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Effects of ocean climate on the length and condition of forage fish in the Gulf of Alaska

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Abstract

Climatic drivers of the size and body condition of forage fish in the North Pacific are poorly known. We hypothesized that length and condition of forage fish in the Gulf of Alaska (GoA) vary in relation to ocean temperature on multiple scales. To test this hypothesis, we analyzed morphometric data for capelin (*Mallotus catervarius*) and Pacific sand lance (PSL; *Ammodytes personatus*) sampled by a seabird (*Cerorhinca monocerata*) in two regions of the GoA, 1993–2016. Based on previous studies, we predicted that capelin length and body condition (Fulton's K) would be negatively related to the Pacific Decadal Oscillation (PDO) and sea surface temperature (SST), whereas PSL length and condition would be positively related. Interannual variation in length and body condition was evaluated relative to seasonal values of ocean climate using regression. Forage fish length and condition varied interannually, between sampling regions, and were dependent on the size/age class of the fish sampled. As predicted, length and body condition of capelin (mostly age 1+) were negatively related to the PDO and SST. Relationships with ocean climate for PSL varied by size/age class: positive for putative age-0 fish and negative for putative age-1+ fish. We conclude that our hypothesis was supported for capelin and partially supported for PSL. This study demonstrates that ocean climate determines key morphometric characteristics of forage fish that may relate to interannual variation in the energetic value of prey, and provides an example of how seabirds can be used to obtain specimens for evaluations of potential prey quality.

Keywords: forage fish, condition, ocean climate, interannual variation, seabird

Running head: Forage fish condition and ocean climate

Introduction

Forage fish quantity and quality have important effects on the ecology and vital rates of marine top predators, including seabirds (e.g., Suryan et al., 2002), marine mammals (e.g., Trites & Donnelly, 2003), and large predatory fish (Rose & O'Driscoll, 2002). In particular, the "junk food" hypothesis describes ways in which lower food quality may negatively affect marine predator population parameters (Alverson, 1992; Rosen & Trites, 2000; reviewed by Osterblom et al., 2008). While it has been well established that prey quality is important to aspects of predator success, drivers of variation in quality remain poorly understood. Only a few studies have been conducted over a long enough period of time to examine interannual or lower-frequency variation in prey quality (e.g., Carscadden et al., 2002; Wanless et al., 2005, 2018). Developing a robust understanding of variation in prey size and energetic value is becoming more important with increasing climate variability and unidirectional change (IPCC, 2013), which are likely to affect prey quality through related factors such as prey size and mass (Sheridan & Bickford, 2011).

Prey quality can be assessed by measurements of whole-body lipid and/or protein content, which directly reflect the energetic and nutritional value of prey (e.g., Van Pelt et al., 1997; Payne et al., 1999; Anthony et al., 2000; Vollenweider et al., 2011; von Biela et al., 2019). Spatial (e.g., Abookire & Piatt, 2005) and temporal variation (e.g., Montevecchi & Piatt, 1984; Robards et al., 1999a; Litz et al., 2010; Vollenweider et al., 2011) in lipid and protein content has been documented and in some cases has been related to the ocean conditions that alter the planktonic prey base that forage fish consume (Litz et al., 2010). Variation in energy content is primarily related to variation in lipid content and length (von Biela et al., 2019). Lipid content can also be inferred by measurements of body condition that index mass (g) scaled to size (mm; Robards et al., 1999a; Logerwell & Schaufler, 2005). Consequently, measurements of body condition, such as the commonly used Fulton's K index (Ricker, 1975), can be used as a proxy for prey quality in space and time (Robards et al., 1999a; Carscadden & Frank, 2002; Davoren & Montvecchi, 2003; Pangle & Sutton, 2005).

In this study, we derive length and a body condition index from forage fish samples obtained during studies of seabird diets in the Gulf of Alaska (GoA) taken over multiple decades (e.g., Hatch & Sanger, 1992; Sydeman et al., 2017a; Piatt et al., 2018). This application of predator-based sampling (e.g., Mills et al., 2007; Thayer et al., 2008), has been used to study basin-scale and annual to decadal variation in forage fish availability in this region (Sydeman et al., 2017a; Piatt et al., 2018) and elsewhere in the world. For example, using common murres (*Uria aalge*) and Atlantic puffins (*Fratercula arctica*) as samplers in the North Sea, Wanless et al. (2005, 2018) showed that the energy content of sandeel (*Ammodytes marinus*) and sprat (*Sprattus sprattus*) prey were extraordinarily low in 2004, and that the overall quality of sandeels declined steadily over a 40-year sampling period. Similarly, in a decade-long study in the Northwest Atlantic, Davoren and Montevecchi (2003) showed that body condition of capelin sampled by murres declined through time, accompanied by a synchronous decline in the condition of murre chicks.

An important assumption in these studies is that seabirds sample prey in proportion to the abundance and/or availability of prey in the environment. Rarely are contemporaneous data collected on diet and prey availability, but in cases where this has been done, diet composition reflects prey abundance. This includes studies on the take of i) age-0 cod (Gadidae) by puffins in the GoA (Hatch & Sanger, 1992), ii) age-0 rockfish (*Sebastes* spp.) by murres in the central California Current (Mills et al., 2007), iii) age-0 and age-1+ Pacific sand lance (PSL; *Ammodytes personatus*) and capelin (*Mallotus catervarius*) by puffins in the Gulf of Alaska and Aleutian archipelago (Piatt et al., 2018), and iv) age-0 and older anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) by Cape gannets (*Morus capensis*) in the southern Benguela ecosystem (Crawford et al., 2019). We therefore assume that sampling in proportion to abundance also occurred in this study. Another critical assumption is that the seabirds sample prey sizes in proportion to those available in the environment.

