**Title:** Spatiotemporal dynamics of nearshore fish communities in Casco Bay, Maine

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**Abstract**

Nearshore regions in the Gulf of Maine facilitate the growth, reproduction, and migration of many fish species, but rapidly increasing temperatures may be impacting these ecosystems. We used 11 years of summer beach seine survey data to explore temperature-linked effects to nearshore fish growth rates, relative abundances, and overall community composition. Atlantic silversides (*Menidia* *menidia*) and Atlantic herring (*Clupea* *harengus*) were used as focal species to identify effects on warm-tolerant and warm-intolerant species, respectively. Growth models based on weekly length-frequency relationships revealed that age-0 silversides grew 2.6-6.2 mm per week, with significantly higher growth occuring in years with anomalously warm surface temperatures. Age-0 herring grew 1.2-5.0 mm per week, with no clear link to temperature. Generalized additive models highlighted strong seasonal patterns of nearshore habitat use by both species. Silverside catch per unit effort (CPUE) was highest in August-September, but elevated CPUE in July could occur if surface temperatures exceeded 18°C. Herring CPUE was positively associated with temperatures between 15-19°C, but consistently declined after mid-July regardless of temperature. We identified patterns of nearshore community composition through nonmetric multidimensional scaling and k-means clustering analyses. Community composition regularly progressed from herring-dominated in the early summer to silverside-dominated in the late summer. At an annual scale, only years with anomalously cold summers had herring-dominated communities. Temperature-mediated changes to the productivity and phenology of the nearshore fish community will likely have far-reaching ecosystem impacts. Nearshore fish dynamics should be monitored to identify potential changes to Gulf of Maine community and trophic ecology.

**Keywords:** distribution, phenology, Gulf of Maine, nearshore, community composition**1 Introduction**

Nearshore regions of the ocean, via a unique combination of tidal mixing, freshwater input, shallow depths, complex habitats (e.g., rocky coastline or emergent macrophytes), and seasonal variation in temperatures, are important habitats for a wide array of aquatic species. The diverse mosaic of static (depth, substrate) and dynamic (tidal currents, wave action, temperature, salinity) environmental characteristics within these relatively small areas allows organisms to target one or more ecosystem services by selecting habitats at fine spatial and temporal scales. Nearshore regions are often used seasonally as spawning grounds (Fairchild et al. 2013) or nursery habitats (Stevenson et al. 2014) for juvenile life stages due to their high productivity and the protective effects of complex habitats and shallow and turbid waters against predation (Beck et al. 2001, Munsch et al. 2016). Nearshore regions also facilitate seasonal resource acquisition (Falke et al. 2024) and migratory pathways by both oceanodromous (Stevenson 1989, Lazzari & Stevenson 1992) and diadromous species (Saunders et al. 2006). The reliance of many commercially important species (e.g. herrings, groundfish, lobsters, bivalves) on nearshore regions for at least a portion of their life histories and the relative accessibility of these areas to human harvest conveys not only ecological importance, but also economic value.

Temperature is a critical factor for habitat selection, growth, and phenology for many aquatic species (Pörtner 2002, Staudinger et al. 2019). Increases in ocean temperatures linked to climate change have been shown to affect habitat selection (Methratta & Link 2007), distributions (Nye et al. 2009, Pershing et al. 2021), mortality and productivity (Pershing et al. 2015, Le Bris et al. 2018), and body sizes (Sheridan & Bickford 2011, Cheung et al. 2013) of marine organisms. The response to increased temperatures can be species-specific and further affected by position along a latitudinal range, leading to varied impacts on species interactions and other aspects of community ecology. The North Atlantic Ocean, and the Gulf of Maine (hereafter, GoM) in particular, has experienced rapid warming in recent decades (Pershing et al. 2015, 2021). Basin-scale hydroclimatic changes have already been linked to changes in nearshore ecosystem use and population dynamics of iconic GoM species like American lobster and Atlantic cod (Pershing et al. 2015, Le Bris et al. 2018, Record et al. 2024). They may also be facilitating northward range expansions of typically mid-Atlantic species like black sea bass and blue crabs (Johnson 2015, Bell et al. 2015, McBride et al. 2018). The GoM has relatively low biodiversity, which could limit the resilience of its ecosystems to biotic and abiotic changes (Steneck & Wahle 2013, McMahan & Grabowski 2019).

As regional warming is expected to continue at an above-average rate in the GoM compared to other oceanic ecoregions (Saba et al. 2016), temperature-linked disturbances to historic nearshore community structure and function may become more frequent, intense, and prolonged. Common species like Atlantic silverside (Menidia menidia) and Atlantic herring (Clupea harengus) could be used to broadly represent the responses of warming-tolerant and warming-intolerant groups, respectively. Though both species are highly abundant in the nearshroe regions of the GoM in the summer, their differing life history strategies and the relative position of the GoM to their overall distributions could lead to varied responses to increasing temperatures.

Atlantic silverside may be the only truly annual fish in the Northwest Atlantic, with little evidence of individuals reaching age 2 (Conover 2024). Spawning occurs in shallow nearshore waters in the spring, and young-of-year migrate to deeper offshore waters in the winter to maintain a warmer thermal habitat. Silverside are distributed from southern Florida, USA to the northern Gulf of St. Lawrence, Canada, implying a diversity of genetic and phenotypic adaptations to a wide range of temperatures. Casco Bay, Maine, is at a relatively high latitude within this spatial range. The rapid generation time and ubiquity of silversides to much of the North American Atlantic coast have made them a useful tool to study the varied effects of temperature on vital rates and local adaptation (see the works of David O. Conover cited within Conover 2024). Silversides have demonstrated sensitivity to temperature; when reared in “common garden” median-temperature experiments, higher-latitude fishes have increased growth rates when compared to lower-latitude conspecifics (Conover & Present 1990). This response is consistent with an expected temperature-mediated growth increase for a species that is not near its thermal maximum.

Atlantic herring are distributed on both sides of the Atlantic, with the Gulf of Maine-Georges Bank complex representing the southernmost spawning population in the western Atlantic (Stevenson & Scott 2005). Adults are oceanodromous and will make seasonal migrations from higher-latitude spawning grounds to lower-latitude overwintering grounds. In the Northwest Atlantic, this overall distribution ranges from South Carolina, USA to Labrador, Canada. Increased temperatures are associated with decreased growth rate (Sswat et al. 2018). There is a consistent cross-population response of smaller body size with increased sea surface temperatures, and herring that spawn and overwinter in the warmer, lower-latitude edge of the population range have the strongest response (Beaudry‐Sylvestre et al. 2024). It has been difficult to definitively link warming ocean temperatures to recent declines in spawning stock biomass of US herring stocks, likely due to confounding effects of historical exploitation (Pershing et al. 2021) and the effects of density-dependence (Becker et al. 2020). Despite this, temperature has been shown to decrease recruitment (Mills et al. 2024) and affect phenology (Boyce et al. 2021). Additionally, several studies predict a decrease in thermally suitable habitat and an associated decrease in abundance for herring in the GoM by 2050 (Kleisner et al. 2017, Allyn et al. 2020).

