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

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**1 Abstract**

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Nearshore regions (0-50 m depth), via a unique combination of tidal mixing, freshwater input, shallow depths, and seasonal variation in temperatures, are utilized by a wide array of aquatic species. The diverse mosaic of static (depth, substrate) and dynamic (tidal currents, temperature, salinity) environmental characteristics within these relatively small areas allows organisms to select habitats at fine spatial and temporal scales to best suit one or more ecosystem services. 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 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. herring, 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 importance.

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 the distributions (Nye et al. 2009, Pershing et al. 2021), mortality and productivity (Pershing et al. 2015, Le Bris et al. 2018), ontogenetic shifts (Methratta & Link 2007), and body sizes (Fisher et al. 2010, 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). This is likely due to the increased influence of the warmer Gulf Stream current, as compared to the more historically influential and colder Labrador Current, on waters entering at depth through the constricted Northeast Channel (Gonçalves Neto et al. 2021, Balch et al. 2022). An increased frequency of warm core eddies from the Gulf Stream entering the GoM since the early 2000s may also have contributed to warming temperatures (Gangopadhyay et al. 2019). This trend has been further punctuated by several pulses of anomalously warm temperatures linked to atmospheric warming, termed marine heatwaves (Mills et al. 2013). Basin-scale hydroclimatic changes have already been linked to dramatic, negative changes in nearshore ecosystem dynamics and 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 (Bell et al. 2015, McBride et al. 2018), and blue crabs (Johnson 2015). 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). Regional warming is expected to continue at an above-average rate as compared to global averages (Saba et al. 2016), and temperature-linked disturbances to historic nearshore community structure and function may become more frequent, intense, and prolonged. Monitoring nearshore regions will be critical to predicting and understanding how increased temperatures may affect biological organization levels from individual species to the overall GoM ecosystem. In this study, we will relate changes in nearshore surface temperature both to shifts in community structure and to changes in the relative abundance and growth rates of common fishes, using Atlantic silverside (*Menidia menidia;* hereafter, silverside) and Atlantic herring (*Clupea harengus;* hereafter, herring) as focal species.

Atlantic silversides are the only truly annual fish in the western North Atlantic (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. It’s expected that less than 1% of the singular year class returns from this overwintering period on the inner continental shelf to recolonize shallow nearshore and estuarine habitats and spawn (Conover & Murawski 1982, Conover 2024). Even less of the population survives beyond age 1. They have a native range spanning 3000 km from southern Florida to the northern Gulf of St. Lawrence, implying a diversity of genetic and phenotypic adaptations to temperature. Casco Bay is in the northern half of this spatial range. The ubiquity of silversides to much of the North American Atlantic coast and rapid generation time has made them a useful tool to study the varied effects of temperature on sex determination, countergradient growth variation, spatial scale of local adaptation, and fisheries-induced evolution (see the works of David O. Conover cited within Conover 2024). The demonstrated sensitivity of silversides to temperature, chiefly the known increased growth rate of higher-latitude fishes when reared in “common garden” median-temperature experiments as compared to lower-latitude conspecifics (Conover & Present 1990), indicates increased temperatures in Casco Bay would result in higher growth rates for local silversides.

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. They can live up to 15 years, with sexual maturity occurring around age 3 in the GoM (O’Brien et al. 1993) and age 4 in northern populations (Chamberland et al. 2022). Spawning occurs in the late summer to fall, with peak spawning occurring in October in the western GoM (Graham et al. 1972b). Demersal eggs are deposited in areas with strong tidal currents, and larvae are dispersed into coastal zones where they overwinter (Graham et al. 1972a, Graham & Townsend 1985). These larvae metamorphose into juveniles by spring and grow rapidly through the summer (Anthony 1972, Lough et al. 1982). Laboratory experiments have indicated that juvenile herring prefer temperatures between 8 and 12°C (Stickney 1969). Until they reach sexual maturity, herring will annually move offshore or to deeper bays to overwinter in more suitable thermal habitats but will not make north-south migrations (Boyar 1968). Tagging studies indicate that juvenile herring remain close to their overwintering grounds (Creaser & Libby 1986, 1988). Adults are oceanodromous and will make extensive north-south seasonal migrations from more northerly spawning grounds to more southerly overwintering grounds. In the western North Atlantic, this overall distribution ranges from South Carolina (southern extent, winter distribution) to Labrador (northern extent, summer distribution). A recent synoptic study of all Northwest Atlantic herring populations indicates that there is a coherent cross-population response of smaller body size with increased sea surface temperatures, but herring that spawn and overwinter in the warmer (southern) edge of the population range are experiencing a more negative response (Beaudry‐Sylvestre et al. 2024). Temperature has also been shown to affect growth rates, with increased temperatures leading to slower growth (Sswat et al. 2018). Though it has been difficult to definitively link shifting temperature regimes to recent declines in spawning stock biomass of US Atlantic herring stocks because of the competing influence of historical exploitation (Pershing et al. 2021) and the known effects of density-dependence (Becker et al. 2020), temperature has been shown to affect recruitment and phenology in Canadian stocks in the Bay of Fundy and Scotian Shelf (Boyce et al. 2021), and several studies predict a decrease in thermally-suitable habitat and associated decrease in abundance for herring in the GoM by 2050 (Kleisner et al. 2017, Allyn et al. 2020).