The samples used in this study were obtained from rhinoceros auklets (*Cerorhinca monocerata*), a medium-sized (~500 g) puffin (Friesen et al., 1996) with the capacity to search and forage to 10–60 m depth (Burger et al., 1993; Kuroki et al., 2003; Cunningham et al., 2018), typically 30–80 km from a breeding colony (Cunningham et al., 2018). Here, we focus on two key forage fish of the Alaskan North Pacific: capelin and Pacific sand lance. Our study region spans the eastern to central-northern GoA, an ecosystem highlighted by a rich and abundant community of marine mammals, fish, and seabirds, as well as valuable fisheries for salmon, cod, and halibut. Biological productivity and the controls of energy flow from lower to upper trophic levels in this region are related to water movement of the Alaska Gyre, winds and upwelling/downwelling, ocean temperatures, and stratification (Brodeur & Ware, 1992; Stabeno et al., 2004, 2016; Waite & Mueter, 2013).

Our focal forage fish species have different habitat preferences within the cool subarctic/boreal waters in which both species reside: PSL prefer warmer, coastal waters (Abookire & Piatt, 2005; Sydeman et al., 2017a; Piatt et al., 2018), whereas capelin are found in deeper, colder shelf waters (Abookire & Piatt, 2005; Logerwell et al., 2007). In this study, we test the hypothesis that forage fish body condition varies in relation to large-scale to regional ocean climate parameters that regulate ecosystem productivity, primarily temperature. We predict that variability in ocean climate affects the size (proxied by length) and body condition of these species in opposing directions, with temperature relating positively to PSL size and body condition and negatively to capelin size and body condition. Past research has primarily focused on species composition and abundance in predator diet studies, but some life history events, such as breeding failures, cannot be explained by diet composition. This study is significant because understanding environmental effects on prey quality is useful for predicting impacts on predator communities and fisheries in the face of continued climate variability.

Methods

Forage fish data

Other than for herring (*Clupea pallasii*), annual abundance estimates are not available for any forage fish species in Alaska. From the 1970s to the present, however, summer studies of puffin food habits have been conducted as part of the Alaska Maritime National Wildlife Refuge (AMNWR) seabird monitoring program as well as the sampling programs conducted by the U.S. Geological Survey Alaska Science Center and the Institute for Seabird Research and Conservation (Byrd, 2007; Hatch, 2013; Schoen et al., 2018). Field research sampling methods are detailed by Hatch and Sanger (1992) and AMNWR (2018) and the database housing the data collected from these monitoring programs, the Alaska Puffin Diet Database, is described in more detail elsewhere (Sydeman et al., 2017a; Piatt et al., 2018). In brief, researchers collected the fish that were caught as prey by adult puffins and brought to colony burrows that contain their chicks. These fish were identified and measured in the field or frozen for measurement in the lab; the vast majority was measured in the field. We used data from two sites in the GoA: Middleton Island (59.438°N, 146.327°W), in the northern GoA region, and St. Lazaria Island (56.987°N, 135.705°W), in the eastern GoA region (Figure 1). These sites were the most suitable for use in our study because of their locations in the GoA and because they had the most complete time series of the sites in the seabird monitoring program.

In this study, we use measurement data for capelin and PSL sampled by rhinoceros auklets between 18 June and 26 August each year, from 1993–2016. These fish are among the most important forage fish in the Gulf of Alaska and there were large sample sizes available for them at our study sites (Table 1). The data were filtered for records with length (mm) and mass (g) measurements on whole fish. Records with no mass or length measurement were omitted from analysis. Our database had more records that included total length than fork length. Therefore, to use all available data, we converted fork length measurements to total length with the following regressions (established from data from fish samples with both measurements): capelin total length = 4.944 + (1.012*fork length), $R^2 = 0.95$, n = 1685; PSL: total length = 0.880 + (1.023*fork length), $R^2 = 0.99$, n = 2298. For further analysis we used the measured or predicted total length data. We assume length to be an indicator of age classes under average environmental conditions; under anomalous circumstances, some fish may be smaller (e.g., von Biela et al., 2019), and may not fall precisely into these age classifications. Nevertheless, under this assumption, length frequency distributions were used to identify size/age classes for each species.

We calculated Fulton's K index of body condition (Ricker, 1975) using the following equation:

$$K = \left(\frac{mass}{length^3}\right) * 100$$

We chose this condition index because it is commonly used in fisheries science (Nash et al., 2006) and was previously found to be a suitable descriptor of variation in body condition in capelin and PSL (Carscadden & Frank, 2002; Baker et al., 2019). Fulton's K represents variation primarily in the mass of fish, which can be variable even at a constant length (see Tables S1, S2).

To obtain robust time series, we omitted "site-years" when <10 individual fish were measured (by species; see Table 1 for final number of years and fish). Trends in the annual K were described with linear and quadratic regression, weighted by sample size in order to adjust for years with few specimens. While a few statistically significant trends were found (Tables S3, S4), these data were not detrended for analysis because most of the variables had no trends. We employed analysis of covariance (ANCOVA) to test for interannual variability in K, adjusted for sampling date. Additionally, we used an unpaired two-sided t-test to test for differences between the mean length and condition at sites within species (Middleton and St. Lazaria for each of capelin, PSL age 0, and PSL age 1+).

Environmental data

We used two environmental data sets to examine the relationship between ocean climate and forage fish length and condition index: the basin-scale Pacific Decadal Oscillation (PDO) index and the local sea surface temperature (SST) over a ~4° latitude x 4° longitude area around each island site, encompassing most of the foraging range of the birds. The PDO is defined as the first Empirical Orthogonal Function of detrended SST poleward of 20°N and represents an index of ocean temperature-climate variability in the North Pacific basin (Mantua & Hare, 2002). Monthly time series were averaged to produce the seasonal values winter: January–March (JFM), spring: April–June (AMJ), and summer: July–September (JAS). Each SST and PDO season was compared to annually-averaged length and condition for each size/age class of fish separately to avoid model over-fitting due to SST autocorrelation and because lagged relationships with the fish sampled in June–August may indicate different mechanisms of environmental influence. SST data were obtained from the Hadley Center HadISST1 reconstructed data set (https://www.metoffice.gov.uk/hadobs/hadisst/), which provides monthly 1-degree data for the study period (1993–2016). We selected a "coastal" box (52–56°N, 136–132°W) for St. Lazaria and a "Gulf of Alaska" box (54–58°N, 144–138°W) for Middleton (Figure 1), over which we averaged SST values to obtain one local SST index for each site. Seasonal SST time series did not have significant linear trends at any site, while quadratic regressions showed significant ($p < 0.05$) fits for spring (April–June) in both regions. This was largely due to the SST anomalies in 2014–2016 associated with the marine heatwave (Figure S5; Di Lorenzo & Mantua, 2016). When the 2015–2016 values were removed, these quadratic regressions were not significant ($p > 0.05$) and therefore we did not detrend the SST or PDO data.

