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ARTICLE

Phase Shift in an Estuarine Finfish Community Associated with Warming Temperatures

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Abstract

Finfish abundance indices, produced from seasonal trawl survey data collected in Long Island Sound, were examined for changes in community composition related to the dynamics of water temperature from 1984 to 2008. In general, seasonal mean catch of species identified a priori as cold adapted significantly decreased while warm-adapted and subtropical species significantly increased over the time series. Bottom water temperature also significantly increased. As a group, annual abundance of cold-adapted species exhibited significant negative correlation with mean bottom water temperatures while warm-adapted species, but not subtropical species, exhibited significant positive correlation. Multivariate analyses identified a shift in community structure producing two primary year-groupings. Spring groupings were clearly delineated as 1984–1998 (cold period) and 1999–2008 (warm period). Autumn groupings were temporally discontinuous in the 1990s with group membership shifting between cold and warm periods, although the distal ends of the time series were clearly divided. These patterns aligned with deviations from the 1984 to 2008 mean bottom water temperature, indicating that this estuary is experiencing a relatively rapid shift consistent with a response to climate warming. The more distinct delineation of community structure in spring suggests that the lack of advantageous spring conditions was a more important factor in the decline of cold-adapted species than increasingly stressful conditions in autumn.

Climate change is a global phenomenon, but the expression of climate-driven changes to regional ecosystems are not uniform, hence different systems and their component communities experience these effects at differing rates and extent (Solomon et al. 2007). Knowledge of the rates of change in climatic factors and responses of communities and component populations within ecosystems is critical for predicting long-term trends and developing strategies for conservation and sustainable use (Nye et al. 2009; Lucey and Nye 2010; ter Hofstede et al. 2010). While responses within some ecosystems can be strong and the links to changes in climate obvious (Rosenzweig et al. 2008),

the role of climate variability versus other drivers may not be clear in all systems. This can be especially true in estuarine ecosystems where the effects of climate, expressed as changes in water temperature over time, can be confounded by migratory patterns and harvest removal, as well as the responses of individual species to normally large fluctuations in salinity and temperature for which these systems are known.

Long Island Sound (LIS) is a large semienclosed estuary in the midlatitude Virginian biogeographic region of the northwestern Atlantic Ocean (Briggs 1974; Wolfe et al. 1991). This region is a component of the larger Eastern Temperate

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biogeographic province, also known as the Boreal or Cold Temperate province (Mondor et al. 1995) which includes the continental shelf from Newfoundland to Cape Hatteras. Others have described a boundary at Cape Cod between the Eastern Temperate and the Warm Temperate or Trans-Atlantic province to the south. Some researchers have identified two subprovinces within the Warm Temperate (i.e., the Virginian, from Cape Cod to Cape Hatteras, and the Carolinian, from Cape Hatteras to Cape Canaveral) and described the Virginian subprovince as a transition zone lacking a unique fauna of its own (Coomans 1962). This level of inconsistency in describing the region's biogeography is based in part on diverse patterns and dynamics of faunal distributions and in part driven by the wide variation in environmental conditions found across the continental shelf and within the coastal regions in particular (Longhurst 1998; Cook and Auster 2007; Friedland and Hare 2007).

Like all midlatitude estuaries, LIS supports a large number of both resident and migratory finfish that are tolerant of large fluctuations in temperature, salinity, and related physical variables. Increasing abundance of warmwater and subtropical migrants into LIS and neighboring Narragansett Bay, Rhode Island, has been recently documented (Wood et al. 2009) and attributed in part to increased water temperatures. However, long-term shifts occurring across the broader finfish community have not been explored. In this study we have examined trends in the LIS finfish community based on data collected in a spatially comprehensive standardized trawl survey conducted over a 25-year time period. Trends in community composition and species abundance were compared to patterns in water temperature to determine if there were significant changes over time and

if such changes are indicative of larger-scale changes in thermal regime.

METHODS

Finfish abundance.—The Long Island Sound trawl survey has been conducted seasonally in Connecticut and New York waters from longitude 72°03'W (New London, Connecticut) to longitude 73°39'W (Greenwich, Connecticut) since 1984. The survey originally (1984–1990) included 40 sampling sites every month from April through November. However, in 1991 sampling was reduced to spring (April, May, and June) and autumn (September and October) periods while retaining the 40 site per month schedule, for a total of 200 sites annually. Although additional sampling has been conducted periodically, only samples taken in those months are included in this study. The survey employs a stratified random design, dividing the region into 1.85-km × 3.70-km (1 × 2 nautical miles) potential sampling sites (Figure 1). Each sample site is assigned to 1 of 12 strata defined by depth interval (0–9.0 m, 9.1–18.2 m, 18.3–27.3 m, 27.4 + m) and bottom type (mud, sand, transitional as defined by Reid et al. 1979). Discrete stratum areas smaller than a sample site and areas inaccessible to the trawl are excluded a priori. For each monthly sampling cruise, sites are selected randomly from within each stratum at a sampling density of 1 per 68 km² (20 mi²) with a minimum of two sites sampled per stratum. During the entire history of the survey, the sampling gear has been a 14-m chain-sweep otter trawl with a 51-mm cod end towed for 30 min at approximately 3.5 knots by a 12.9-m or 15.2-m aluminum hull research trawler during daylight hours. The entire finfish catch captured in each sample is sorted by

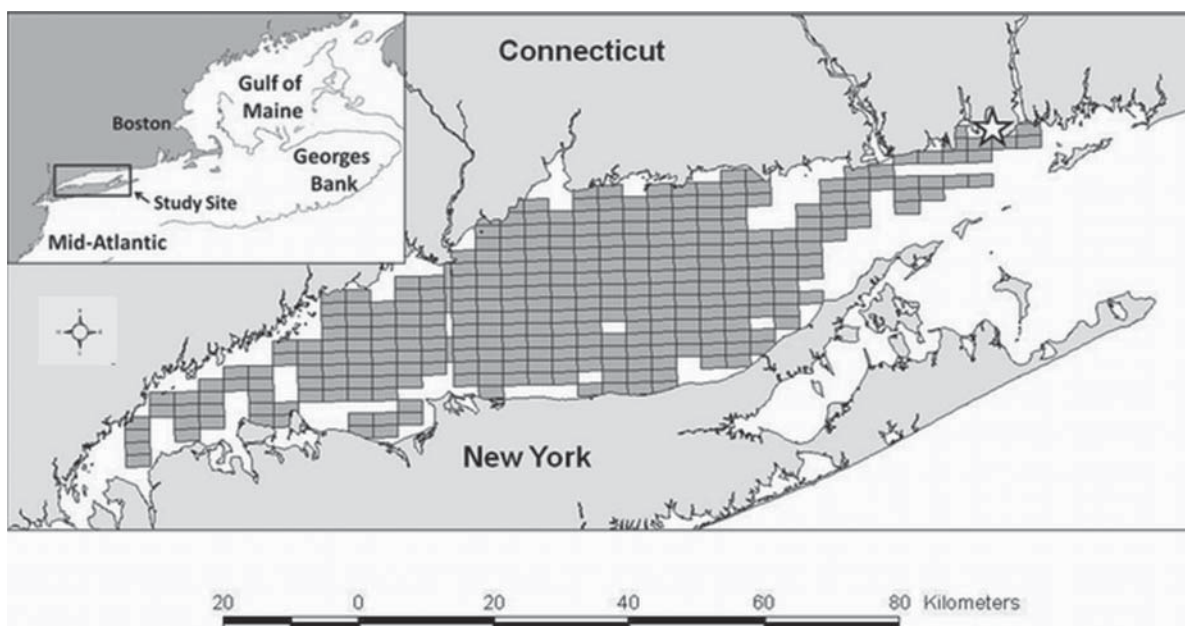


FIGURE 1. Long Island Sound Trawl Survey sampling area. Each sampling site grid in the shaded area is 1.85 km × 2.70 km. The location of Millstone Power Station (white star) is shown for reference.

species and counted. Two senior staff are responsible for species identification. Raw count per tow is log transformed ($\log_e + 1$) to normalize skewed catch frequencies typical of clustered fish distributions, and the log mean is retransformed to a geometric mean with 95% confidence intervals. Complete details of the survey methodology can be found in Gottschall et al. (2000).