Paragraph on community structure.

In this study, we use 11 years of summer beach seine data collected in Casco Bay, Maine to explore the effect of nearshore temperature on the summer growth rates and relative abundances of herring and silverside. We also use these data to examine spatiotemporal changes in community structure. Seasonal warming and the linked phenology of nearshore species should result in juvenile stages of spring-spawning oceanodromous and diadromous fishes dominating species assemblages in the early summer. Alternatively, summer-spawning oceanodromous fishes and nearshore residents should dominate in the late summer. Average annual community composition across all of Casco Bay may shift from herring-dominated in cooler years to silverside-dominated in recent, warmer years.

Final PP:

**2 Methods**

2.1 Field data collection

Since 2014, the Gulf of Maine Research Institute has conducted summer beach seines at 12 sites within the western half of Casco Bay as part of the Casco Bay Aquatic Systems Survey (CBASS) program. Sites range from just north of the Presumpscot River mouth to just north of Trundy Point, Cape Elizabeth (Fig. 1), resulting in samples arranged along a gradient of salinity. Bottom substrate type varies across sites from fine-grained mud at the sites within the Presumpscot River to coarse-grained gravel at sites along the Cape Elizabeth coast. Sites were sampled at approximately 2-week intervals from early June through mid-September (weeks 24-39), with scattered omissions or delays due to weather or mechanical issues. All samples were collected using a 45.7 m x 2.4 m seine with a 2.4 m x 2.4 m x 2.4 m central bag. Detailed seine deployment methods can be found in the supplemental material. Specimens collected by seine were sorted by species and enumerated. A subsample of 25 individuals per species was measured to the nearest mm. After completion of seine operations, surface temperature was measured using a YSI multiparameter sonde, and general weather conditions were recorded. Data cleaning and processing were accomplished before beginning any statistical analyses. Data from 2019 were excluded from all analyses because sampling effort was too low to accurately characterize the ecosystem in this year. Data from observations that noted an issue with the setting of the seine (water depth below the minimum standard, net coming in tangled, etc.) were also excluded. Of 707 initial seine sampling records, 659 remained after data cleaning.

2.2 Nearshore surface temperature anomaly

Temperature data from each sampling event characterizes instantaneous local conditions but cannot characterize long-term changes in nearshore surface temperature. To create a more synoptic index of nearshore surface temperature, we used data from the NOAA Portland Harbor tide gauge (Station ID: 8418150). We extracted temperature data from January 2003 through December 2024, cleaned to remove ecologically unlikely values (sudden spikes indicative of the instrument being removed from water, or temperatures above 30°C), and calculated the mean daily temperature. The climatological reference period (CRP) was defined as January 2003 through December 2020, which is the closest possible match of the instrument record to the 1991-2020 CRP currently used by the NOAA National Centers for Environmental Information. A Generalized Additive Model (GAM) was used to estimate daily mean temperature over the CRP. Day of year and year were used as the explanatory variables. The *mgcv* package (Wood 2004) was used to fit the model. Predictions of mean temperature per day of year, excluding the effects of individual years, were extracted.

Daily temperature anomalies within the sampling period (2014-2024) were calculated as the difference between the mean daily temperature at the Portland Harbor tide gauge and the predicted daily temperature of the CRP. The temporal frame of reference was shifted so that day 1 of each modeled year was December 1st. This was done to best align the categorization of temperature anomalies with seasonal temperature changes that would impact summertime ecosystem dynamics; winter (December-February) and spring (March-May) temperatures are critical for the timing and success of reproduction and growth for many GoM species. Mean annual temperature anomalies were calculated according to this frame of reference (December 1st through the following November 30th). Years with mean temperature anomalies below the CRP average were categorized as “cooler,” and years with mean temperature anomalies above the CRP average were categorized as “warmer.”

2.3 Statistical analyses

2.3.1 Weekly growth rates

Estimates of weekly growth rates for both of the focal species were carried out separately for each year of data collection, as we expected interannual variation in spawning timing and growth. This analysis was limited to probable age-0 individuals; the process for initially identifying these individuals is detailed within the supplemental material.

Bayesian inference through the R package *LaplacesDemon* (Statisticat LLC 2021) was used to estimate the number of discrete length distributions within each week. A mixed modeling approach using an expectation-maximization (EM) algorithm was then used to estimate the mean length of each discrete group; the *mixtools* R package (Benaglia et al. 2009) was used for this step. A 95% confidence interval was estimated as 2 standard deviations around each identified mean length and stood in for the estimated size range of each group.

We then developed a set of rules to exclude biologically invalid or improbable estimates of age-0 weekly size ranges. For the former, this included length estimates with minimum lengths below 0 mm or maximum lengths above the literature-derived maximum asymptotic body length. For the latter, this included length estimates where the range of possible lengths exceeded 40% of the value of the maximum asymptotic body length. It is unlikely that fish of the same age and captured in the same location would have such extreme variation in achieved lengths. We also merged groups with more than 50% overlap in estimated size confidence intervals, as this is not enough separation to identify distinct age groups. From the remaining data, we identified the first week each summer in which probable age-0 fish were identified, then tracked the growth of that cohort through the following weeks.

In some years, infrequent herring observations resulted in only 2-5 weeks of data per year to estimate weekly growth rates. Herring were caught in only the first week of sampling in 2023, so growth rates could not be estimated for that year. Growth rates for both species in 2024 were estimated from data that had no sampling in weeks 32 to 38 because of vessel mechanical issues; we therefore had low confidence in the results for this year and did not include them in further analyses.

Next, linear models were fit to the upper and lower limits of age-0 cohort length ranges in each week. This was necessary to create a continuous time series of estimated lengths; data volume limitations prevented the Bayesian and mixed modeling approach from identifying an age-0 cohort in some weeks. The relatively short duration of the observation window (typically 15 weeks a year) supported estimating the observed growth rate as a linear relationship. Fish with lengths outside the modeled age-0 limits of each week were removed from further growth analyses. Finally, weighted least squares regressions were used to control for heteroskedasticity and estimate average weekly growth rates in each year. Two-sided Welch’s t-tests were then used to compare weekly growth rates in “warmer” years (annual temperature above CRP average) and “cooler” years (annual temperature below CRP average).

2.3.2 Effects on catch

Generalized additive models were used to model changes in herring and silverside catch along environmental gradients and through time. Catch data for herring and silverside were filtered to only include observations where the time of the observation and the surface temperature were recorded. It is important to note that, unlike the growth analysis, these GAMs use all catch data and do not focus on only age-0 individuals. GAMs were fit with a negative binomial error distribution family and a log-link function due to the zero-inflated and overdispersed nature of the catch data. Thin-plate regression splines were fit to all continuous numeric variables and interaction terms.