Modeling the relationships between fish indices (length, K condition index) and ocean climate time series (SST, PDO) was done using weighted multiple regressions. Each regression included one fish index as a dependent variable and only one seasonal ocean climate index at a time as the independent variable. We tested linear and quadratic (2nd degree polynomial) values of the ocean climate indices. The models were first evaluated by discarding any non-significant models using a p-value ($p < 0.05$) criterion. In no case were the quadratic models significant (Tables S5, S6). From the resulting significant models, we selected the best model for each fish index and each climate index, but across all seasons, based on the lowest Akaike information criterion (AIC) statistic. Secondarily, we verified the selection of the best model by examination of the R^2 value; a higher R^2 value indicated greater explanatory power.

Results

Length-frequency distributions

Due to the timing of sampling corresponding to the May–July spawning period for capelin, most capelin sampled by rhinoceros auklets were age 1 and older fish (hereafter age 1+), though a few small, probably age-0 fish, were also sampled (Figure 2 a,b; also see Naumenko, 1966; Pahlke, 1985). Owing to the few age-0 fish in our samples, we did not stratify capelin by size/age class for analyses. In contrast, a distinct bimodal structure for length was evident for PSL (Figure 2 c,d). Typically, PSL < 100 mm in length during summer are assumed to be age-0 fish, whereas fish ≥ 100 mm are assumed to be primarily age 1+ (Robards et al., 1999b; Arimitsu et al., 2018; Cunningham et al., 2018). It is possible, however, that in years of anomalous environmental conditions, PSL growth diminishes sufficiently such that some age-1 fish are misclassified as age 0 (von Biela et al., 2019). Since our data set included large samples of both smaller and larger PSL, we stratified analyses by these size/assumed age classifications to examine differences between these groups. There were significant differences in average length of fish sampled between regions (capelin: $t = -12.26$, $p < 0.0001$; PSL: $t = 4.60$, $p < 0.0001$), with larger fish for both species (PSL age 1+) found at Middleton in the northern GoA (Figure S1).

Fulton's K index of body condition

Condition indices of capelin and age-0 PSL were significantly higher in the eastern GoA (St. Lazaria) in comparison with the northern region (Middleton), however, there was no significant difference in K between regions for age-1+ PSL (Table 2). There was significant interannual variability in fish condition for capelin and age-1+ PSL at both sites and age-0 PSL at Middleton (Table 3, Figures 3, S2). For capelin and PSL age 1+ we found that anomalies oscillated between positive and negative over the course of the time series in cycles of 4–5 years. Age-0 PSL showed less interannual variability in general (Table 3). There was a significant effect of sample date for capelin and both PSL age classes at Middleton, and PSL age 1+ at St. Lazaria, but not for capelin and PSL age 0 at St. Lazaria Island (Table 3). In all cases, the regression coefficient for sampling date was negative, indicating a slight decline in condition over the course of the summertime sampling period (Figure S3).

Relationships with environment

Capelin length was inversely related to spring (AMJ) SST and PDO at Middleton (Table 4, Figure 4). Spring SST was a better predictor of capelin length than the PDO, with 52% of the variation in length explained by SST (Table 4). No relationship between capelin length and SST or PDO was established at St. Lazaria. At both Middleton and St. Lazaria islands, capelin body condition was inversely related to SST and the PDO, explaining between 42% and 68% of the variation in capelin body condition (Table 5, Figure 5). The summer (JAS) SST effect was more pronounced at Middleton and spring (AMJ) temperature (SST and PDO) was the most important at St. Lazaria.

Environmental relationships for PSL varied by size/age class. Winter (JFM) SST and PDO explained 41–46% of the variance in the length of age-0 PSL at Middleton, and the relationships were positive, in accordance with predictions (Table 4, Figure 4). However, no relationships were found for length of age-0 PSL at St. Lazaria. Spring (AMJ) SST and PDO explained 23%–26% of the variance in the length of age-1+ PSL at Middleton, but these relationships were negative, in contrast to our predictions (Table 4, Figure 4). Summer (JAS) PDO explained 25% of the variance in the body condition of age-0 PSL at St.

Lazaria, but no relationships were found with Middleton data (Table 5, Figure 5). For age-1+ PSL, winter (JFM) SST accounted for 36% of the variance at Middleton, but no relationships were found for St. Lazaria (Table 5).

Discussion

Based on previous work that showed apparent habitat affinities with opposing responses by capelin and PSL to cool vs. warm ocean temperatures (Sydeman et al., 2017a), we predicted that capelin length and body condition would show negative relationships with both SST and the PDO, whereas the relationships for PSL length and body condition would be positive. We found support for our hypothesis for capelin, however, temperature effects on the length and condition of PSL depended on their size/assumed age classes. For age-0 PSL, our findings suggest a positive relationship between length and winter SST, supporting our hypothesis, which may reflect earlier hatch dates and/or higher metabolic and growth rates (using length as a proxy) under warmer winter ocean conditions.