To understand the effects of thermal regime on finfish community structure, we first examined the response of finfish species grouped by temperature preference. All finfish species captured in the survey were included except American sand lance *Ammodytes americanus*, bay anchovy *Anchoa mitchilli*, and striped anchovy *A. hepsetus*, which were considered substantially undersampled by the gear. All other finfish species (total $N = 95$, Appendix 1) were classified a priori as cold-adapted species (primarily distributed in cold temperate regions), warm-adapted species (primarily distributed in warm temperate regions), or subtropic-adapted species (primarily distributed in subtropical and tropical regions). These classifications were based on published life history literature (Murphy et al. 1997; Collette and Klein-MacPhee 2002; Able and Fahay 2010) describing their distribution relative to LIS, their temperature tolerance and preference range, and most importantly whether they spawn at the upper or lower end of their preferred temperature range (see full group definitions in Appendix 1). Divided by adaptation group, 33 species were classified as cold adapted, 34 were classified as warm adapted, and 28 were classified as subtropic adapted. The seasonal abundance index (\log_e mean number/tow) for each group was regressed over the 25-year time series and tested for correlation with seasonal mean water temperature using the Spearman rank test. For the subtropical group, analyses were conducted for autumn catch data only because too few species were captured in spring. Additionally, the seasonal \log_e abundance for each species captured in at least 1% of total tows ($N = 2,753$ spring tows; 1,910 autumn tows) was regressed over the 25-year time series to determine trends of individual species. Regression coefficients were adjusted for unequal sample size and autocorrelation using the SAS AUTOREG procedure (SAS 2011). To address the potential role that fisheries might play in confounding the interpretation of our results we classified the generalized harvest history of each species using the same reference materials used to classify adaptation groups above (Appendix 1). Species were classified as (1) targeted by both commercial and recreational fisheries, (2) targeted by either a commercial or a recreational fishery, (3) incidental or bycatch harvest only, or (4) no known fishery.

Changes in the finfish community were examined using multivariate statistical techniques. Annual log-transformed ($\log_e + 1$) standardized catch data for all species ($N = 95$) were analyzed to identify changes in community structure over time for each season. We computed Bray–Curtis similarity coefficients among years and then applied nonmetric multidimensional scaling (MDS), verified using hierarchical cluster analysis, to determine similarities in community composition over the years of the time series. Resultant groupings were used to assign

years as factors for an Analysis of Similarities (ANOSIM). The null hypothesis for ANOSIM is that there are no differences in species composition between different factors. The resultant global R value of this test is a measure of variation between groups compared to variation within groups, with high R values indicating greater dissimilarity (Clarke 1993). Similarity percentage routines (SIMPER) were used to identify species that contributed most to the average dissimilarity between groups. We used the PRIMER version 5 software package to produce the Bray–Curtis matrix and conduct the multivariate analyses (Clarke and Gorley 2001).

Water temperature.—Although several water temperature time series are available for LIS, the most consistent and spatially comprehensive data set is near-bottom (within 1 m) temperature readings at fixed stations recorded in the Connecticut Department of Energy and Environmental Protection Water Quality Survey. These stations span the length of LIS (Figure A.1) and temperatures have been recorded monthly since 1991. March–June (spring) and August–October (autumn) temperature data were averaged to correspond to the months that fisheries data were gathered plus one month prior. Both seasonal time series exhibited significantly increasing trends from 1991 to 2008 ($r^2 = 0.26$ – 0.27 , $P < 0.02$). In order to extend this data set backward to encompass the same 25-year time period as the fish data set, annual means were compared to spring (March–June) and autumn (August–October) mean temperatures recorded at the Millstone Power Station located in the northeastern region of LIS near its opening to the Atlantic Ocean (Figures 1, A.1). The Millstone data series is spatially limited but daily mean ambient temperature has been calculated from continuous temperature recorders at the power station's intakes (4.6–7.6 m below mean sea level; 1–2 m off bottom) since plant operations began in 1976 (DNC 2009). Regression of spring and autumn averages for the two data sets over their coinciding 18 years (1991–2008) demonstrate that both datasets have strong functional relationships ($df = 17$, spring $r^2 = 0.50$, $P < 0.001$; autumn $r^2 = 0.61$, $P < 0.001$). These relationships were used to hindcast seasonal mean values for the Sound-wide water quality survey for the years 1976–1990 (Figure 2, Appendix 2). Deviations from the 1984 to 2008 mean temperature for spring and autumn were also computed (Figure 3).

RESULTS

The overall geometric mean number per tow of the 95 finfish species, examined collectively over the 25-year time series (1984–2008), exhibited a clear seasonal shift. Mean catch in the spring significantly decreased over time while mean catch in the autumn increased (Figure 4). Species richness (mean number of species/tow) in autumn also increased linearly ($r^2 = 0.39$, $P < 0.001$) from an average of approximately 11–13 species. Spring catches showed no change in richness, averaging about 10 species per tow over the entire time series ($r^2 = -0.04$, $P = 0.99$).

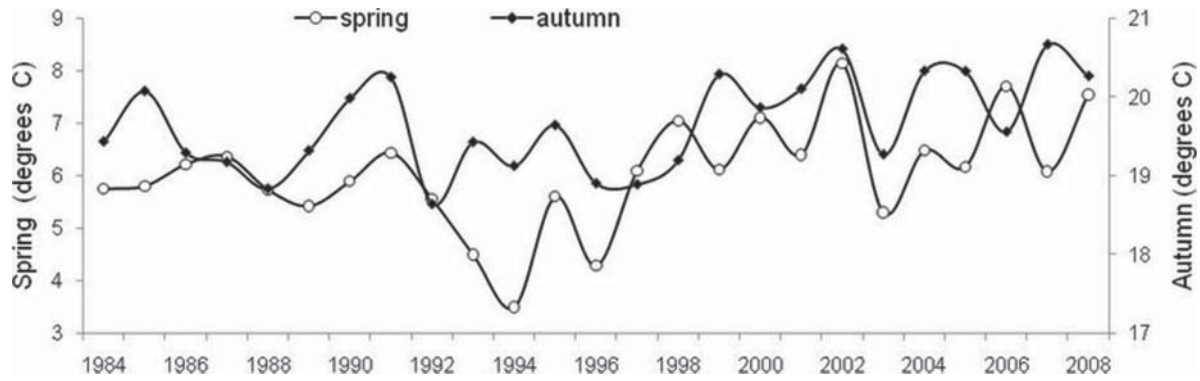


FIGURE 2. Bottom water temperature readings in Long Island Sound. Spring and autumn annual means show a significant positive slope: spring $r^2 = 0.13$, $P = 0.04$; autumn $r^2 = 0.20$, $P = 0.01$. Data are detailed in Appendix 2.

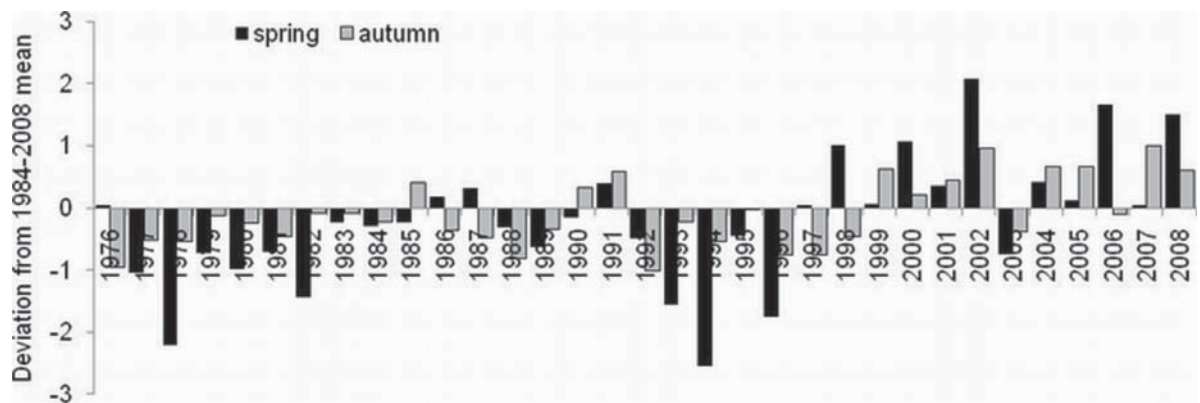


FIGURE 3. Annual deviations from the 1984 to 2008 mean bottom water temperature in spring and autumn showing a distinct positive shift after 1998.