Both silverside and herring are highly abundant in the nearshore regions of the GoM in the summer. However, their distinct life history strategies and differences in the relative position of the GoM to their overall distributions (northern half of range for silverside, southern half of range for herring), could lead to opposing responses to environmental change. Increases in nearshore GoM surface temperatures may be advantageous to silverside growth and reproduction, while conversely altering patterns of nearshore habitat use and reducing the growth of herring. In this study, we will use 11 years of summer beach seine data collected in Casco Bay, Maine to explore these dynamics. We will also use these data to examine changes in spatiotemporal community structure. We expect seasonal shifts in species assemblage for the entire sampled area, where juvenile stages of spring-spawning oceanodromous and diadromous fishes dominate catch in the early summer, but summer-spawning oceanodromous fishes and nearshore residents dominate in the late summer. Differences in salinity and benthic substrate will drive variation in species assemblages between sites. Finally, we expect to see the overall Casco Bay summer community composition shift from herring-dominated to silverside-dominated with increasing average surface temperatures.

**3 Methods**

3.1 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. X – map). 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 summer through early fall, with scattered omissions or delays due to weather or mechanical issues.

All samples were collected using a 45.7 m long, 2.4 m tall seine built of 4.8 mm knotless delta-style nylon mesh with a central bag. The bottom line was weighted with lead sinkers and the top line was fitted with buoyant spongex floats. The seine was connected to a bridle and 2m of spare line on both ends. Seines were deployed with the help of a skiff. For each sample, one end of the seine was held on the beach while the net was flaked out from the bow of the skiff as it backed off the beach. The skiff was moved to extend the seine to the near edge of the bag, then pivoted to return to shore. The remaining length of the seine was flaked out until the skiff landed back on the beach. This resulted in a generally U-shaped deployment of the seine with approximately 20 m between the ends on the beach. Sampling trips were timed with the tides so that the deepest point sampled was between 1.5 and 2.2 m. Once both ends of the seine were on the beach, one person on each end hand hauled the net in. The bag was left partially in the water to limit specimen mortality. The contents of the bag were sorted by species and enumerated. The first 25 individuals of each species were measured to the nearest mm and species with sexually dimorphic features (i.e., crabs) were sexed. All organisms were released immediately after they were counted and/or measured. After completion of seine operations, surface temperature and salinity were measured using a YSI multiparameter sonde, and general weather conditions were recorded.

Data cleaning and processing was accomplished before beginning any statistical analyses. Minimal sampling occurred in 2019 and therefore 2019 data are excluded from all analyses. The most consistently sampled period each year was between weeks 24 and 39 (early June through mid-September). Sporadic data outside this period were removed. Data from observations that noted an issue with the setting of the seine (water depth below minimum standard, the net coming in tangled) were also excluded. Of 707 initial seine sampling records, 659 remained after data cleaning.

3.2 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 pulled data from the NOAA Portland Harbor tide gauge (Station ID: 8418150). Although this station records the temperature of only one point within Casco Bay, it is the most complete and consistent dataset available for historical nearshore water temperature information. The station has reliably recorded surface water temperature at 6-minute intervals since August 2002 with minimal disruption. Wider spatial scale data sources, such as NOAA’s Optimum Interpolated Sea Surface Temperature (OISST) product, do not predict the temperature of the extreme nearshore shallows sampled in this study, and thus may not create a precise or accurate index of temperatures in these areas.