Assuming growth is slower for age-1+ PSL than age-0 PSL, the decrease in PSL age-1+ body condition with increasing temperatures could be related to poorer feeding conditions under warmer ocean conditions (Daly & Brodeur, 2015; Brodeur et al., 2019). This mechanism could potentially affect both age-1+ PSL and capelin. In support of this idea, von Biela et al. (2019) found that age-1 PSL experienced unusually low growth in 2015–2016 during the marine heatwave in the region (see Figure S1c; Di Lorenzo & Mantua, 2016). Slow growth and low abundance in sandeel populations in the North Sea was related to poor feeding conditions (MacDonald et al., 2019) and it's reasonable to assume similar effects during the Northeast Pacific marine heat wave. Moreover, our selected models almost always included a lag of at least one season to the summer season of fish sampling. As noted in other studies (e.g., Byrd et al., 2008; Shultz et al., 2009; Zador et al., 2013; Sydeman et al., 2017b), these relationships indicate that ocean climate in seasons prior to the summer growing period has notable effects, presumably operating through changes in production at lower trophic levels.

A key assumption of this study is that the samples provided by rhinoceros auklets are representative of the size and age classes of these forage fish in the environment. Differences in the lengths of capelin and PSL by region and year may be related to the availability of different size fish in the foraging habitat surrounding the islands where sampling took place. Recent work has shown that seabirds and other predators sample species in proportion to their availability (Bertram & Kaiser, 1993; Piatt et al., 2018) and tagging studies indicate that seabirds sample PSL where net sampling methods underperform (Cunningham et al., 2018). Less is known, however, about whether seabirds sample size of prey in proportion to size availability. This same assumption would presumably also apply to any sampling device used, including net sampling techniques.

Length frequency distributions and life history characteristics

In the GoA, capelin spawn inshore during May–July, and coastal areas may provide nursery grounds for larval fish (Brown, 2002; Brown et al., 2002; Arimitsu et al., 2008). In comparison, PSL spawn in shallow water during an extended period in fall and winter and peak hatching occurs in February–March (Robards et al., 1999b; Doyle et al., 2009). Sand lance begin spawning at roughly 20 months (age 1), and most spawn at age 2 or 3, while smaller percentages survive to age 4–6 (Robards et al., 1999b).

Since spawning occurred during the previous fall/winter, age-0 PSL are of suitable size for seabird predation in the June–August sampling period. In contrast, due to the timing of the capelin spawning season, few age-0 capelin would be of the size suitable for sampling by the birds during summer, and correspondingly we see few age-0 capelin in our samples. Indeed, the timing of capelin spawning may have a stronger effect on sampling at Middleton, which is roughly 100 km offshore of the nearest known spawning location (Arimitsu et al., 2018). On the other hand, St. Lazaria is coastal, so larval/juvenile capelin may be more abundant in this region. While we did not specifically analyze age (e.g., using otoliths) at either site, the bimodal distribution corresponding with small (< 100 mm) and larger (≥ 100 mm) classes of PSL generally indicate that both age-0 and age-1+ fish were taken, and in similar amounts. In Prince William Sound in 2016, however, von Biela et al.

(2019) found that age-0 and age-1 PSL lengths overlapped, but this was during the intense marine heatwave in the region. Potential bias in our ability to correctly classify age class from length is a possible issue in our study, which included these years. However, the 2014–2016 marine heatwave in the North Pacific has been described as unprecedented (Di Lorenzo & Mantua, 2016), meaning that the data from Prince William Sound during these years are probably anomalous. Otherwise, such extreme length-at-age anomalies are rare in *Ammodytes* (Macer, 1966; Wanless et al., 2018).

Seasonal variability condition indices

The body condition of capelin and PSL varied seasonally and depending on the date of sampling. Two main factors influence seasonal variability in condition. First, the condition of females of both capelin and PSL varies with the stage of reproductive maturity because gravid females have higher mass/length ratio and energy density than males (Montevecchi & Piatt, 1984; Carscadden & Frank, 2002; Robards et al., 1999a). This can create a substantial difference because egg masses can increase the weight of gravid female capelin by up to 30% (Montevecchi & Piatt, 1984). Thus, a sample containing both males and females could produce a slightly biased (higher) condition index if a large proportion of the sample was gravid females. This could have affected our findings for capelin because sampling of fish (June–August) partially overlaps with the spawning period of capelin (May–July) in Alaska (Arimitsu et al., 2008). It should not have affected our PSL samples, however, since they typically spawn later in the year (Robards et al., 1999a). Second, seasonal variability in body mass may be related to life history strategies for lipid storage. Capelin store lipid in the fall and use it slowly over winter (Montevecchi & Piatt, 1984), and then more rapidly as they migrate from offshore to nearshore for spawning in the spring. Lipid content is lowest prior to and during spawning (Montevecchi & Piatt, 1984; Buren et al., 2014). By August, juveniles and surviving adults begin to quickly regain lipid reserves. PSL exhibit a similar seasonal cycle, except that peak lipid storage occurs in June–August and stored fat declines steadily until they spawn in the fall (Robards et al., 2002). Thus, for both capelin and PSL, the seasonal variability in timing of spawning and lipid storage probably contributes to the annual variability in body condition described here.

Regional and interannual variation in condition

Condition values for capelin and age-0 PSL were generally higher in the eastern GoA (St. Lazaria Island) than in the northern GoA (Middleton Island); no differences between the sites were found for age-1+ PSL (Table 2). Though the differences between these sites were small, there are a number of factors that may explain them, including environmental factors and/or variation in sample size. St. Lazaria Island is a coastal site located < 20 km offshore (56°N), whereas Middleton is situated at the edge of the continental shelf, 75 km offshore in the northern GoA (59°N). Both islands and their biota may be influenced by the Alaska Current, formed as the northern bifurcation of the North Pacific Current (Hollowed & Wooster, 1992). Local physical oceanographic processes, however, differ substantially. St. Lazaria is located closer to the bifurcation streamline of the North Pacific Current (Cummins & Freeland, 2007), and in a coastal domain where freshwater runoff and downwelling are important factors to ecosystem productivity. In contrast, Middleton is located in more oceanic waters and is less influenced by coastal enrichments. Conditions at both locations are influenced by the PDO, although larger influence has been hypothesized for the northern GoA than on the eastern side (Lluch-Cota et al., 2001). Due to this oceanographic variation, it is possible that the coastal waters near St. Lazaria are, in general, more productive than the offshore waters near Middleton. Indeed, Waite and Mueter (2013) showed that satellite-derived chlorophyll-a indices in May–July, prior to and overlapping the beginning of our sampling period, were generally higher in southeast GoA than in the northern-central GoA. Whether this variation in phytoplankton standing stocks links to variation among higher trophic levels is currently unknown.