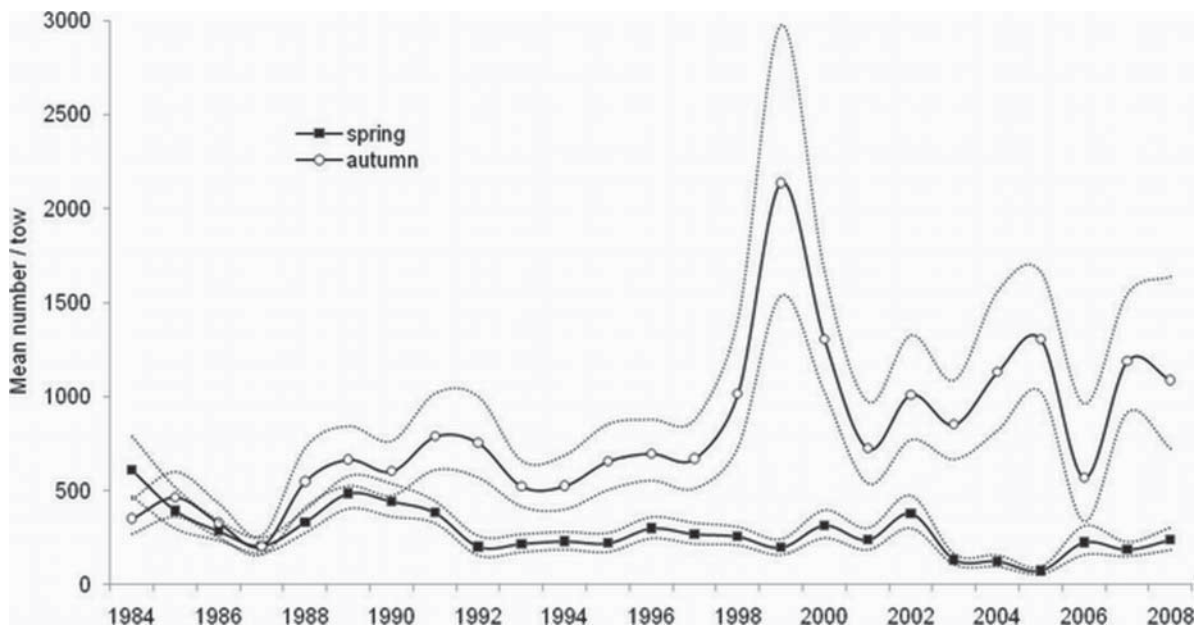


FIGURE 4. Long Island Sound Trawl Survey annual geometric mean catch of all finfish in spring and autumn, 1984–2008. Dotted lines show 95% confidence intervals. Spring catch significantly decreased ($r^2 = 0.36$, $P < 0.001$) while fall catch significantly increased ($r^2 = 0.37$, $P < 0.001$).

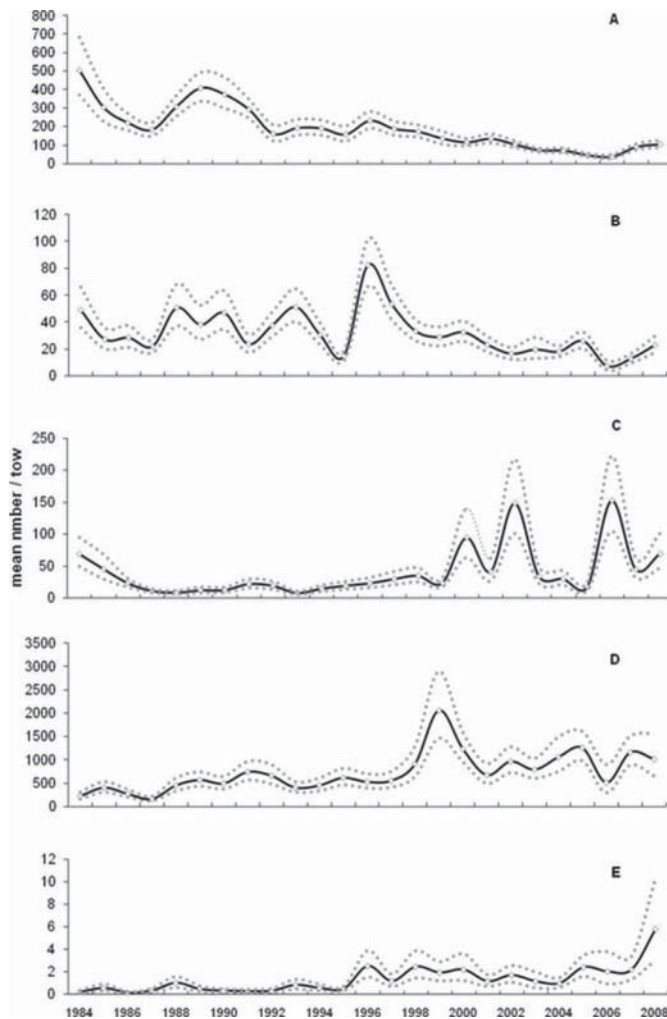


FIGURE 5. Annual abundance trends in the three adaptation groups by season. Mean catches have significant trends for cold-adapted species in (A) spring and (B) autumn, warm-adapted species in (C) spring and (D) autumn, and subtropic-adapted species in (E) autumn, shown with 95% confidence intervals (dotted lines). Regression statistics are as follows: cold-adapted species: spring $r^2 = 0.68$, $P < 0.001$, autumn $r^2 = 0.15$, $P = 0.031$; warm-adapted species: spring $r^2 = 0.15$, $P = 0.032$, autumn $r^2 = 0.39$, $P < 0.001$; subtropic-adapted species: autumn $r^2 = 0.49$, $P < 0.001$.

Collectively the abundance of cold-adapted species declined significantly over the time series in both spring and autumn (Figures 5A–B). In contrast, the abundance of warm-adapted species increased significantly in both seasons (Figures 5C–D). Subtropic-adapted species were present almost exclusively in autumn catches, and also increased significantly over the time series (Figure 5E). Species richness by adaptation group followed similar trends (Figure 6): Cold-adapted species declined significantly in spring while warm-adapted species increased significantly in spring as well as autumn. Species richness of cold- and subtropic-adapted species in autumn catches had no significant trend over the time series.

Seasonal abundance indices of the cold and warm adaptation groups showed strong rank correlation with water temperature over the entire time series (Figure 7). For the cold-adapted group, abundance was negatively correlated with water temperature in both spring and autumn. Abundance of the warm-adapted group was positively correlated to water temperature in both spring and autumn. Autumn abundance of the subtropic-adapted group showed no correlation with autumn water temperature.

The MDS and hierarchical cluster analysis of spring and autumn survey data identified a shift in community structure over time producing two primary groupings that are in phase with increasing temperatures (Figures 8A–B). Interestingly, the division of spring (cold period) surveys into groups based on year was much clearer than the results from autumn (warm period) surveys. That is, spring groupings were clearly delineated along the time series as 1984–1998 and 1999–2008 (Figure 8A). Autumn groupings were temporally discontinuous (Figure 8B), with group membership shifting back and forth from cold to warm periods in the 1990s, while the distal ends of the time series were clearly divided by group (i.e., 1980s in the cold group and 2000s in the warm). Results of ANOSIM procedures for both seasons were significant ($P < 0.10$) but only marginally so. These groupings align with a clear change in temperature. Deviations from 1984 to 2008 mean spring and autumn bottom temperatures changed in 1998 (Figure 3): prior to that year, deviations were primarily negative or slightly positive; after 1998, 9 out of the 10 spring deviations are positive as were 8 out of the 10 autumn deviations.