Potential explanatory environmental variables included substrate type, weather conditions, tidal state (rising or falling), water level (m) compared to the Mean Lower Low Water (MLLW) datum, and surface temperature (°C). Substrate type, weather conditions, and tidal state were included as fixed-effect factor variables. Water level data from the Portland Harbor tide gauge were used to determine the tidal state and approximate water level at the time of each seine haul. Though the gauge measurements are specific to Portland Harbor, the time offsets for high and low tides at subordinate NOAA tidal prediction stations near the edges of Casco Bay are between 1 and 2 minutes, and tidal height offsets are between 0 and 0.3 m. All our sampled sites are relatively close to Portland Harbor and would likely have temporal and tidal height offsets within this range, which is small enough that we would not likely be able to detect any ecological effects.

Temporal variables included year and numeric week of year. Year was treated as a fixed-effect factor variable so that the effect of each year on catch could be estimated independently, as is most appropriate for generating indices of relative abundance. Week was incorporated as an interaction term with surface temperature. This was done to account for the effect of seasonal warming on the phenology of the focal species.

A random effect for each site was also included as a model term. Though we were not interested in characterizing the difference in catch between sites, including this term was necessary to account for the temporal autocorrelation introduced by the repeated measures sampling design. Site was included as a random rather than a fixed effect because it is likely that the catch of fish at any location is a function of the interaction of multiple local conditions, including those beyond what was explicitly included in the model (e.g., bathymetric features or shoreline shapes that influence currents, concentration of planktonic prey items, salinity). Term selection was conducted according to the “double penalty,” or “null space penalization,” approach (Marra & Wood 2011).

2.3.3 Spatiotemporal community structure

The relative proportion of observed species is variable across the different sampling sites within Casco Bay, as each site has a unique set of dynamic environmental characteristics that can influence species-specific habitat selection patterns. To get a fine-scale assessment of nearshore community structure, the catch per unit effort (CPUE) of every encountered species was calculated at each site within three seasonal periods, pooled across all years. The seasonal periods were defined as early summer (weeks 24-28 of each year), mid summer (weeks 29-33), and late summer (weeks 34-39). CPUE per seasonal period for each species was calculated as the number of individuals caught divided by the number of seine hauls. The data were filtered so that only species that were caught in more than 1% of all seine hauls and across 8 of 10 sampling years remained. This approach was used to limit the influence of uncommon and possibly misidentified species. Encounter rates were used as thresholds rather than total abundance to avoid bias towards schooling or shoaling species. After this process, 10 species remained of 42 total species encountered.

Community composition analysis was conducted using nonmetric multidimensional scaling (NMDS) (Clarke 1993). This approach was applied to Bray-Curtis similarity matrices. Because catch was standardized by effort in the previous step, no transformation was applied. The goodness of fit of the data across the ordination axes was indexed by the stress coefficient. If the calculated stress coefficient was less than 0.2, the NMDS plot was deemed an acceptable representation of the data (Field et al. 1982, Clarke 1993).

After NMDS, k-means clustering was used to identify groups with similar community structures. The silhouette and total within sum of squares (WSS) methods were used to identify the most appropriate number of clusters. We did not assign data points *a priori* to clusters by seasonal period or location within the study area, as we expected both spatial location and seasonal warming to affect community composition and did not want to assume the nature of that interaction. A permutation-based, one-way Analysis of Similarities (ANOSIM) test was used to identify whether community composition was statistically significantly different between clusters (Clarke 1993). This was followed by a Similarity Percentages (SIMPER) test, which was used to identify the species that contributed the most to the dissimilarity between identified clusters’ community composition (Clarke 1993). All statistical tests except k-means clustering were performed using the *vegan* R package, version 2.6-8 (Oksanen et al. 2024).

Interannual differences in community structure, driven by larger-scale and longer-term processes than those encompassed by the previous analysis, were also of interest. We applied the same sequence of tests—NMDS, k-means clustering, ANOSIM, and SIMPER—on species CPUE when pooled across all sampling sites and seasonal periods per year.

**3 Results**

3.1 Species caught

In total, 659 seine hauls across 132 sampling days met data collection standards and were included in our analyses (Table 1). The total catch was 159,590 individuals across 42 species. The 10 species that met encounter thresholds to be included in community composition analyses were, in order of increasing encounter percentage, bluefish (*Pomatomus* *saltatrix*), northern pipefish (*Syngnathus* *fuscus*), American sand lance (*Ammodytes* *americanus*), Atlantic tomcod (*Microgadus* *tomcod*), Atlantic herring (*C. harengus*), river herring (*Alosa* spp.), mummichog (*Fundulus* *heteroclitus*), winter flounder (*Pseudopleuronectes* *americanus*), Atlantic silverside (*M.* *menidia*), and green crab (*Carsinus* *maenas*). Note that river herring is an umbrella term for both alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*). We did not differentiate between the two, as they are difficult to identify without lethal sampling. Combined, these 10 commonly encountered species comprised over 99% of all individuals caught. Atlantic silverside was the most abundant species at nearly 42% of total catch and was encountered in 56% of all seine hauls. Atlantic herring were also highly abundant (nearly 35% of total catch), but were encountered in only 15% of all seine hauls. Both species were encountered in every year of the sampling period. Green crabs had the widest range of spatiotemporal distribution and were encountered in 68% of all seine hauls. With few exceptions, they were detected at least once at every site in every year. Green crabs are the only non-teleost included in the analyses; other benthic invertebrates like horseshoe crabs (*Limulus polyphemus*) and various species of shrimp and hermit crabs were occasionally encountered but not enumerated.

3.2 Nearshore surface temperature anomaly

GAMs fit to average daily surface temperature data from the Portland Harbor tide gauge explained 95.9% of the deviance. Results indicated that 2014-2015 and 2017-2019 had average annual temperature anomalies below the CRP average (Table 2) These cooler years were characterized by sustained periods of daily temperatures beneath the modeled daily average in winter and spring, and limited time above the modeled daily average in summer (Fig. S2). In contrast, daily temperatures in both summers and winters of warmer years (2016, 2020-2024) typically remained above the modeled daily average. Notably, summer temperatures have been more than 1°C greater than modeled averages in each year since 2020 (Table 2).

3.3 Weekly growth rates

The earliest week of age-0 herring detection was generally in week 25 (SD: 1.2 weeks), and the latest week of detection varied between week 26 and week 36 (mean: week 30, SD: 3.2 weeks). The wide range of the latest week of detection is partially caused by variability in sampling season end dates but is also caused by high interannual catch variability, decreasing herring catch through the sampling season, and infrequent encounters after the early summer period. Weekly growth rates for age-0 herring varied from 1.4 to 3.9 mm per week in warmer years and from 1.2 to 5.0 mm per week in cooler years (Fig. 2). Welch’s t-tests indicated no significant difference when comparing mean growth rates between warmer and cooler years (t(4.907) = 0.467, p = 0.661).