Interannual variability in body condition for capelin and PSL was significant in almost all cases, with an exception of age-0 PSL at St. Lazaria. Young-of-the-year fish typically distribute energy toward growth rather than lipid storage (Robards et al., 1999a; Burril et al., 2018), so this finding is not surprising (Brosset et al., 2015). In another study overlapping with ours in study period, the energy density of age-0 PSL in Prince William Sound did not vary in 2012–2016, despite large variation in physical conditions between years (von Biela et al., 2019). Similarly, there was relatively low interannual variability in condition of age-0 PSL at Middleton, though condition for these fish was much lower in one year, 2008, following a very cold and late spring (Figure 3; Hatch, 2013).

Temperature and variation in condition

Models including SST or the PDO explained a relatively large percentage (25–68%) of the variance in capelin and PSL body condition in the GoA. SST and PDO had negative effects on capelin and age 1+ PSL body condition, indicating lower body condition with warming for these larger and older fish. The effects of SST and the PDO, however, were positive for age-0 PSL, suggesting that warmer ocean temperatures are important for younger, developing fish, provided that food for them is not limited. It was summertime SST or PDO that related positively to body condition of age-0 PSL, whereas wintertime ocean climate was related negatively to body condition of older fish.

In contrast, Carscadden and Frank (2002) found no correlation between capelin body condition and temperature in Newfoundland, however, they did find high capelin condition during the 1980s followed by a decade of low condition in the 1990s. Later studies revealed that this decadal-scale change in condition coincided with a regime shift in which capelin and cod (*Gadus morhua*) populations both crashed after 1990 and remained extremely low until after the mid-2000s (Rose & Rowe, 2015; Buren et al., 2014, 2019). In this region, zooplankton stocks also crashed during the 1990s so the food supply for capelin may have been limited (Carscadden & Frank, 2002). Buren et al. (2014) found evidence that capelin population biomass was indirectly affected by temperature via effects on timing of spring sea ice retreat and a corresponding change in phenology of primary and secondary productivity. Elsewhere, evidence suggests that changes in zooplankton prey communities from rich- to poor-quality species, coupled with an increase in fish metabolic rate under warming, were responsible for a reduction in body condition of juvenile salmonids off Oregon (Daly & Brodeur, 2015; Brodeur et al., 2019). Similarly, long-term studies of anchovy and sardine in the Mediterranean Sea suggest that while temperature changes may be associated with changes in body condition (especially in sardine), the most consistent and significant predictor of body condition was meso-zooplankton concentration (Brosset et al., 2015). In summary, evidence suggests that marked, persistent changes in body condition indicate changes in bottom-up processes that affect food webs and these are often coincident with or driven by temperature changes that may or may not be associated with regime shifts.

That said, there were no obvious signs in our study of effects from the 1997–1998 El Niño event, or the unusual climate conditions that took place in 2005 that affected marine food webs around the northeast Pacific (Brodeur et al., 2006). On the other hand, the persistence of the 2014–2016 marine heatwave (Bond et al., 2015; Di Lorenzo & Mantua, 2016) was evident in the length-frequency distribution of PSL at Middleton, which was largely unimodal in 2015 and 2016 and consisted primarily of the small/age-0 class (Figure S4). Additionally, body condition of PSL age 1+ at Middleton in 2016 was the lowest value of the time series, and nearly the same as the average condition for the small PSL (~0.29). von Biela et al. (2019) reported that in Prince William Sound, the energy density of age-1 PSL began to decline in 2015, and the 2015 PSL year class experienced little growth over the winter of 2015–2016. This anomalous growth was an 89% decline in whole body energy for age-1 PSL compared to cooler years, which may have occurred because of poor feeding conditions, particularly during the 2015 summer/fall PSL growth season.

Conclusion

We found species-specific, regional, and interannual variation in forage fish length and body condition, suggesting that climate variability in the North Pacific can have substantial impacts on prey species morphometrics, hence energy density, in the Gulf of Alaska. Changes in condition of key prey species may have cascading effects in marine food webs, and this will be a topic of future analyses. For example, condition of capelin and PSL were among the lowest of the time series in 2015–2016 and may have contributed to the large-scale die-off of seabirds and unusual mortality of marine mammals in the region during the fall and winter of 2015–2016 (Walsh et al., 2018). This study thus provides another step toward a greater understanding of variation in forage fish length and condition to climate variability in the Gulf of Alaska.

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Conflict of interest

The authors of this paper have no conflict of interest to declare.

Author contributions

JFP, SAH, and MGR contributed data to the study. SAT, WJS, and MGR were responsible for data analysis. SAT, WJS, MLA, MGR, and JFP wrote, edited, and revised the manuscript.

Data availability statement

The Pacific Decadal Oscillation index is available at https://oceanview.pfeg.noaa.gov/erddap/tabledap/cciea_OC_PDO.htmlTable?time,PDO. Sea surface temperature data were obtained from the Hadley Center HadISST1 reconstructed data set (https://www.metoffice.gov.uk/hadobs/hadisst/). The forage fish data that support the findings of this study are available on request from the corresponding author. Those data are not publicly available due to privacy or ethical restrictions.

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Table 1. Sample sizes and summary statistics (mean, standard deviation, and coefficient of variation; calculated based on the number of fish) condition indices for capelin and Pacific sand lance by site, 1993–2016. See text for details on Fulton's K calculations.