When the seasonal abundance of the cold- and warm-adapted groups were separated into the two time periods identified in the ANOSIM procedure (Figure 9) and plotted against bottom temperature, a shift in species abundance with temperature thresholds is evident. The abundance of the cold-adapted group was low while the abundance of the warm-adapted group was high in years with mean temperature above 6°C in spring and 19.5°C in autumn. These temperature ranges were relatively rare before 1998 but much more common afterward.

The SIMPER analyses (Tables 1, 2) identified a limited group of species that were drivers of the grouping patterns. In spring 11 warm-adapted and 10 cold-adapted species contributed to the differences in groupings; in autumn 11 warm-adapted, 7 cold-adapted, and 1 subtropical species contributed to the pattern. Eleven species (seven cold-adapted and four warm-adapted species) contributed to the pattern in both seasons. All species captured in at least 1% of the total tows ($N = 49$; 18 cold-adapted, 22 warm-adapted, and nine subtropic-adapted species) were regressed separately, resulting in 34 of the 49 showing a statistically significant increasing or decreasing trend in abundance over the time-series for one or both seasons (Appendix 1). Note that for species showing a trend in both seasons, the direction of the trend was the same. The majority of cold-adapted species (12 of 18) declined in abundance while only 4 increased. In contrast, only 4 of 22 warm-adapted species declined while 11 increased. Three of the nine subtropic-adapted species

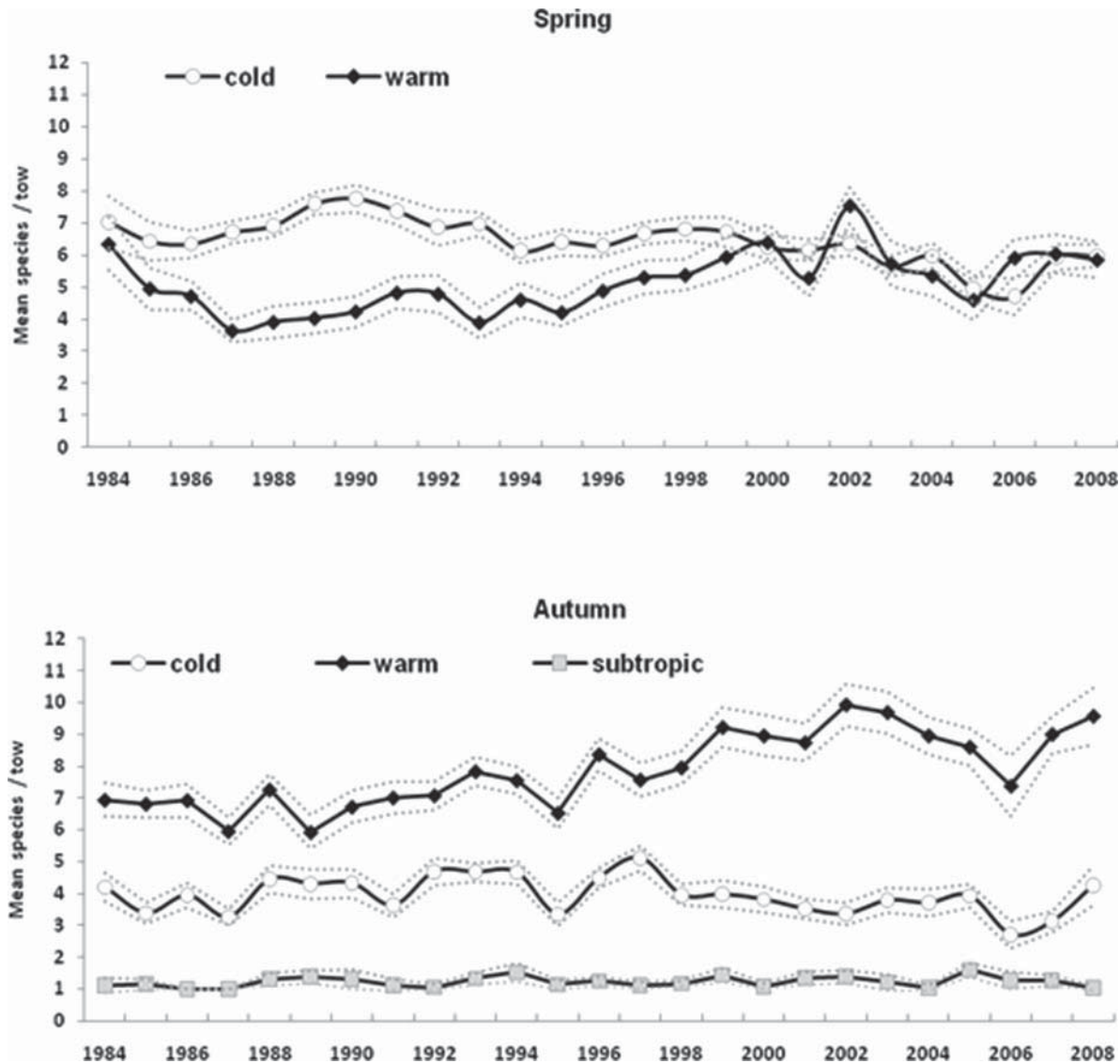


FIGURE 6. Long Island Sound Trawl Survey annual mean species richness by adaptation group and season, 1984–2008. Mean species numbers/tow have significant trends for cold-adapted and warm-adapted species in spring and warm-adapted species in autumn, shown with 95% confidence intervals (dotted lines). Regression statistics are as follows: spring cold-adapted species $r^2 = 0.47$, $P < 0.001$; spring warm-adapted species $r^2 = 0.25$, $P = 0.007$; autumn warm-adapted species $r^2 = 0.62$, $P < 0.001$; autumn cold-adapted and subtropical species, no trend, $r^2 < 0.10$, $P > 0.13$.

taken in at least 1% of samples showed a trend, all increasing in abundance.

Fisheries effects on both cold-adapted and warm-adapted groups, based on our coarse-grained harvest classification, were approximately even. Those species that were direct targets of either or both commercial and recreational fisheries (harvest classes 1 and 2) made up 58% (19 of 33) of cold-adapted species and 59% (20 of 34) of warm-adapted species examined here. Only 18% (5 of 28) of the subtropical-adapted group were in these categories. It is noteworthy that all 4 of the cold-adapted species showing an increasing trend, and 8 of 11 of the warm-adapted species exhibiting the same increasing trend, are the subject of directed fisheries. None of the subtropical-adapted

species exhibiting an increasing trend are the target of a regional fishery.

DISCUSSION

The LIS finfish community has shifted from one in which cold-adapted species dominate in spring and warm-adapted species dominate in fall, to one in which warm-adapted species are increasingly abundant in both seasons. Many of the species in the warm-adapted group have historic ranges centered off the mid-Atlantic and a northward shift of these populations into LIS is consistent with trends and forecasts at larger biogeographic scales (Murawski 1993; Nye et al. 2009; Hare et al.

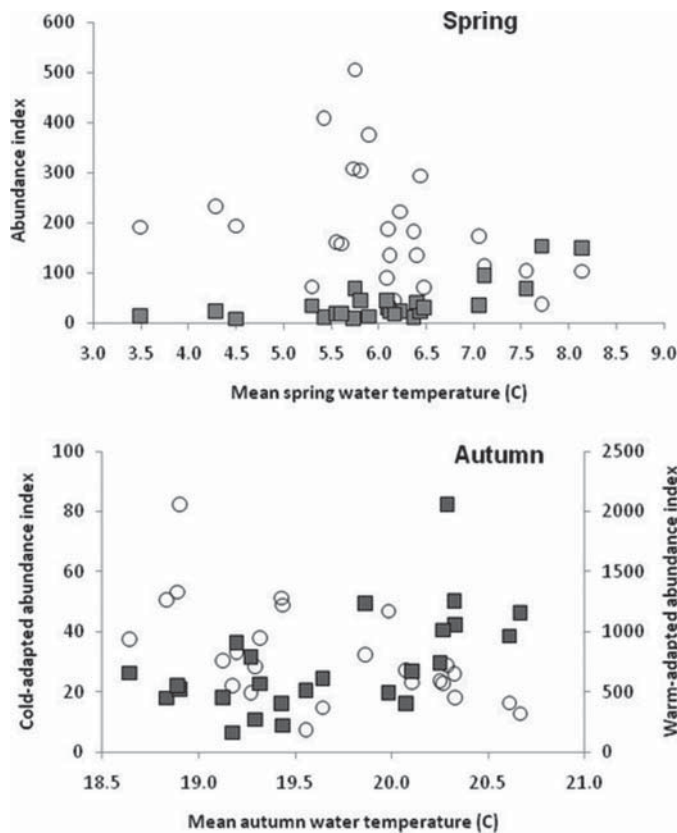


FIGURE 7. Relationship between adaptation group abundance and annual mean water temperature by season. The cold-adapted group (open circles) was negatively correlated in spring (Spearman $R = -0.48$, $P = 0.013$) and autumn ($R = -0.59$, $P = 0.002$); the warm-adapted group (shaded squares) was positively correlated in spring ($R = 0.60$, $P = 0.001$) and autumn ($R = 0.59$, $P = 0.002$). The subtropic-adapted group (not shown) showed no correlation ($R = 0.25$, $P = 0.224$).