The earliest week of age-0 silverside detection was generally in week 29 (SD: 1.8 weeks), and the latest week of detection was usually the last week of the sampling season (mean: week 36, SD: 2.2 weeks). Silversides grew 4.5 to 6.2 mm per week in warmer years and 2.6 to 4.9 mm per week in cooler years (Fig. 2). Welch’s t-tests indicated growth rates were significantly different between warmer and cooler years (t(4.758) = -3.298, p = 0.035), with a mean growth of 3.5 mm per week in cooler years and a mean growth of 5.3 mm per week in warmer years.

3.4 Effects on catch

Herring catch was significantly affected by the interaction of week and temperature, tidal height, surface temperature, and factor variables for bottom substrate and year (Fig. 3). Factor variable terms for weather and tidal stage and the random effect based on site were identified as not significant predictors and removed. The final model explained 56.7% of the deviance in catch. There was a strong effect of week on catch, as evidenced by the smooth representing the interaction of week and temperature. The strongest positive effect of week on catch occurred in weeks 30 and earlier and when temperatures were between 15 and 20°C. After week 30, there was an increasingly negative effect of week on catch regardless of temperature. The relationship between catch and tidal height was shaped like a sigmoidal curve, with a negative effect when the Portland Harbor tide gauge was lower than approximately 1.5m above MLLW. Above this point, increasing tidal height had a slowly increasing positive effect. The relationship between catch and temperature had a more complicated polynomial shape, but there was a clear positive effect when temperatures were between approximately 15 and 19°C. The effect of sand and sand/gravel substrate on catch was not significantly different, but there was a significant negative effect of mud substrate compared to sand/gravel. All years except 2017 and 2020 had a significantly negative effect on catch compared to 2014. The strongest negative effect was for 2023, which had the lowest mean herring catch per unit effort. Herring were caught in only the first week of sampling in this year. This low catch may be more reflective of a timing mismatch than a true decrease in abundance; sampling started later than usual and anecdotal observations indicated that herring had already used the nearshore region and left before the first seine operations were conducted.

Explanatory variables included in the final silverside catch model were the interaction of week and temperature, factor variables for weather conditions and year, and a random effect based on site (Fig. 4). Terms for temperature, tidal height, substrate type, and tidal stage were identified as not significant predictors of catch and removed. The final model explained 53.5% of the deviance in catch. In general, there was a positive relationship between catch and week, with the highest catches and a positive effect occurring in week 32 or later. However, the shift from week having a negative effect to week having a positive effect on catch could occur earlier in the summer (as early as week 30) if surface water temperatures were at or above approximately 18°C. The strongest negative effect on catch occurred in cool (>15°C) waters before week 30, and the strongest positive effect occurred in moderate temperatures (15-19°C) in weeks 33-38. Weather conditions also affected silverside catch. Compared to full sun, overcast conditions had a positive effect. There was no significant effect of partly cloudy or rainy conditions compared to full sun, though it should be noted that there were few samples taken in the rain. When holding all other variables fixed, the random effect of site had the highest variability in the sites near the mouth of the Presumpscot River (Audubon to Brothers North sites). For all years but 2015, there was a significant positive effect of year on catch compared to 2014. The strongest positive effect was for 2020, which also had the highest mean silverside catch per unit effort.

3.5 Spatiotemporal community structure

NMDS analysis compressed site-specific seasonal community compositions to two ordination axes. The resulting stress coefficient was 0.13, indicating a sufficient goodness of fit and limited distortion. Fitting species as vectors within the ordination plot revealed that sand lance, herring, and silversides have the strongest associations with the ordination configuration (Fig. 5). Visualizing the total within sum of squares and average silhouette width for *k* in 1 to 20 clusters indicated the most support for *k* = 3 clusters of similar community composition. ANOSIM confirmed a significant difference in community composition between these three clusters (r = 0.761, p < 0.0001). The average CPUE for each species in each cluster was calculated and visualized, which revealed that cluster A typically had high herring catch, cluster B had generally low catch for all species, and cluster C had high silverside catch (Fig. 5).

SIMPER analysis across clusters provided quantitative confirmation of this visual analysis. When comparing the composition of cluster A to cluster B, herring (p = 0.001, Contribution = 62.5%), sand lance (p = 0.007, Contribution = 12.4%), and green crabs (p = 0.016, Contribution = 3.9%) combined to contribute more than 90% of the dissimilarity. Winter flounder, Atlantic tomcod, and northern pipefish contributed smaller, but still significant, amounts of dissimilarity. Cluster A had higher average CPUE for all species identified as significantly contributing to dissimilarity except sand lance, which had higher average CPUE in cluster B. When comparing clusters A and C, only catch of silverside (p = 0.002, Contribution = 49.6%) and herring (p = 0.017, Contribution = 31.0%) had significant contributions to dissimilarity. Herring had a higher average CPUE in cluster A, and silverside had a higher average CPUE in cluster C. Dissimilarity between clusters B and C was driven by catch of silverside (p = 0.001, Contribution = 66.2%), mummichog (p = 0.025, Contribution = 12.4%), and bluefish (p = 0.031, Contribution = 0.09%). All three of these species had higher average CPUE in cluster C compared to cluster B.

When plotted across space and time, divergent spatiotemporal patterns of habitat use can be identified (Fig. 5). In the early summer period, most sampling sites (9 of 12) are best described by cluster A. Only one site belongs to cluster A in the mid- or late summer periods, which matches the noted trend in decreasing herring catch through the summer. Cluster B is present across all three seasonal periods. The mixed-composition community structure of this cluster best describes sites with low CPUE for all species included in the modeling efforts. Sand lance has the highest CPUE of all species within this cluster, but it should be noted that sand lance catch was uncommon and mostly observed in the late summer period at the two southernmost sites. In early summer period, but many sites were best described by this cluster in the mid-summer (7 sites) and late summer (9 sites) periods. This matches the noted trend in increasing silverside catch through the summer.

NMDS ordination of community composition aggregated across all sampling sites per year also had sufficient goodness of fit across two ordination axes (stress = 0.08). Herring, silverside, and northern pipefish had the strongest associations with ordination configuration, and k-means clustering analysis supported the selection of two clusters (Fig. 6). ANOSIM confirmed a significant difference in community composition between clusters (r = 0.81, p = 0.021). Visual representations of ordination plots and average CPUE per species within both clusters indicated that cluster A was characterized by high silverside catch and cluster B was characterized by high herring catch (Fig. 6). SIMPER results highlighted herring as the only species contributing a statistically significant amount of the dissimilarity between the clusters (p = 0.001, Contribution = 67.6%). Casco Bay community composition in 2014 and 2017 was best characterized by cluster B, and all remaining years were best characterized by cluster A. Though there was no clear connection between average annual temperature anomaly and community composition cluster, it should be noted that both 2014 and 2017 were cooler than the CRP and had extended periods in the spring and summer with below-average daily temperatures.