				Fulton's K		
Species	Location	N years	N fish	Mean	S.D.	CV
<u>Capelin</u>						
	Middleton	12	2351	0.478	0.172	0.359
	St. Lazaria	21	1688	0.507	0.090	0.178
Total			4039			
<u>Pacific sand lance</u>						
Age 0 (< 100 mm)	Middleton	12	2649	0.269	0.081	0.300
	St. Lazaria	16	924	0.311	0.280	0.901
Age 1+ (≥ 100 mm)	Middleton	13	1551	0.322	0.139	0.431
	St. Lazaria	18	1315	0.329	0.056	0.171
Total			6439			

Table 2. Results of unpaired two-sided t-test to test for differences in mean condition between each site by species and size/age class. PSL: Pacific sand lance.

Species	Site	N	Mean	S.E.	t	p (|T| > |t|)
Capelin	Middleton	2340	0.478	0.0036	-4.714	<0.0001
	St. Lazaria	1139	0.503	0.0020		
PSL age 0	Middleton	1055	0.267	0.0030	-7.132	<0.0001
	St. Lazaria	497	0.300	0.0022		
PSL age 1+	Middleton	876	0.329	0.0035	1.684	0.092
	St. Lazaria	451	0.320	0.0019		

Table 3. Results of ANCOVA on body condition (Fulton's K) by year and sampling date for capelin and Pacific sand lance (PSL) at each site, 1993–2016. Gray shading indicates significant ($p < 0.05$) correlations.

Species	Site	N fish	Variable	df	F	p > F	Coefficient
Capelin	Middleton	2351	model	12	9.81	<0.001	
			year	11	9.98	<0.001	
			sample date	1	13.83	<0.001	-0.0013
Capelin	St. Lazaria	1688	model	21	7.25	<0.001	
			year	20	7.55	<0.001	
			sample date	1	0.55	0.457	-0.0001
PSL age 0	Middleton	2649	model	12	7.64	<0.001	
			year	11	7.82	<0.001	
			sample date	1	4.80	0.029	-0.0003

PSL age 0	St. Lazaria	924	model	16	1.16	0.294	
			year	15	1.22	0.248	
			sample date	1	0.14	0.706	-0.0003
PSL age 1+	Middleton	1551	model	13	3.93	<0.001	
			year	12	3.51	<0.001	
			sample date	1	8.64	0.003	-0.0010
PSL age 1+	St. Lazaria	1315	model	18	9.50	<0.001	
			year	17	9.84	<0.001	
			sample date	1	18.68	<0.001	-0.0006

Table 4. Best models based on AIC (lowest) and R^2 (highest) from regressions of the PDO and regional SST by season on average annual body size (length, mm). PSL : Pacific sand lance; JFM: winter, January–March; AMJ: spring, April–June; JAS: summer, July–September.

		Model									
Species	Site	AIC	R^2	df	p-value	Term	β	SE of β	t-stat	p-value	Figure
Capelin	Middleton	y = 1 + SST_AMJ									
		242.0	0.52	20	<0.0005	Intercept	109.360	1.123	97.38	<0.0001	4a
						SST_AMJ	-8.090	1.743	-4.64	<0.0005	
		y = 1 + PDO_AMJ									
		250.0	0.29	20	<0.01	Intercept	107.440	1.380	77.71	<0.0001	4b
						PDO_AMJ	-4.770	1.680	-2.85	<0.01	
	St. Lazaria	none									
PSL age 0	Middleton	y = 1 + SST_JFM									4c

		269.0	0.41	22	<0.001	Intercept	79.660	1.151	69.23	<0.0001	
						SST_JFM	4.960	1.276	3.89	<0.001	
		y = 1 + PDO_JFM									
		267.0	0.46	22	<0.0005	Intercept	79.980	1.032	77.53	<0.0001	4d
						PDO_JFM	3.550	0.825	4.30	<0.0005	
	St. Lazaria	none									
PSL age 1+	Middleton	y = 1 + SST_AMJ									
		297.0	0.26	22	0.011	Intercept	123.180	1.911	69.16	<0.0001	4e
						SST_AMJ	-6.150	2.225	-2.76	0.011	
		y = 1 + PDO_AMJ									
		292	0.23	22	0.018	Intercept	131.400	1.832	71.72	<0.0001	4f
						PDO_AMJ	-4.640	1.820	-2.55	0.018	
	St. Lazaria	none									

Table 5. Best models based on AIC (lowest) and R^2 (highest) from regressions of the PDO and regional SST by season on average annual body condition (Fulton's K). PSL : Pacific sand lance; JFM: winter, January–March; AMJ: spring, April–June; JAS: summer, July–September.

		Model									
Species	Site	AIC	R^2	df	p-value	Term	β	SE of β	t-stat	p-value	Figure
Capelin	Middleton	y = 1 + SST_JAS									
		14.7	0.42	10	0.023	Intercept	0.48	0.009	54.27	<0.0001	5a
						SST_JAS	-0.02	0.009	-2.67	0.05	
	St. Lazaria	y = 1 + SST_AMJ									5b
		-17.3	0.61	19	<0.0001	Intercept	0.513	0.004	131.24	<0.0001	

						SST_AMJ	-0.032	0.006	-5.46	<0.0001	
		y = 1 + PDO_AMJ									
		-21.1	0.68	19	<0.0001	Intercept	0.503	0.003	148.9	<0.0001	5c
						PDO_AMJ	-0.024	0.004	-6.29	<0.0001	
PSL age 0	Middleton	none									
	St. Lazaria	y = 1 + PDO_JAS									
		6.27	0.25	14	0.048	Intercept	0.325	0.011	28.91	<0.0001	5d
						PDO_JAS	0.017	0.008	2.17	0.048	
PSL age 1+	Middleton	y = 1 + SST_JFM									
		-1.26	0.36	11	0.029	Intercept	0.330	0.006	51.72	<0.0001	5e
						SST_JFM	-0.018	0.007	-2.50	0.029	
	St. Lazaria	none									