2010; Lucey and Nye 2010). The three adaption groups appear to have responded directly to water temperature as an abiotic forcing variable but with neither total abundance nor total diversity greatly increasing or declining over the 25-year time series examined here.

Long-term water temperature data confirms that LIS is experiencing a warming trend comparable to that documented in neighboring estuaries and the western Atlantic Shelf off the northeastern United States (Oviatt et al. 2003; Nixon et al. 2004; Oviatt 2004; Friedland and Hare 2007; Collie et al. 2008; Taylor et al. 2009; Smith et al. 2010). Historic sea surface temperature data recorded from 1875 to 2007 show a significant warming trend along the U.S. coast north of Cape Hatteras that exceeds local atmospheric temperature increases and is comparable to the warming rates of the Arctic and Labrador (Shearman and Lentz 2010). These authors conclude that the regional coherence of this warming trend points to the along-shelf transport of water from Labrador to the Middle Atlantic Bight as the mechanism controlling coastal ocean warming north of Hatteras. Therefore,

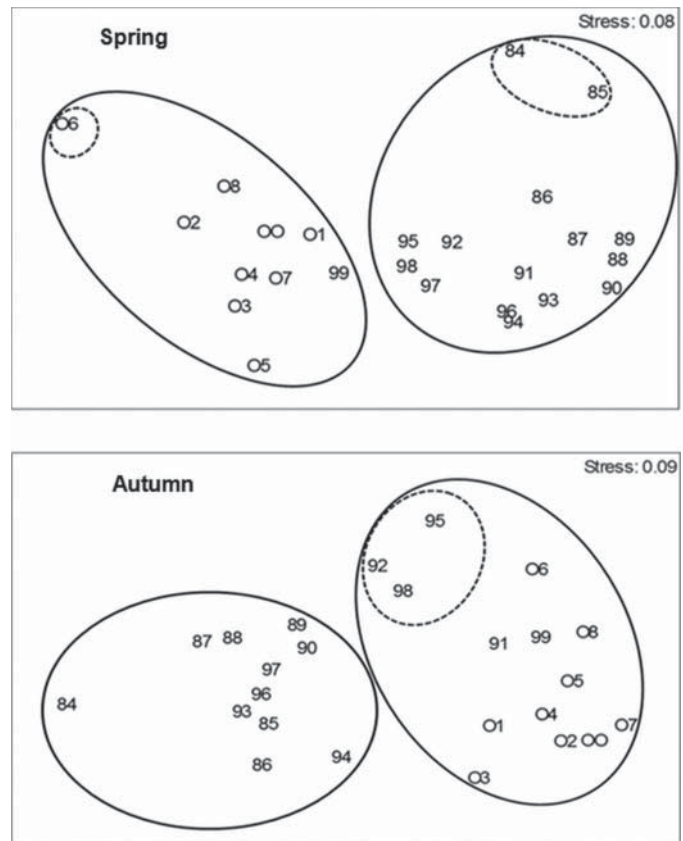


FIGURE 8. Results of spring and autumn MDS analyses based on 10 restarts. Major groupings (solid lines) were assigned from results of hierarchical clustering and assigned as factors for subsequent ANOSIM procedures. Subsets of years (dotted lines) indicate minor groupings at higher levels of similarity.

it should be expected that the warming trend along the northeastern U.S. coast will continue.

Species showing the greatest dissimilarity coefficients in our SIMPER analysis are known to have considerable sensitivity to temperature. Scup *Stenotomus chrysops*, which had among the greatest dissimilarity coefficients, avoid temperatures below 7°C (Fritz 1965) and have a history of large die-offs during sudden cold spells in shallow water (Collette and Klein-MacPhee 2002). Since spring temperatures above 6°C have become more common in LIS, this species is no longer excluded from the area due to unfavorable temperatures. Winter flounder *Pseudopleuronectes americanus* also showed large dissimilarity coefficients and are equally sensitive to increasing temperatures. Lethality at temperatures as low as 19.3°C have been reported (Collette and Klein-MacPhee 2002) with larger fish showing a lower temperature tolerance than smaller fish (McCracken 1963). The specialized blood proteins which protect this species from freezing (Duman and DeVries 1976) have diminishing competitive value in warming waters. The importance of subtle temperature shifts in determining spawning success can be seen by contrasting the temperature tolerances of windowpane *Scophthalmus aquosus* and butterfish *Peprilus triacanthus*, two other species

TABLE 1. Similarity percentage routines analysis of spring trawl survey annual mean abundances of species contributing more than 1% to annual spring dissimilarity. Total mean dissimilarity was 29.39. Species adaptation group (C = cold adapted; W = warm adapted; S = subtropic adapted) is listed with the common name. Species scientific names and group definitions are listed in Appendix 1.

Species	Group	Average abundance		Dissimilarity		Percent contribution	Cumulative percent
		1984–1998	1999–2008	Mean	SD		
Scup	W	2.88	19.37	3.88	1.92	13.22	13.22
Butterfish	W	2.60	4.96	2.20	1.47	7.50	20.71
Windowpane	C	53.52	7.87	2.20	1.52	7.47	28.19
Spotted hake	C	0.11	1.52	1.90	3.48	6.47	34.66
Silver hake	C	3.37	5.72	1.75	1.22	5.97	40.62
Summer flounder	W	0.68	1.90	1.71	2.04	5.82	46.44
Little skate	C	12.57	5.04	1.31	1.25	4.45	50.90
Striped searobin	W	1.05	1.82	1.27	1.68	4.33	55.23
Winter flounder	C	84.89	24.39	1.24	1.04	4.21	59.44
Alewife	C	0.87	1.31	1.22	1.58	4.15	63.59
Striped bass	W	0.29	0.87	1.19	1.75	4.03	67.62
Atlantic herring	C	2.80	0.86	1.12	1.32	3.81	71.43
Red hake	C	5.16	3.11	1.03	1.38	3.51	74.95
Northern searobin	W	2.32	1.35	0.89	1.35	3.02	77.97
Smooth dogfish	W	0.41	0.73	0.84	2.30	2.87	80.84
Fourspot flounder	C	6.27	3.14	0.80	1.54	2.72	83.56
Blueback herring	W	0.55	0.24	0.48	1.14	1.65	85.21
Tautog	W	0.88	0.58	0.46	1.43	1.55	86.76
Fourbeard rockling	C	0.72	0.40	0.40	1.49	1.37	88.13
American shad	W	0.65	0.40	0.39	1.38	1.34	89.47
Black seabass	W	0.10	0.23	0.37	1.67	1.26	90.73