**4 Discussion**

Many studies have identified responses to hydroclimatic changes at a species-specific level (Pershing et al. 2015, Le Bris et al. 2018), and others have focused on responses at higher levels of ecological organization and at large spatial scales like the Northeast US Continental Shelf Large Marine Ecosystem (Lucey & Nye 2010, Fenwick et al. 2024). Fewer studies have explored temperature-linked changes to the community ecology of GoM nearshore regions. We were interested in characterizing seasonal and interannual patterns of Casco Bay species assemblages, with an emphasis on the effect temperature has on these patterns. Many ecologically and economically important species use this area, connecting it to larger spatial scales and several levels of biological organization. Atlantic silverside and Atlantic herring, as highly abundant and important forage species with differing adaptability to temperatures experienced in Casco Bay, were used as focal species to estimate the effects of temperature on growth and abundance.

The phenology and relative abundances of Casco Bay nearshore fishes, and the effects of increasing nearshore surface temperatures, were illustrated through the analysis of 11 years of seine survey data. Catch was dominated by 10 commonly encountered species. . However, a few unusual species were observed. These include

There was a clear seasonal progression to community structure, which is closely tied to the relative abundances of these focal species. Most sites in the early summer period (weeks 24-28) were best described by high herring catches and relatively low catches of other species.

Similarly, GAMs indicated a strong positive effect of both early weeks and cooler temperatures on herring abundance, but a strong negative effect for the same conditions on silverside abundance. The mid-summer period (weeks 29-33) is a transitional period, where temperatures rapidly increase and community assemblage shifts to generally be more silverside-dominated as YOY silverside recruit to the seine and herring leave the nearshore area. Note that we have no information on how far or deep juvenile herring go when then leave the reach of our beach seine, though concurrent collection of environmental DNA (eDNA) samples may shed light on fine-scale herring spatiotemporal distributions. This is especially true of sites in and around the Presumpscot River estuary, which are typically warmer than the sites with less freshwater influence. The late summer period (weeks 34-39) had a strong negative effect on herring regardless of temperature. Though there was generally a strong positive effect on silverside abundance in this period, this effect was weakened when surface temperatures exceeded 20°C.

The ties between community structure and seasonal warming were evident when analyzing at site-specific and short-time scales. We hypothesized that longer-term warming would also result in changes in community structure and somatic growth at larger spatial and temporal scales. It was expected that years with average temperatures exceeding the CRP average would benefit silverside and disadvantage herring, resulting in altered community structure and opposing effects on growth. Community structure viewed through an annual, whole-Bay lens did not clearly follow this pattern. Though two years categorized as cooler than the CRP average (2014 and 2017) had relatively high herring abundance and were best described by a herring-dominated community structure, the remaining cool years (2015 and 2018) had relatively low herring abundance and were best described by a silverside-dominated community structure. All years categorized as warmer were best described by a silverside-dominated community structure.

Interestingly, some of the lowest estimated herring weekly growth rates occurred in years with high herring relative abundance (2014 and 2017), while years with low herring relative abundance (2015 and 2018) had the two highest estimated growth rates. This may indicate a density-dependent effect on growth, which has previously been noted in GoM herring populations (Becker et al. 2020), although this was for adult herring. Though there was a trend of decreased herring weekly growth rates in warmer years, this trend was not significant. Population dynamics of herring have notably high interannual variability, with a wide range of biotic and abiotic factors and selective processes acting on recruitment, growth, distribution patterns, and mortality (Becker et al. 2020, Burbank et al. 2023, Beaudry‐Sylvestre et al. 2024). The characteristics of the population observed in nearshore Casco Bay seines are likely influenced by processes at much larger spatial and temporal scales than captured in this study.

Posthave been reported Silverside weekly growth rates were significantly higher in warmer years than cooler years. Silverside relative abundance increased over the 11-year study period, which may also be related to the increasing summer nearshore temperatures experienced in the study area over this time. The short lifespan, early summer spawning, and nearshore distribution of the YOY silverside primarily caught in our seine surveys closely links their population dynamics to short-term, local processes. This, combined with their highly abundant and ubiquitous nature, may make them a useful indicator species for coarse-scale structure and functioning of the Casco Bay ecosystem.

Reduced relative abundance of certain forage species in nearshore GoM ecosystems, including herring, could negatively impact nearshore trophic dynamics. Changes in prey size, distribution, relative abundance, and community structure will impact piscivorous predators that have evolved to exploit nearshore forage fishes (Ball et al. 2007, D. McGowan et al. 2019, A. McGowan et al. 2022, Falke et al. 2024). Our study has illustrated temperature-related changes in seasonal herring nearshore habitat use and indicates that long-term temperature increases could alter temporal patterns of distribution in nearshore GoM areas. Though silverside may grow faster and increase in abundance with warmer temperatures, they may not fill the same role in trophic dynamics as herring. In the early summer, silverside in the nearshore region were much larger than herring. This size difference could preclude silverside from being a prey item for juvenile piscivorous fishes using the nearshore region as a nursery area. Prey size is an important limiting factor in the ontogeny of piscivory in striped bass and bluefish, both of which are important sportfish and predators in the GoM (Scharf et al. 2009). Herring and silverside also have differing spatial distribution patterns; silverside typically inhabit extremely shallow nearshore regions (Conover & Ross 1982), while herring are more widely distributed (Boyar 1968, Creaser & Libby 1986, 1988). If biomass of forage fishes shifts closer to shore and into shallow areas, it may alter prey availability to larger-bodied predators or force changes in predator distributions.

The dynamics of shallow nearshore ecosystems and the forage species that use them are relatively understudied (Lankowicz et al. 2020, McGowan et al. 2022). The abundances and distributions of taxonomic groups in these highly heterogeneous areas are spatially and temporally variable along environmental gradients. Some environmental gradients may directly influence the behavior of a species (temperature, dissolved oxygen, salinity); this may modify interspecific interactions (competition, predation) and lead to further indirect effects. Identifying the environmental patterns that drive fish distribution and community structure could provide predictive insight under alternate climate scenarios, as well as for much larger spatial scales and biological organization levels.

The results of this study indicate that increasing surface water temperatures will likely lead to altered timing of nearshore habitat use by Atlantic herring, which may affect their population dynamics. Further exploration into interannual variation in juvenile herring population dynamics and individual growth may add context to the steep decline in recruitment and associated reduction in spawning stock biomass seen since 2012, which has persisted despite reduced fishing pressure (NOAA 2024). This produces natural follow-up questions regarding altered interspecific interactions within nearshore ecosystems, trends in average energetic content of herring compared to silverside, as well as the potential of interspecies competition between herring and silverside for prey in the nearshore regions. Though answering these questions is beyond the scope of this paper, it is clear that current Casco Bay nearshore temperatures are still within the thermal tolerances of Atlantic silverside, which has led to increased abundance and faster growth. Monitoring efforts like the Casco Bay Aquatic Systems Survey should be continued, and possibly expanded in temporal scope, to further explore the effects of shifting community structure on the trophic ecology of nearshore regions.