We extracted all 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. Standard practice, as described by the NOAA National Centers for Environmental Information, is to use a defined 30-year period to calculate climatological norms. The current United States national CRP is 1991-2020. The Portland Harbor tide gauge does not have an instrument record extending back this far, so we chose to use the longest uniform period in the instrument record as our CRP. 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, which explained 95.9% of the deviance. 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 CRP-predicted daily temperature as calculated in the previous step. We decided to shift the temporal frame of reference so that day 1 of each modeled year was December 1st of the previous calendar year. 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 anomalies below 0 were cooler than the CRP and years with mean anomalies above 0 were warmer.

3.3 Statistical analyses

3.3.1 Weekly growth rates

Growth rate fluctuates with age, so it is necessary to separate fish captured in summer beach seine operations into discrete year classes. When direct measurements of age are not available (counting annuli of otoliths or other hard structures), statistical length-frequency models can be used to estimate the age of temperate fishes with short, distinct spawning seasons (Macdonald & Pitcher 1979). Both focal species (herring and silverside) can be aged in this way. At least two year classes of each focal species are present in the nearshore region during our sampling period, though the timing of use may vary by age class (Fig. X – Herring and Silverside Weekly Lengths). Larval herring metamorphose to juveniles at 40-55 mm standard length by the first spring after hatching (Lough et al. 1982) and grow to lengths of 90-125 mm by the end of their first year (Anthony 1972). The size range of herring caught in our beach seines indicates they were mostly age-0 fish spawned the previous fall (mean 64 mm, SD 13 mm), but occasionally larger herring were captured. For silverside, weekly average lengths were consistently around 100 mm in the first third of the sampling season but rapidly decreased to a low of 67 mm in week 31. This indicates that mostly age-1+ silversides were caught early in the season, but recently-spawned silversides recruit to the seine and dominate catch by late July. This is consistent with phenological patterns and growth rates reported in the literature (Conover & Ross 1982, Conover & Present 1990, Gao & Munch 2013). We are interested in calculating growth rates for the youngest cohort of each focal species and therefore must identify age-0 fishes. This begins with an assumption that the lengths of sampled conspecifics in the same cohort at the same time come from an identifiable distribution. Commonly, lengths of a cohort of conspecifics are assumed to come from a normal distribution (Macdonald & Pitcher 1979, Zhou et al. 2022). It is therefore possible to identify cohorts by their unique modal lengths along a cumulative length distribution (Macdonald & Pitcher 1979).

The following analyses were carried out separately for each year of data collection, as we expected year-specific effects on spawning and growth. Bayesian inference through the R package LaplacesDemon (Statisticat LLC 2021) was used to estimate the number of length distribution modes within each week. This was accomplished through the Modes function, which is a deterministic function that differences the kernel density of a continuous variable and reports a number of modes equal to half the number of changes in direction. This allows for the statistical determination of the number of age groups, as opposed to traditional length frequency analysis methods that require either a priori knowledge or graphical analysis to identify age groups (Petersen 1891, Fournier et al. 1990, Zhou et al. 2022). If the assumption that the lengths of a cohort come from a normal distribution holds, the location of each mode would represent the mean length of fish belonging to that distinct cohort. The location of modes was estimated using a mixed modeling approach via the mixtools R package (Benaglia et al. 2009). An expectation-maximization (EM) algorithm for mixtures of univariate normals applied to the number of modes identified in the previous step was applied. A 95% confidence interval around each mode was estimated as 2 standard deviations around each identified mode and stood in for estimated size range of each cohort.

This approach to length-frequency analysis is similar to established software and methods (Gayanilo et al. 1996, Mildenberger et al. 2017, Zhou et al. 2022). Like these other approaches, an expert is required at this point to apply informative priors and make decisions about the validity of the identified cohorts. We developed a set of rules to exclude biologically invalid or improbable estimates of cohort size range. For the former, this included cohort length estimates with minimum lengths below 0mm or maximum lengths above the literature-derived maximum asymptotic body length. For the latter, this included cohort length estimates where the range of possible lengths exceeded 40% of the value of maximum asymptotic body length for the latter. It is unlikely that fish of the same age and captured in the same location would have such extreme variation in achieved sizes. We also merged identified cohorts with more than 50% overlap in estimated size confidence intervals, as this is not enough separation to clearly identify distinct age groups. From the remaining data, we identified the first week each summer in which age-0 fish were identified, then tracked the growth of that cohort through the following weeks.