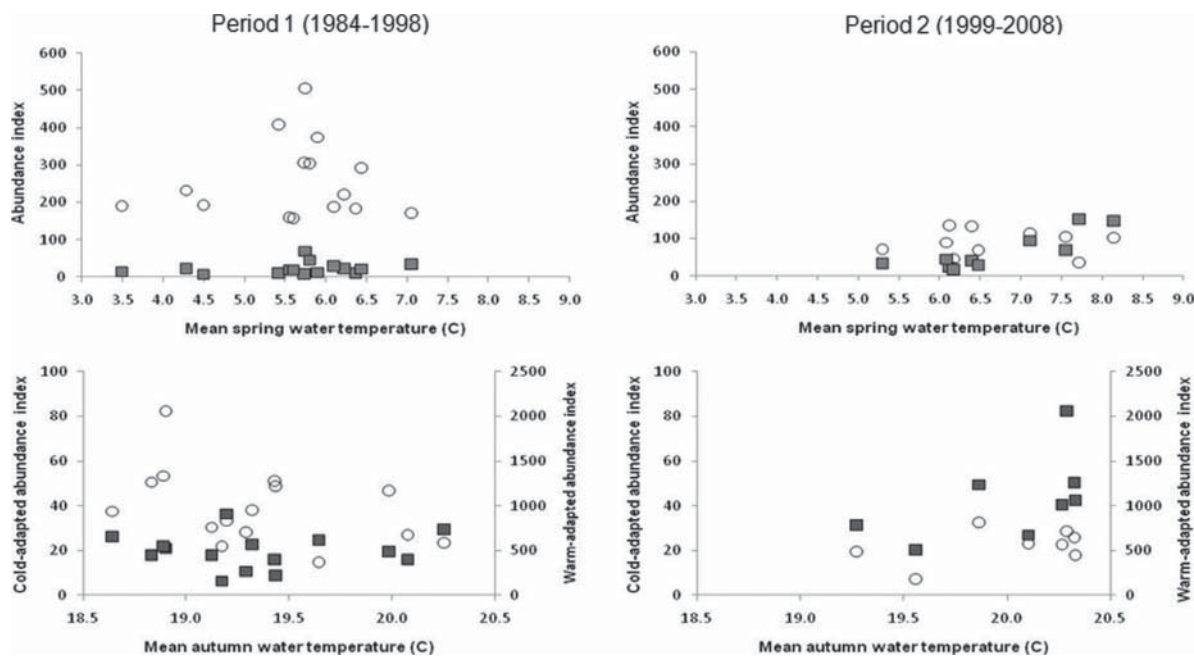


FIGURE 9. Annual abundance of the cold-adapted (open circles) and warm-adapted (shaded squares) groups versus mean bottom temperature during the two time periods identified in the MDS analyses in spring and autumn.

TABLE 2. Similarity percentage routines analysis of autumn trawl survey annual mean abundances of species contributing more than 1% to annual autumn dissimilarity. Total mean dissimilarity was 26.57. Species adaptation group (C = cold adapted; W = warm adapted; S = subtropic adapted) is listed with the common name. Species scientific names and group definitions are listed in Appendix 1.

Species	Group	Average abundance		Dissimilarity		Percent contribution	Cumulative percent
		1984–1998	1999–2008	Mean	SD		
Windowpane	C	11.88	3.75	3.60	2.46	13.55	13.55
Winter flounder	C	8.30	3.80	2.92	2.76	11.00	24.55
Scup	W	48.42	278.99	2.48	1.84	9.33	33.88
Weakfish	W	7.63	29.44	2.23	1.54	8.40	42.28
Little skate	C	6.32	4.02	2.21	2.55	8.33	50.60
Bluefish	W	22.34	25.75	1.91	1.76	7.20	57.80
Butterfish	W	116.59	215.83	1.33	1.60	4.99	62.79
Striped searobin	W	2.86	3.47	1.06	1.52	4.00	66.79
American shad	W	1.31	0.78	0.89	1.04	3.36	70.15
Fourspot flounder	C	1.39	1.05	0.78	1.82	2.95	73.09
Smooth dogfish	W	1.03	1.45	0.77	1.12	2.88	75.97
Summer flounder	W	1.28	2.41	0.76	1.50	2.85	78.82
Silver hake	C	0.79	0.21	0.69	0.94	2.59	81.41
Red hake	C	0.88	0.48	0.68	1.72	2.56	83.98
Moonfish	S	0.40	1.39	0.49	1.11	1.83	85.81
Spotted hake	C	0.44	0.57	0.37	0.99	1.40	87.21
Blueback herring	W	0.32	0.12	0.31	1.20	1.15	88.36
Hogchoker	W	0.27	0.16	0.33	0.85	1.14	89.51
Atlantic menhaden	W	0.45	0.86	0.29	1.05	1.08	90.59

that also had large dissimilarity coefficients. Catch distributions in the New York Bight have shown that windowpane can tolerate a wide range of water temperatures, however this species displayed continuous spawning activity only during colder summers (Wilk et al. 1990), as they cease to spawn at temperatures above 15°C (Collette and Klein-MacPhee 2002). In contrast, the temperature tolerance range of butterfish is 4–22°C, but spawning appears to be quite limited in waters below 15°C (Colton 1972). Shifts in water temperature of only a single degree can therefore change not only the distribution of these species but also the prospects of successful spawning. Although water temperature appears to have exerted a straightforward effect on the finfish community when grouped by affiliation to thermal regime, it is probable that there are multiple physical, behavioral, and physiological factors working in concert with temperature to produce the changes we have observed in individual species. These include physiological and energetic responses to variation in dissolved oxygen levels which are exacerbated by rising temperature, temperature driven changes in species interactions including predator–prey relationships, the role of environmental stress in the transmission of diseases, direct and indirect effects of change in land use practices, and the synergies of these responses that result in variation in reproductive success and somatic growth of component species. The subtle effects of these secondary factors can dictate the ultimate composition

of the local finfish community and possibly obscure the more direct effects of temperature.

Rising temperatures may have caused cold-adapted species to experience energy losses while also making them more readily available prey to warm-adapted predator species. Guderley and Pörtner (2010) argue that higher water temperatures increase metabolic demand in cold-adapted species such as Atlantic cod *Gadus morhua*, as well as reduce prey abundance or quality, all of which increase foraging time and exposure to predators. Even if only young age-groups are affected, the resulting lack of growth or increased mortality could depress an entire population (Biro et al. 2003). This sequence supports the hypothesis of a competitive feed-back mechanism, where initial modest declines due to metabolic stress or increased foraging activity in the most vulnerable size-classes in cold-adapted species allowed initial modest increases in the warm-adapted group, thereby increasing losses in the cold-adapted group and creating a self-accelerating cascade favoring the warm-adapted group over the cold. Such a scenario of replacement would explain why the MDS analysis of spring data showed a more distinct temporal grouping compared with the more variable pattern seen in the autumn data when temperatures were highest. The disadvantage (or lack of previous advantage) for cold-adapted species would be most pronounced in spring rather than autumn when these species have always experienced stressful conditions. These

results suggest that the absence of advantageous temperatures could be a greater controlling factor than the presence of stressful temperatures.

Individual trajectories for single species varied, with a few species showing trends contradictory to their adaptation group. Some of this variance can be explained by the biology of these species, each responding with varying sensitivity to environmental conditions. For example, four of the eight species showing trends contradictory to their adaptation group are either anadromous (alewife *Alosa pseudoharengus*, American shad *Alosa sapidissima*, Atlantic sturgeon *Acipenser oxyrinchus*) or, in the case of the hogchoker *Trinectes maculatus*, are highly euryhaline brackish species (Collette and Klein-MacPhee 2002), and their abundance patterns may be as much a reflection of conditions in adjacent freshwater rivers as conditions in LIS.

Harvest practices also undoubtedly affect the abundance of heavily exploited species to some extent, although harvest for human consumption is only part of the predator field that all species are subjected to. In general, trends in abundance for the species examined here do not track their harvest history as closely as they appear to align with predictions based on their adaptation group. However, changes in the natural predator field may exert as great or greater effects than changes in thermal regime. For example, spiny dogfish *Squalus acanthias* and winter skate *Leucoraja ocellata* are cold-adapted elasmobranchs that are increasing in abundance. While such patterns could reflect population changes due to modification in harvest regimes, shifting interactions between competitors could have resulted in opportunistic population increases for these dominant species (Link and Auster, in press) in spite of a suboptimal temperature regime. Ecological drivers, including predator-prey and competitor interactions, while not the sole determinant of community composition, could have exerted a far greater effect than harvest removals. These results are consistent with an examination of the distributions of both harvested and non-harvested North Sea fishes (Perry et al. 2005) which have responded markedly to recent increases in sea temperature, with nearly two-thirds of species shifting in mean latitude or depth or both over 25 years. The changes in species abundance reported here are also similar to the changes in the spatial distribution reported by Nye et al. (2009) for outer continental shelf fish populations in the northwestern Atlantic Ocean, where changes related to long-term warming due to the Atlantic multidecadal oscillation were evident for species representing many families, habitat preferences, and fishing histories.