**Acknowledgements**

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**7 Figures & Figure captions**

A map of the ocean

AI-generated content may be incorrect.

Figure 1: (A) Location of sampling sites (bounded by blue outline) relative to the Gulf of Maine. (B) Location of sampling sites along the western coast of Casco Bay. Sites are, from north to south, Presumpscot Moorings (PM), Skitterygusset (SK), Mussel Cove (MC), Audubon (AD), Brothers Island North (BN), Mackworth Island North (MN), Mackworth Island Beach (MB), Back Cove (BC), Great Diamond Island (GD), Southern Maine Community College (SM), Cushing Island (CI), and Alewife Cove (AC). The city of Portland is also labeled for spatial context.

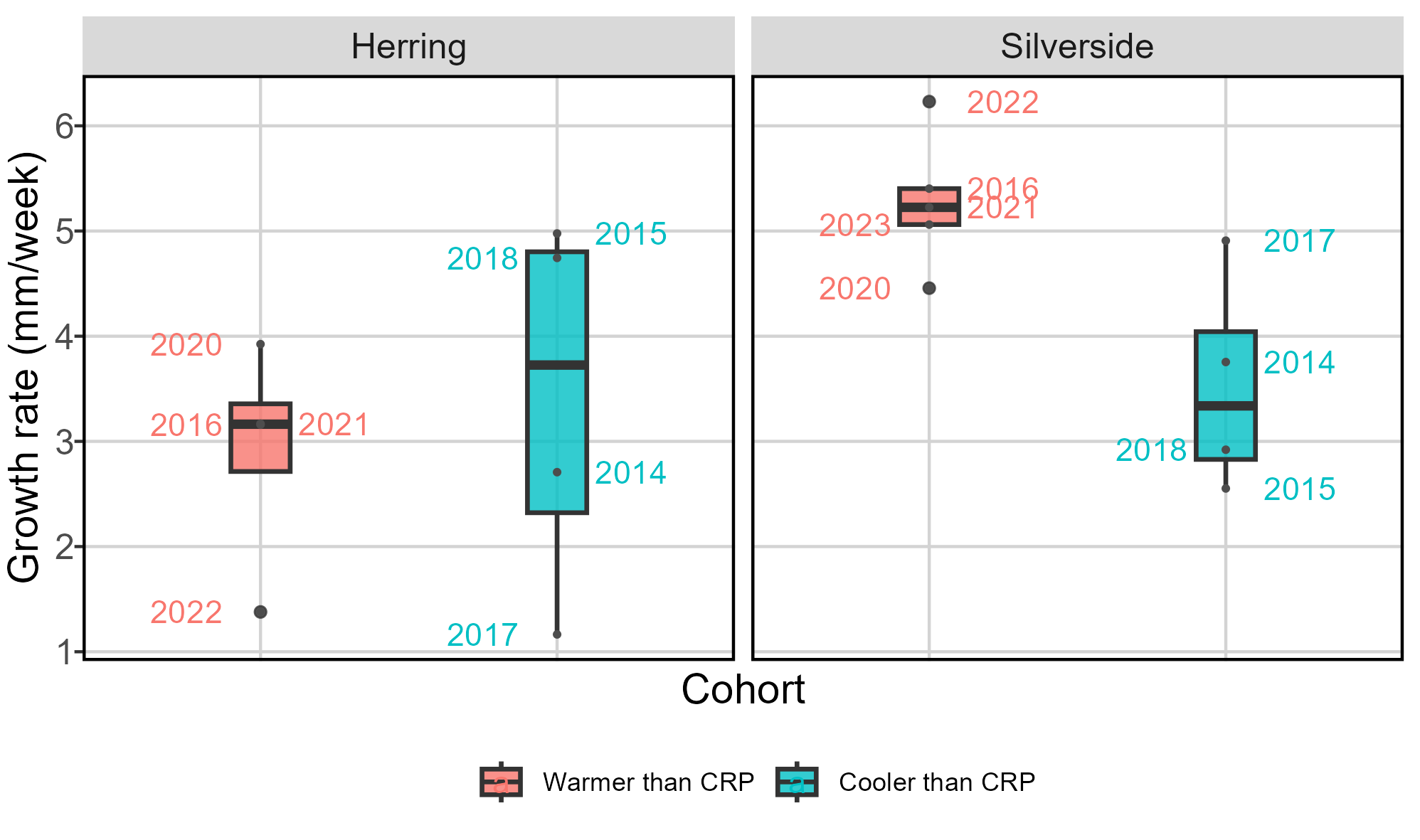
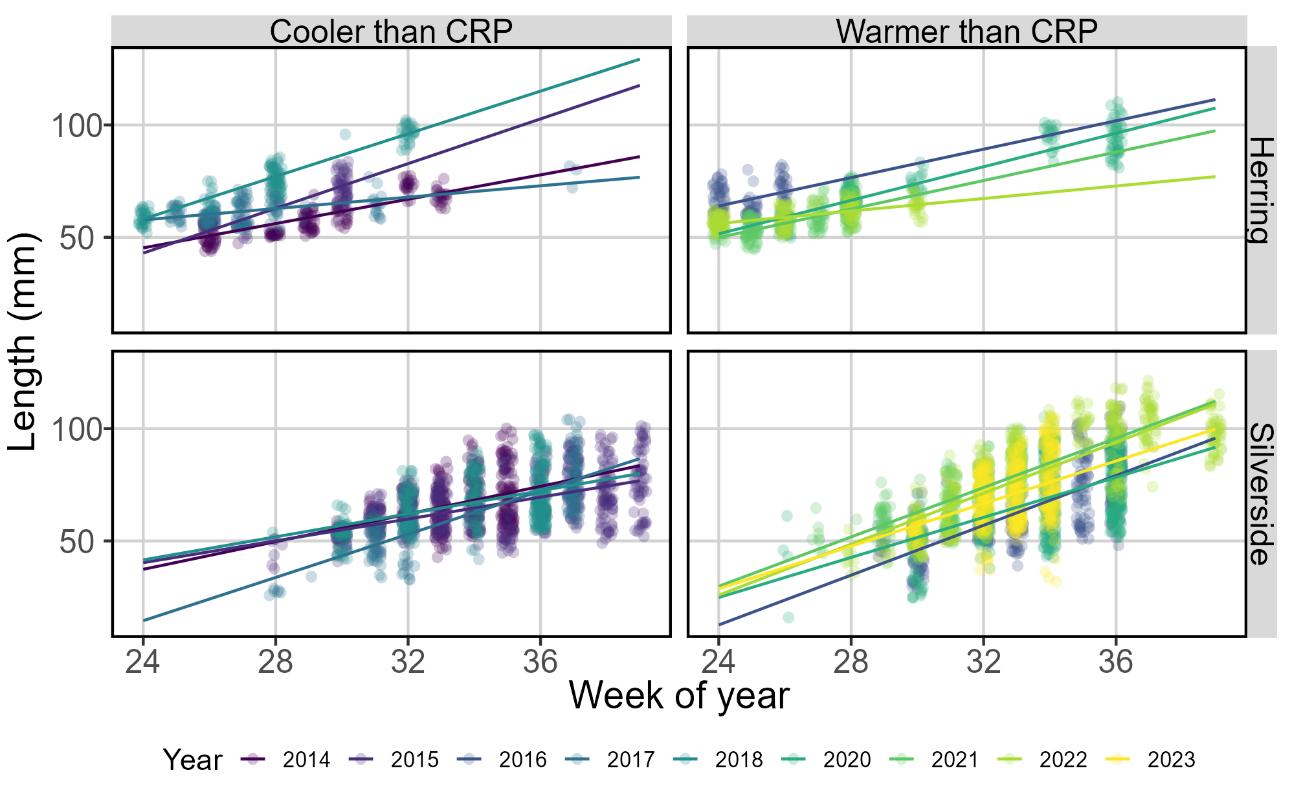