Next, the lower and upper limits of length range of the age-0 cohort for every week in the sampling period was estimated. This was necessary because data volume limitations in some weeks prevented the Bayesian and mixed modeling approach from identifying an age-0 cohort. Lifetime fish growth is usually modeled using the von Bertalanffy equation, which is a specialized case of logistic growth. Beach seine operations took place over 15 weeks in each summer, with the focal species only persisting in the area for a portion of that time. Rapid growth over this relatively short period supports treating the observed growth rate as a linear function. Therefore, linear models were fit to the weekly upper and lower limits of cohort length range as estimated in the previous step. Fish with lengths within the modeled limits of each week were assigned to the age-0 cohort. Fish not assigned to the age-0 cohort were removed from further growth analyses.

The weekly length distribution of both age-0 silverside and age-0 herring in each year often exhibited higher variance in later weeks as compared to earlier weeks. Weighted least squares regressions were used to control for this heteroskedasticity. In these models, lengths of the selected fishes were the response variable and week of year was the explanatory variable. The weekly growth rate of the age-0 cohort of each species (in millimeters) in each year was therefore defined as the slope of the regression fit to the weekly age-0 cohort length frequency distribution data. Two-sided Welch’s t-tests were used to compare weekly growth rates within each species between years with an annual temperature above the CRP average (“warmer” years) and those with an annual average temperature below the CRP average (“cooler” years).

3.3.2 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 was 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, the catch data used in these GAMs encapsulates the entire size range of fishes and does not focus on a single age cohort. 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.

Environmental variables tested as explanatory variables included surface temperature (C), substrate type, weather conditions, tidal state (rising or falling), and water level (m) as compared to the Mean Low Low Water (MLLW) datum at the time and location of each seine haul. Surface temperature data were collected immediately after each seine. Though salinity data were also collected, there were several long gaps in data availability from sensor failures. Thus, salinity could not be included as an environmental variable. Substrate type at each sampling site was categorized as mud, sand, or sand/gravel mixture according to an estimate of average grain size and substrate presence within the swept area. Weather conditions were categorized into sunny, partly cloudy, overcast, or rainy. Both substrate type and weather conditions were included as fixed-effect factor variables. Tidal data were extracted from the nearby Portland Harbor tide gauge. Water level data were extracted at native 6-minute frequency, then interpolated and smoothed to a 1-minute frequency over every summer when sampling occurred. The timestamp of each seine set was then used to determine tidal state (rising or falling; fixed-effect factor variable) and approximate water level as compared to the MLLW datum. 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. It is unlikely that such small shifts will result in noticeable ecological changes.

Temporal variables included week of year and year. Year was treated as a fixed-effect factor variable so that the effect of each year on catch could be estimated independently. Week was incorporated as an interaction term with surface temperature. This was done to address our hypothesis that increasing temperatures would result in shifting seasonal phenology for herring. If warming signals and temperature maxima are earlier each year, herring use of the nearshore area will end earlier, and herring catch may decrease. The interaction between week of year and surface temperature could also highlight age-specific temperature preferences, particularly for silversides.

The final term included was a random effect for each site. We were not necessarily interested in characterizing the difference in catch between sites, but it 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 phytoplankton, salinity). The sites in our study design can be thought of as random samples along the gradients of those unmeasured environmental conditions. Including site as a random effect will better capture the full variability of catch along these gradients than if site was a fixed effect, where levels are assumed to be independent. Sites were ordered roughly north to south, with the first three sites inside the Presumpscot River. Term selection was conducted according to the “double penalty,” or “null space penalization,” approach (Marra & Wood 2011). This enables shrinkage for all smoothed terms and essentially penalizes insignificant terms to 0 through shrinking function components both in the range space and in the null space.

3.3.3 Spatiotemporal community structure

The abundances and distributions of taxonomic groups are spatially and temporally variable along environmental gradients in highly heterogeneous ecosystems like nearshore areas. 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 help predict fish distributions and community structures under alternate climate scenarios and environmental patterns.

It should be expected that the relative proportion of species is variable across the different sampling sites within Casco Bay, as each site has a unique set of static and dynamic environmental characteristics. Seasonal warming will also trigger shifts in habitat use patterns, especially for diadromous and oceanodromous fishes. 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. Interannual variability was not considered at this stage, so results were pooled across all years. The seasonal periods were set to Early Summer (weeks 24-28 of each year, inclusive), Mid Summer (weeks 39-33), and Late Summer (weeks 34-39). CPUE for each species was calculated as the number of conspecifics caught divided by the number of seine hauls per seasonal period. We then filtered the data 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. We chose to use encounter rates rather than total abundance as thresholds in this test to avoid bias towards schooling or shoaling fishes. After this process, 10 species remained of 42 total species encountered.