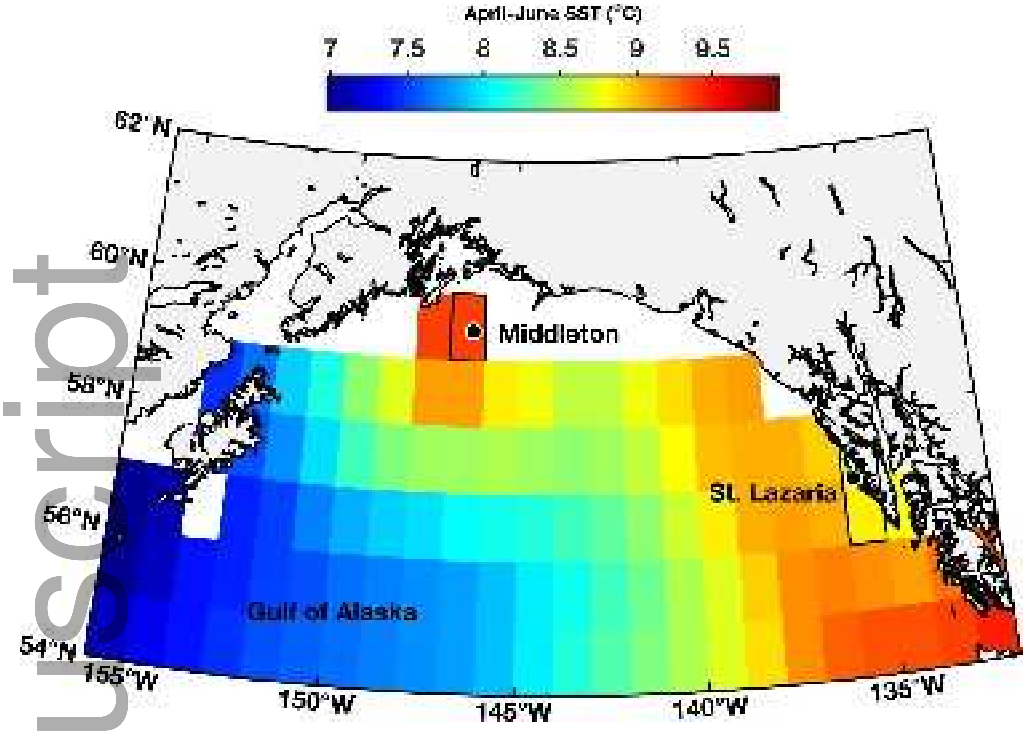
Figure 1. Map showing the Gulf of Alaska with the two study sites Middleton Island (59.438°N, 146.327°W) and St. Lazaria Island (56.987°N, 135.705°W). Colors indicate average SST from April–June (°C). The boxes around each of the sites indicate the bounds for determining local SST; see methods for details.

Figure 2. Length frequency histograms for capelin at A) Middleton and B) St. Lazaria islands, and Pacific sand lance at C) Middleton and D) St. Lazaria islands.

Figure 3. Average annual body condition (Fulton's K) anomalies over time at Middleton (black bars) and St. Lazaria (grey bars) for A) capelin, B) age-0 Pacific sand lance (PSL), and C) age-1+ PSL. Dashed lines indicate ±1 standard deviation.

Figure 4. Predicted (line) and observed (asterisks) values of average annual length (mm) based on best models (see Table 4 for model results) for environmental parameters. Dashed lines reflect 95% confidence intervals for predictions. A) capelin at Middleton by spring SST, B) capelin at Middleton by spring PDO, C) Pacific sand lance (PSL) age 0 at Middleton by winter SST, D) PSL age 0 at Middleton by winter PDO, E) PSL age 1+ at Middleton by spring SST, and PSL age 1+ at Middleton by spring PDO. No model was selected for any of the fish at St. Lazaria.

Figure 5. Predicted (line) and observed (asterisks) values of average annual body condition based on best models (see Table 5 for model results) for environmental parameters. Dashed lines reflect 95% confidence intervals for predictions. A) capelin at Middleton by summer SST, B) capelin at St. Lazaria by spring SST, C) capelin at St. Lazaria by winter PDO, D) Pacific sand lance (PSL) age 0 at St. Lazaria by summer PDO, and E) PSL age 1+ at Middleton by winter SST. No model was selected for PSL age 0 at Middleton or PSL age 1+ at St. Lazaria.