Figure 2: A. (Top panel) Weekly length distributions (in mm) of age-0 herring (top row) and silverside (bottom row) in years designated as having average annual temperature anomalies cooler (left column) and warmer (right column) than expected given the climate reference period (CRP). Lines indicate the calculated slope, or weekly growth rate. Colors of lines and dots indicate year. B. (Bottom panel) comparison of calculated weekly growth rates (in mm) for herring (left column) and silverside (right column) in years warmer than the CRP (red boxplots) and cooler than the CRP (blue boxplots). The year of each calculated growth rate is annotated.

A collage of graphs

AI-generated content may be incorrect.

Figure 3: Smooth terms for the herring weekly catch GAM. Terms include (a) the interaction of week and temperature, (b) temperature, (c) tidal height (m) compared to MLLW, (d) factor effect of year, and (e) factor effect of substrate type.

A collage of graphs

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Figure 4: Smooth terms for the silverside weekly catch GAM. Terms include (a) the interaction of week and temperature, (b) random effect of site, (c) factor effect of year, and (d) factor effect of weather conditions.

A diagram of different colors

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Figure 5: Nonmetric multidimensional scaling and k-means cluster analysis of community composition among all sampling sites. Clockwise from top left, the panels illustrate (a) the clusters of similar community composition found at each sampling site in the early summer (weeks 24-28 of each year), mid summer (weeks 29-33), and late summer (weeks 34-39) periods; (b) the NMDS ordination of each site-period combination (points) with coloring indicating the same clustering structure and herring (h), silverside (ss), and sand lance (sl) association to the ordination structure illustrated as vectors; and (c) the log-scaled average catch per unit effort (CPUE) for all species by cluster. Species are bluefish (bf), northern pipefish (pf), Atlantic tomcod (tc), winter flounder (fl), green crab (gc), river herring (aw), Atlantic herring (h), Atlantic silverside (ss), mummichog (mm), and American sand lance (sl).

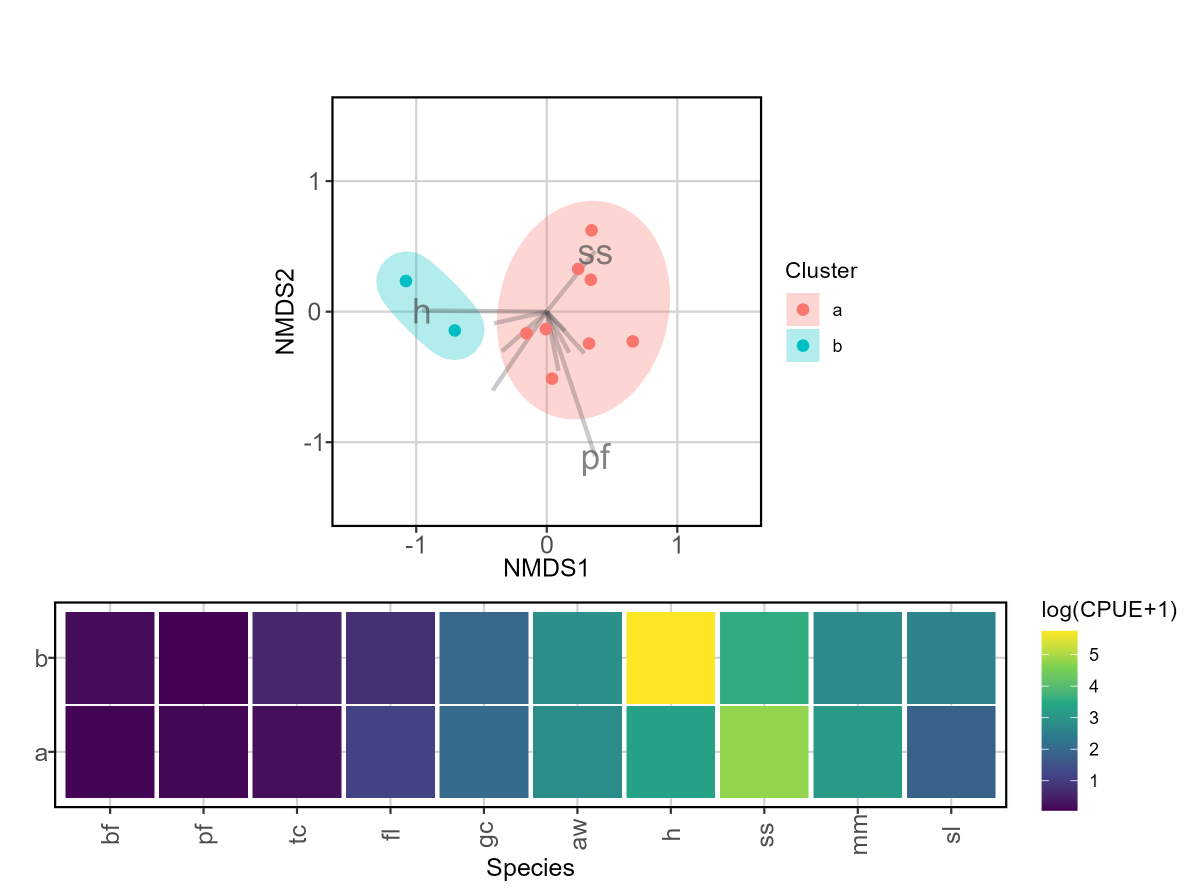


Figure 6: Nonmetric multidimensional scaling and k-means cluster analysis of community composition among all sampling sites. The top panel illustrates the NMDS ordination of each annual Casco Bay-wide annual community compositions, with the color of the points indicating the cluster and herring (h), silverside (ss), and northern pipefish (pf) association to the ordination structure illustrated as vectors. The top panel illustrates the log-scaled average catch per unit effort (CPUE) for all species by cluster. Species are bluefish (bf), northern pipefish (pf), Atlantic tomcod (tc), winter flounder (fl), green crab (gc), river herring (aw), Atlantic herring (h), Atlantic silverside (ss), mummichog (mm), and American sand lance (sl).