Community composition analysis was conducted using nonmetric multidimensional scaling (NMDS), which ordinates data without assuming linear relationships or distance metric properties (Clarke 1993). This approach was applied to Bray-Curtis similarity matrices. Because we standardized catch by effort in the previous step, no transformation was applied. The goodness of fit of the data across the two ordination axes was indexed by the stress coefficient, which represents the distortion involved in reducing multidimensional data to fewer dimensions. If the resulting 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. This is a non-hierarchical method used to minimize the distance between data points and the center of an assigned cluster. The silhouette and total within sum of squares (WSS) methods were used to identify the most appropriate number of clusters. We did not *a priori* assign data points to clusters by seasonal period or location within the study area, as we expected both spatial location and seasonal progression 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 dissimilarity between the identified clusters’ community composition (Clarke 1993). Average CPUE for each species within each cluster was plotted on a log scale to help visualize both SIMPER results and the change in community composition in space and time. 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 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.

**4 Results**

4.1 Species caught

In total, 659 seine hauls across 132 unique sampling days met data collection standards and were included in our analyses (Table 1 – Catch). Total catch was 159,590 individuals across all 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 sandlance (*Ammodytes* *americanus*), Atlantic tomcod (*Microgadus* *tomcod*), Atlantic herring (*Clupea* *harengus*), alewife (*Alosa* *Pseudoharengus*), mummichog (*Fundulus* *heteroclitus*), winter flounder (*Pseudopleuronectes* *americanus*), Atlantic silverside (*Menidia* *menidia*), and green crab (*Carsinus* *maenas*). These species comprised over 99% of total fish caught in all seine hauls. 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, as they were encountered in 68% of all seine hauls and with few exceptions were detected at least once at every site, every year.

The remaining 32 species were mainly juvenile fishes native to the Gulf of Maine or connecting freshwater systems, but also included permit (*Trachinotus* *falcatus*), crevalle jack (*Caranx* *hippos*), white mullet (*Mugil* *curema*), and summer flounder (*Paralychthis* *dentatus*). Permit and crevalle jack are among an assemblage of tropical or subtropical species that typically reside south of Cape Cod, but may be advected northward into the Gulf of Maine by eddies or warm core rings of the Gulf Stream Current (Hare et al. 2002, Wood et al. 2009, O’Neill et al. 2025). Species within this group are colloquially known as “Gulf Stream Orphans.” Though not officially recognized as part of this group, white mullet and other Mugilidae fishes are also subtropical species unknown to be breeding in or regularly migrating to regions north of Cape Cod (Bigelow & Schroeder 1953, Ayvazian et al. 1992). Summer flounder are a temperate species more commonly found south of Cape Cod, but some individuals may make seasonal migrations to coastal Maine and are not considered Gulf Stream Orphans (Bigelow & Schroeder 1953).

4.2 Nearshore surface temperature anomaly

Smoothed surface temperature data from the Portland Harbor tide gauge indicated that 2014-2015 and 2017-2019 had average annual temperature anomalies below the CRP average (Figure X – Temperature). These “cooler” years were characterized by sustained periods of daily temperatures beneath the modeled daily average in winter (December-February, inclusive) and spring (March-May, inclusive), and limited time above the modeled daily average in summer (June-August, inclusive). 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 – Seasonal Temperature).

4.3 Weekly growth rates

The process of filtering length frequency distribution data to include only the age-0 cohorts of fish produced between 2 and 5 weeks of data per year to estimate herring 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. Herring growth rates 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. The earliest week of age-0 herring detection was generally in week 25 (SD: 1.2 weeks), and the latest week detection varied between week 26 and week 36 (mean: week 30, SD: 3.2 weeks). The wide range of 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 years warmer than the CRP average and from 1.2 to 5.0 mm per week in years cooler than the CRP average. There are many studies on larval herring growth rates in the western North Atlantic, but few for post-metamorphosis juveniles with which we can compare our results. There is some evidence supporting growth rates of 2-2.5 mm per week for age-0 herring in the Bay of Fundy during the spring and early summer, but this is based on a single year of data collection (Das 1972). Welch’s t-tests indicated no significant difference when comparing mean growth rates between warm and cool years (t(4.907) = 0.467, p=0.661).

