in the feeding habits of the 25 top species. The community has shifted from fish that specialize on molluscs and crustaceans to unspecialized predators of benthic and pelagic invertebrates. Several of the benthic species that were more abundant in the 1960s (tautog, cunner, sea stars) feed primarily on mollusks, which presumably were also more abundant then. This dietary shift is consistent with a shift in production from benthic filter feeders (e.g., bivalve molluscs) to enhanced pelagic production (e.g., ctenophores). A shift in production has not yet been documented in Narragansett Bay, but it is consistent with similar benthic-to-pelagic shifts in other estuaries, especially Chesapeake Bay (Jackson et al. 2001).

In summary, there are two long-term patterns in the GSO trawl survey data. The gradual decline of demersal fish, increase in invertebrates, and decrease in mean size in the community appear to be driven primarily by increased SST and secondarily by fishing. We attribute the more rapid shift from benthic to pelagic species starting in 1980 to changes in the pelagic food web that strongly correlate with an increase in winter NAO and a reduction in chlorophyll *a* concentration. Are the observed shifts in species composition reversible? Does the more recent community structure represent an alternate stable state, or will the community structure continue to shift? Pelagic species have become less dominant since 1994, but there is little indication that the species composition is returning to that of the 1960s. If the species composition is largely driven by environmental forcing (SST, NAO) and coastal temperatures continue to increase, it is likely that the fish community will continue

to shift toward a more warm-water and pelagic community resembling those of more southern estuaries such as Delaware Bay and Chesapeake Bay.

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