**8 Tables & table captions**

Table 1: Summary of seine catch data of 11 year time series. Species are arranged by number of individuals caught, number of seine hauls where at least one individual of the species was encountered (Encounters), and number of years where at least one individual of the species was encountered (Years encountered). The percentage of total catch (number caught divided by 159,590 total organisms enumerated) and percentage of encounters (number of seine hauls seen divided by 659 total seine hauls) are also calculated.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Common name** | **Scientific name** | **# Individs.** | **% of total catch** | **Encounters** | | **% of encounters** | | **Years encountered** | |
| cunner | *Tautogolabrus adspersus* | 1 | < 0.01 | | 1 | | 0.2 | | 1 |
| eastern silvery minnow | *Hybognathus regius* | 1 | < 0.01 | | 1 | | 0.2 | | 1 |
| spotted hake | *Urophycis regia* | 1 | < 0.01 | | 1 | | 0.2 | | 1 |
| summer flounder | *Paralichthys dentatus* | 1 | < 0.01 | | 1 | | 0.2 | | 1 |
| northern puffer | *Sphoeroides maculatus* | 2 | < 0.01 | | 2 | | 0.3 | | 2 |
| red hake | *Urophycis chuss* | 2 | < 0.01 | | 2 | | 0.3 | | 2 |
| American eel | *Anguilla rostrata* | 3 | < 0.01 | | 3 | | 0.5 | | 3 |
| crevalle jack | *Caranx hippos* | 3 | < 0.01 | | 2 | | 0.3 | | 2 |
| lumpfish | *Cyclopterus lumpus* | 3 | < 0.01 | | 2 | | 0.3 | | 2 |
| American plaice | *Hippoglossoides platessoides* | 4 | < 0.01 | | 1 | | 0.2 | | 1 |
| shortfin squid | *Illex illecebrosus* | 4 | < 0.01 | | 1 | | 0.2 | | 1 |
| Atlantic butterfish | *Peprilus triacanthus* | 5 | < 0.01 | | 4 | | 0.6 | | 4 |
| rainbow smelt | *Osmerus mordax* | 5 | < 0.01 | | 3 | | 0.5 | | 2 |
| striped bass | *Morone saxatilis* | 6 | < 0.01 | | 6 | | 0.9 | | 3 |
| smallmouth bass | *Micropterus dolomieu* | 7 | < 0.01 | | 3 | | 0.5 | | 2 |
| white hake | *Urophycis tenuis* | 7 | < 0.01 | | 2 | | 0.3 | | 2 |
| American shad | *Alosa sapidissima* | 8 | 0.01 | | 4 | | 0.6 | | 4 |
| largemouth bass | *Micropterus salmoides* | 9 | 0.01 | | 4 | | 0.6 | | 3 |
| permit | *Trachinotus falcatus* | 9 | 0.01 | | 2 | | 0.3 | | 1 |
| Atlantic cod | *Gadus morhua* | 10 | 0.01 | | 2 | | 0.3 | | 1 |
| white wucker | *Catostomus commersonii* | 19 | 0.01 | | 6 | | 0.9 | | 5 |
| blueback herring | *Alosa aestivalis* | 20 | 0.01 | | 6 | | 0.9 | | 3 |
| longhorn sculpin | *Myoxocephalus octodecemspinosus* | 20 | 0.01 | | 7 | | 1.1 | | 2 |
| threespine stickleback | *Gasterosteus aculeatus* | 21 | 0.01 | | 15 | | 2.3 | | 7 |
| rock gunnel | *Pholis gunnellus* | 25 | 0.02 | | 11 | | 1.7 | | 6 |
| fallfish | *Semotilus corporalis* | 28 | 0.02 | | 3 | | 0.5 | | 1 |
| pollock | *Pollachius virens* | 35 | 0.02 | | 6 | | 0.9 | | 5 |
| ninespine stickleback | *Pungitius pungitius* | 42 | 0.03 | | 6 | | 0.9 | | 4 |
| shorthorn sculpin | *Myoxocephalus scorpius* | 47 | 0.03 | | 21 | | 3.2 | | 6 |
| northern pipefish | *Syngnathus fuscus* | 82 | 0.05 | | 41 | | 6.2 | | 10 |
| grubby sculpin | *Myoxocephalus aenaeus* | 83 | 0.05 | | 32 | | 4.9 | | 6 |
| bluefish | *Pomatomus saltatrix* | 84 | 0.05 | | 21 | | 3.2 | | 8 |
| white mullet | *Mugil curema* | 180 | 0.11 | | 9 | | 1.4 | | 6 |
| Atlantic tomcod | *Microgadus tomcod* | 231 | 0.15 | | 70 | | 10.6 | | 10 |
| Atlantic menhaden | *Brevoortia tyrannus* | 682 | 0.43 | | 4 | | 0.6 | | 3 |
| winter flounder | *Pseudopleuronectes americanus* | 1331 | 0.83 | | 247 | | 37.5 | | 10 |
| green crab | *Carcinus maenas* | 4463 | 2.8 | | 446 | | 67.7 | | 10 |
| sandlance | *Ammodytes americanus* | 4688 | 2.94 | | 65 | | 9.9 | | 9 |
| alewife | *Alosa pseudoharengus* | 10184 | 6.38 | | 140 | | 21.2 | | 10 |
| mummichog | *Fundulus heteroclitus* | 14579 | 9.14 | | 199 | | 30.2 | | 10 |
| Atlantic herring | *Clupea harengus* | 55768 | 34.95 | | 97 | | 14.7 | | 10 |
| Atlantic silverside | *Menidia menidia* | 66887 | 41.91 | | 369 | | 56 | | 10 |

Table 2: Portland Harbor tide gauge average annual temperature anomalies, calculated as the mean difference between daily average temperature and the expected daily average temperature as determined from the 2003-2020 climate reference period (CRP). Summer (June-August) anomalies are also presented. Negative values are cooler temperatures than expected compared to the CRP, and positive values are warmer temperatures than expected compared to the CRP.

|  |  |  |
| --- | --- | --- |
| **Year** | **Annual anomaly (°C)** | **Summer anomaly (°C)** |
| 2014 | -0.74 | -0.62 |
| 2015 | -0.41 | 0.06 |
| 2016 | 0.69 | 0.57 |
| 2017 | -0.37 | -1.05 |
| 2018 | -0.11 | 0.58 |
| 2019 | -0.27 | 0.35 |
| 2020 | 0.66 | 1.86 |
| 2021 | 1.24 | 1.7 |
| 2022 | 0.97 | 1.51 |
| 2023 | 1.12 | 1.42 |
| 2024 | 0.9 | 1.09 |