Wood et al. (2009) found that species with warmwater affinities increased in abundance over time (1987–2000) in both LIS and adjacent Narragansett Bay, Rhode Island. These authors found that temperature between the two study areas was highly correlated; however, the fish faunas were significantly different. These results suggest that while geographically similar sites may experience similar regional-scale effects of climate change, responses in areas with distinct ecological milieus can

vary considerably and are therefore difficult to predict on a species-specific level. As a consequence, an adaptation group may exhibit a coherent and predictable response, but the species-specific composition of the group may vary considerably. This same type of response has been observed in trophic guild structure of shelf fishes off the northeastern USA, where five of seven guilds remained stable over four decades but composition within guilds varied considerably (Auster and Link 2009). The concept of thermal guilds may be a useful paradigm to aid in addressing the uncertainties in predicting the effects of climate variability in estuarine finfish communities.

Time series trends from survey data reveal a finfish community that is making a quick transition from a cold tolerant winter–spring community coupled with a warm tolerant summer–autumn community to a single community adapting to increasing water temperatures. Both population and community level trends are consistent with a response to climate warming. Continued high species diversity indicates that this community shift has not diminished the ecological health of the estuary. However, that such change can be identified in a temperate estuarine fish community, which is nominally adapted to a thermally dynamic environment, is indicative of the kinds of changes that environmental managers will need to understand to conserve these communities while allowing for continued sustainable use of their biological diversity.

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APPENDIX 1: ADAPTATION GROUPINGS OF SPECIES CAPTURED IN THE LONG ISLAND SOUND TRAWL SURVEY AND TRENDS IN ANNUAL ABUNDANCE INDICES

The temperature adaptation groups used to classify the finfish species captured in the survey are defined as indicated below; the trends in the annual abundance indices are given in Table A.1.1.

- Adapted to cold temperate waters (cold-adapted species):
 - more abundant north of Cape Cod, Massachusetts, than south of New York
 - behaviorally adapted to cold temperatures, including subfreezing ones

- preferred temperature range approximately 3–15°C
 - spawns at lower end of temperature tolerance
2. Adapted to warm temperate waters (warm-adapted species):
- more abundant south of New York than north of Cape Cod, Massachusetts
 - behaviorally avoids temperatures <7–10°C
 - preferred temperature range approximately 11–22°C
 - spawns at higher end of temperature tolerance
3. Adapted to subtropical or tropical waters (subtropic-adapted species):
- rare north of Chesapeake Bay and occasional or rare in the mid-Atlantic
 - strays captured north of mid-Atlantic are usually juveniles
 - generally not tolerant of temperatures <10°C
 - spawns only south of New York Bight

TABLE A.1.1. Direction of significant trends (decreasing [–], increasing [+], or no trend [nt]) in the annual abundance indices for the 49 species taken in at least 1% of all samples, spring and autumn 1984–2008; $P < 0.10^*$, $P < 0.05^{**}$, $P < 0.01^{***}$. The extent of coastwide harvest activity was classified into four categories: 1 = targeted by commercial and sport fisheries, 2 = targeted by either a commercial or sport fishery, 3 = incidental or by-caught harvest only, and 4 = no known fishery in the western Atlantic Ocean.

Species	Spring trend	Autumn trend	Harvest class
Cold adaptation group			
Alewife <i>Alosa pseudoharengus</i>	+ ***	+ **	2
American plaice <i>Hippoglossoides platessoides</i>			2
Atlantic herring <i>Clupea harengus</i>	nt	nt	1
Atlantic cod <i>Gadus morhua</i>			1
Atlantic mackerel <i>Scomber scombrus</i>	– ***	nt	2
Atlantic salmon <i>Salmo salar</i>			3
Atlantic seasnail <i>Liparis atlanticus</i>			4
Atlantic sturgeon <i>Acipenser oxyrinchus</i>	nt	+ **	2
Atlantic tomcod <i>Microgadus tomcod</i>			3
Barndoor skate <i>Dipturus laevis</i>			2
Cunner <i>Tautoglabrus adspersus</i>	– ***		2
Fawn cusk-eel <i>Lepophidium profundorum</i>			4
Fourbeard rockling <i>Enchelyopus cimbrius</i>	– **	– *	4
Fourspot flounder <i>Paralichthys oblongus</i>	– **	nt	3
Grubby <i>Myoxocephalus aeneus</i>			4
Haddock <i>Melanogrammus aeglefinus</i>			1
Little skate <i>Leucoraja erinacea</i>	– ***	nt	2
Longhorn sculpin <i>Myoxocephalus octodecemspinosus</i>	– ***	nt	3
Lumpfish <i>Cyclopterus lumpus</i>			3
Monkfish (also known as goosfish) <i>Lophius americanus</i>	– **	nt	2
Northern pipefish <i>Syngnathus fuscus</i>			4
Ocean pout <i>Zoarces americanus</i>	– **	nt	3
Pollock <i>Pollachius virens</i>			2
Rainbow smelt <i>Osmerus mordax</i>			2
Red hake <i>Urophycis chuss</i>	– *	nt	2
Rock gunnel <i>Pholis gunnellus</i>			4
Sea raven <i>Hemitripterus americanus</i>	– ***	nt	3
Spiny dogfish <i>Squalus acanthias</i>	nt	+ **	2
Silver hake (also known as whiting) <i>Merluccius bilinearis</i>	nt	nt	2
Windowpane <i>Scophthalmus aquosus</i>	– ***	– **	3
Winter flounder <i>Pseudopleuronectes americanus</i>	– ***	– ***	1
Winter skate <i>Leucoraja ocellata</i>	nt	+ **	2
Yellowtail flounder <i>Limanda ferruginea</i>			1

TABLE A.1.1. Continued.

Species	Spring trend	Autumn trend	Harvest class
Warm adaptation group			
American eel <i>Anguilla rostrata</i>			1
American shad <i>Alosa sapidissima</i>	— **		1
Atlantic bonito <i>Sarda sarda</i>			2
Atlantic croaker <i>Micropogonias undulates</i>			1
Atlantic menhaden <i>Brevoortia tyrannus</i>	— ***	nt	1
Atlantic silversides <i>Menidia menidia</i>			4
Black sea bass <i>Centropristis striata</i>	nt	+ ***	1
Blueback herring <i>Alosa aestivalis</i>	nt	nt	1
Bluefish <i>Pomatomus saltatrix</i>	nt	nt	1
Butterfish <i>Peprilus triacanthus</i>	nt	nt	2
Clearnose skate <i>Raja eglanteria</i>	nt	+ ***	2
Conger eel <i>Conger oceanicus</i>			3
Gizzard shad <i>Dorosoma cepedianum</i>			3
Hickory shad <i>Alosa mediocris</i>	nt	+ ***	2
Hogchoker <i>Trinectes maculatus</i>	— *	— **	4
Lined seahorse <i>Hippocampus erectus</i>			4
Naked goby <i>Gobiosoma bosc</i>			4
Northern kingfish <i>Menticirrhus saxatilis</i>	nt	nt	3
Northern puffer <i>Sphoeroides maculatus</i>	nt	nt	3
Northern searobin <i>Prionotus carolinus</i>	nt	+ ***	3
Oyster toadfish <i>Opsanus tau</i>			4
Scup (also known as porgy) <i>Stenotomus chrysops</i>	nt	+ ***	1
Sea lamprey <i>Petromyzon marinus</i>			4
Smallmouth flounder <i>Etropus microstomus</i>	+ ***	+ ***	4
Smooth dogfish <i>Mustelus canis</i>	+ ***	nt	2
Spot <i>Leiostomus xanthurus</i>	nt	nt	1
Spotted hake <i>Urophycis regia</i>	+ ***	nt	2
Striped bass <i>Morone saxatilis</i>	+ ***	+ ***	1
Striped cusk-eel <i>Ophidion marginatum</i>			4
Striped searobin <i>Prionotus evolans</i>	nt	nt	3
Summer flounder <i>Paralichthys dentatus</i>	+ ***	+ ***	1
Tautog (also known as blackfish) <i>Tautoga onitis</i>	— ***	nt	1
White perch <i>Morone americana</i>			1
Weakfish <i>Cynoscion regalis</i>	nt	+ ***	1
Subtropic adaptation group			
African pompano <i>Alectis ciliaris</i>			2
Atlantic moonfish <i>Selene setapinnis</i>		+ ***	4
Banded rudderfish <i>Seriola zonata</i>			3
Bigeye scad <i>Selar crumenophthalmus</i>		nt	3
Bigeye <i>Priacanthus arenatus</i>			4
Blue runner <i>Caranx crysos</i>			2
Crevalle jack <i>Caranx hippos</i>		nt	2
Dwarf goatfish <i>Upeneus parvus</i>			4
Glasseye snapper <i>Heteropriacanthus cruentatus</i>			4
Grey triggerfish <i>Balistes capriscus</i>			3
Inshore lizardfish <i>Synodus foetens</i>		+ ***	3
Lookdown <i>Selene vomer</i>			3
Mackerel scad <i>Decapterus macarellus</i>			4

TABLE A.1.1. Continued.