Silversides were caught more consistently than herring, and between 2 and 8 weeks of age-0 length frequency data remained after data filtering. We excluded growth rates estimated for 2024 because of the gap in sampling data noted above. The earliest week of age-0 silverside detection was generally in week 29 (SD: 1.8 weeks), and the last 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 years warmer than the CRP average and 2.6 to 4.9 mm per week in years cooler than the CRP average. Growth rates for post-metamorphic age-0 Atlantic silversides reported by other studies using a variety of methods to calculate growth have converged on estimated average growth rates around 5 mm per week for silverside populations in coastal New England (Conover & Ross 1982, Barkman & Bengtson 1987, Pringle & Baumann 2019). Welch’s t-tests indicated growth rates were significantly different between warm and cool years (t(4.758)=-3.298, p=0.035), with a mean growth of 3.5 mm per week in cool years and a mean growth of 5.3 mm per week in warm years.

4.4 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. 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 were not significantly different, but there was a significant negative effect of mud substrate as compared to sand/gravel. All years except 2017 and 2020 had a significantly negative effect on catch as compared to 2014. The strongest negative effect was for 2023, which had the lowest mean herring catch per unit effort because herring were caught in only one week during the sampling period.

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. 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 catch. Compared to full sun, overcast conditions had a positive effect on catch. There was no significant effect of partly cloudy or rainy conditions, though it should be noted that there were few samples taken in the rain. When holding all other variables fixed, the random effect by site has 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 as compared to 2014. The strongest positive effect was for 2020, which also had the highest mean silverside catch per unit effort.

4.5 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 reveals that sandlance, herring, and silversides have the strongest associations with the ordination configuration. 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 groups (r= 0.761, p < 0.0001). Average CPUE for each species in each cluster was calculated and visualized, which made obvious that cluster a typically has high herring catch, cluster c has high silverside catch, and cluster b has generally low catch for all species. SIMPER analysis across clusters provided quantitative confirmation of this visual analysis. When comparing composition of cluster a to cluster b, herring (p=0.001, Contribution = 62.5%), sandlance (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 sandlance, 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 higher average CPUE in cluster a, and silverside had higher average CPUE in cluster b. 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 as compared to cluster b.

When plotted across space and time, divergent spatiotemporal patterns of habitat use can be identified. 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. Sandlance has the highest CPUE of all species within this cluster, but it should be noted that sandlance catch is uncommon and mostly occurred in the late summer period at the two southernmost sites. In early summer, sites in and near the Presumpscot River had generally low CPUE for all species and were best described by this cluster. In the mid-summer period, four sampling sites across the study region were best described by cluster b. One of these sites was near the mouth of the Presumpscot River and, again, had a generally low CPUE for all species of interest. The other three sites were all in the southern half of the study area and had relatively high CPUE for sandlance. By the late summer period, only the site furthest up the Presumpscot River (with generally low CPUE for all species of interest) and the site furthest south (with generally high sandlance CPUE) were best described by cluster b. Cluster c was absent in the early summer period, but by the mid-summer period seven sites in and around the Presumpscot River were best described by this cluster. In the late summer period, nine sites across the study area belonged to this cluster.

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 distinct clusters. ANOSIM confirmed a significant difference in community composition between groups (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. SIMPER results highlighted herring as contributing a statistically significant amount of the dissimilarity between the clusters (p=0.001, Contribution= 67.6%), with higher average CPUE in cluster b. 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 we did not see an obvious fit between average annual temperature anomaly and community composition, 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.

**5 Discussion**

The complicated nature of nearshore ecosystems makes them inherently difficult to comprehensively observe. Many studies have identified individual North Atlantic species’ responses to hydroclimatic changes (Pershing et al. 2015, Le Bris et al. 2018), and others have focused on responses at higher levels of ecological organization at large spatial scales like the Northeast US Continental Shelf Large Marine Ecosystem (NEUS LME; Lucey & Nye 2010, Fenwick et al. 2024). We were interested in identifying temperature-linked changes to community ecology in GoM nearshore regions due to their connections to many ecologically and economically important species and several levels of biological organization. We hypothesized that the growth rates and annual abundances of Atlantic herring and Atlantic silverside, as focal species

, would result in opposing responses to increased surface temperature.