Species	Spring trend	Autumn trend	Harvest class
Northern sennet <i>Sphyraena borealis</i>			3
Orange filefish <i>Aluterus schoepfii</i>			3
Planehead filefish <i>Stephanolepis hispidus</i>		nt	4
Red cornetfish <i>Fistularia petimba</i>			4
Red goatfish <i>Mullus auratus</i>			4
Rough scad <i>Trachurus lathami</i>		nt	4
Roughtail stringray <i>Dasyatis centroura</i>			3
Round herring <i>Etrumeus teres</i>			4
Round scad <i>Decapterus punctatus</i>		+ ***	4
Sandbar shark <i>Carcharhinus plumbeus</i>			1
Spanish mackerel <i>Scomberomorus maculatus</i>		nt	1
Sharksucker <i>Echeneis naucratus</i>			4
Short bigeye <i>Pristigenys alta</i>			4
Striped burrfish <i>Chilomycterus schoepfii</i>			4
Yellow jack <i>Caranx bartholomaei</i>		nt	3

APPENDIX 2: LONG ISLAND SOUND BOTTOM WATER TEMPERATURE DATA

Table A.2.1. Mean temperatures (°C; SDs in parentheses) recorded at Millstone Power Station and Connecticut Water Quality (WQ) Survey stations in spring (March–June) and autumn (August–October) (see Figure A.2.1). The regression relationship for the seasonal data taken in 1991–2008 was used to estimate Long Island Sound–wide WQ values for 1976–1990. Millstone data were provided courtesy of Dominion Nuclear Connecticut (DNC 2009; D. Landers, Millstone Power Station, personal communication).

Year	Spring		Autumn	
	Millstone	WQ	Millstone	WQ
1976	9.56 (4.0)	6.10	17.86 (2.4)	18.71
1977	8.54 (5.0)	5.00	18.44 (2.3)	19.14
1978	7.47 (4.9)	3.84	18.40 (1.8)	19.11
1979	8.84 (4.8)	5.32	18.98 (2.5)	19.54
1980	8.60 (4.7)	5.06	18.82 (2.2)	19.42
1981	8.86 (4.8)	5.34	18.52 (2.9)	19.19
1982	8.17 (4.5)	4.60	19.02 (2.6)	19.56
1983	9.29 (4.1)	5.81	19.04 (1.8)	19.58
1984	9.23 (4.6)	5.75	18.84 (1.9)	19.43
1985	9.28 (4.2)	5.80	19.71 (1.9)	20.07
1986	9.67 (4.6)	6.22	18.65 (1.9)	19.29
1987	9.80 (4.4)	6.37	18.49 (2.3)	19.17
1988	9.22 (4.1)	5.73	18.03 (2.6)	18.83
1989	8.93 (4.6)	5.42	18.69 (2.2)	19.32
1990	9.37 (4.0)	5.89	19.59 (1.7)	19.98
1991	10.65 (4.4)	6.44 (3.1)	19.19 (1.7)	20.25 (1.2)
1992	9.34 (4.3)	5.55 (2.1)	18.00 (2.2)	18.64 (1.4)
1993	9.06 (5.0)	4.50 (3.0)	18.70 (2.7)	19.43 (1.7)
1994	8.69 (4.8)	3.49 (3.8)	18.77 (2.0)	19.12 (1.6)
1995	9.81 (4.0)	5.60 (3.4)	19.94 (1.4)	19.64 (1.6)
1996	8.00 (4.6)	4.28 (4.0)	17.88 (2.0)	18.90 (1.2)
1997	8.43 (3.8)	6.09 (3.2)	18.12 (1.9)	18.89 (1.6)
1998	9.88 (4.1)	7.05 (2.7)	19.20 (2.2)	19.20 (1.6)

TABLE A.2.1. Continued.

Year	Spring		Autumn	
	Millstone	WQ	Millstone	WQ
1999	10.74 (4.7)	6.12 (3.1)	19.97 (2.1)	20.29 (1.3)
2000	10.11 (4.5)	7.11 (4.1)	19.53 (2.0)	19.86 (1.0)
2001	9.81 (4.8)	6.40 (4.5)	19.64 (2.2)	20.10 (1.2)
2002	10.42 (4.0)	8.14 (3.6)	19.96 (2.3)	20.61 (0.7)
2003	8.51 (5.1)	5.30 (4.9)	19.59 (2.1)	19.27 (0.9)
2004	9.68 (5.2)	6.48 (5.2)	19.31 (2.2)	20.33 (1.0)
2005	8.97 (5.1)	6.17 (4.8)	19.66 (2.2)	20.33 (1.1)
2006	10.37 (4.1)	7.71 (5.0)	19.67 (2.1)	19.56 (1.6)
2007	9.47 (4.9)	6.08 (4.9)	20.03 (1.4)	20.67 (0.7)
2008	10.35 (4.3)	7.55 (4.2)	19.54 (2.0)	20.27 (1.3)

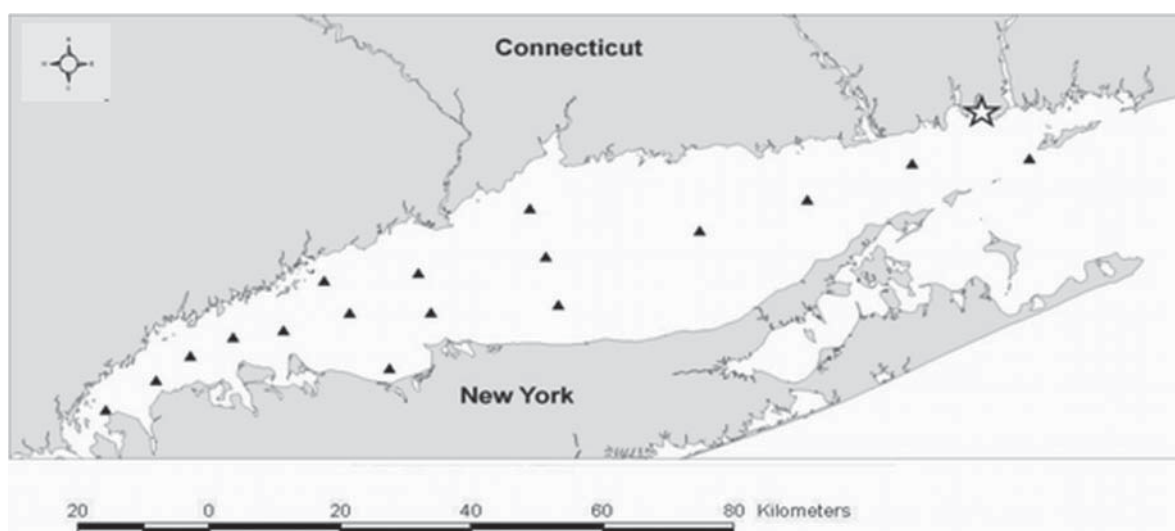


FIGURE A.2.1. Long Island Sound Water Quality Survey sampling stations. Bottom water temperature data were also gathered at Millstone Power Station, indicated by the white star.