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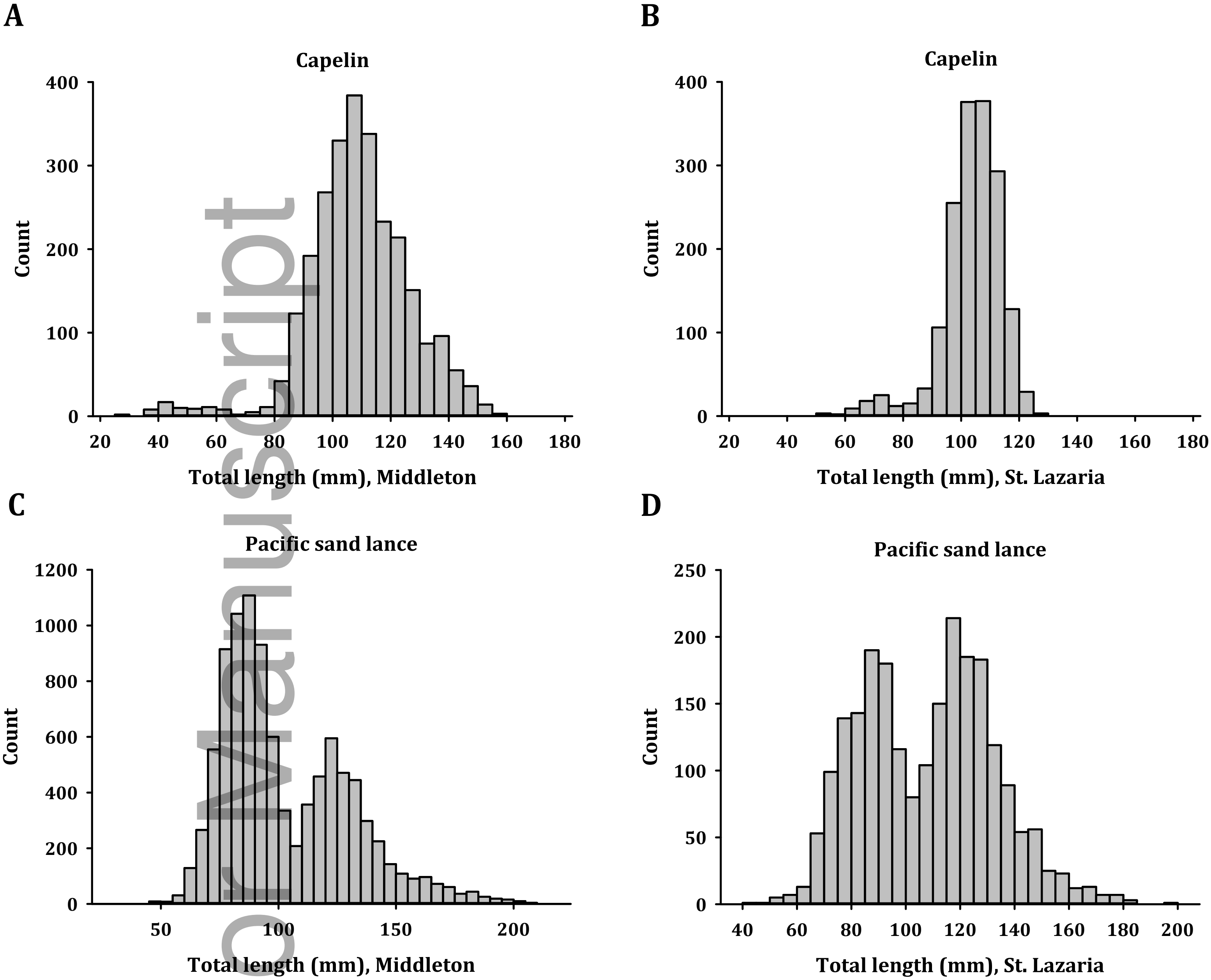

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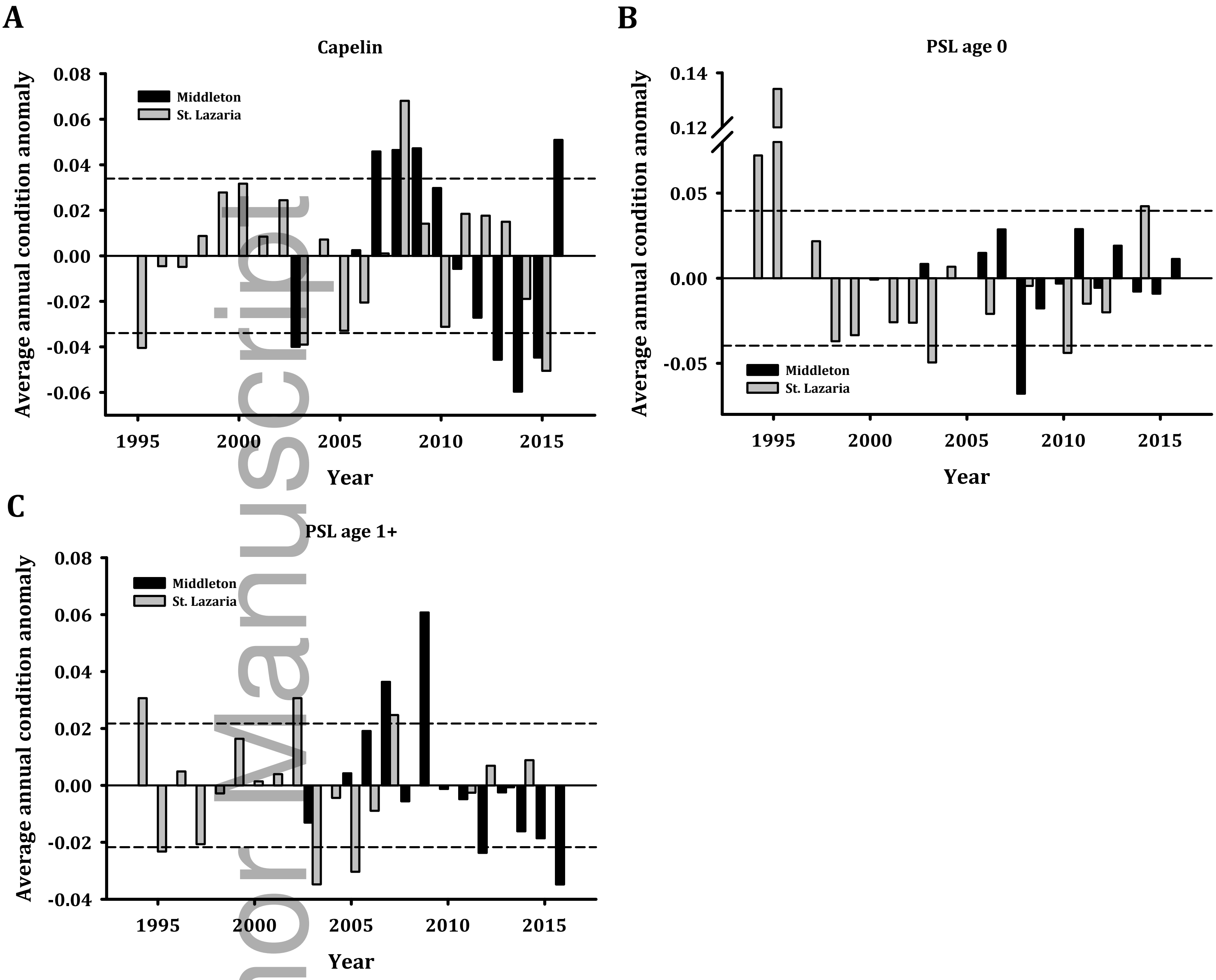

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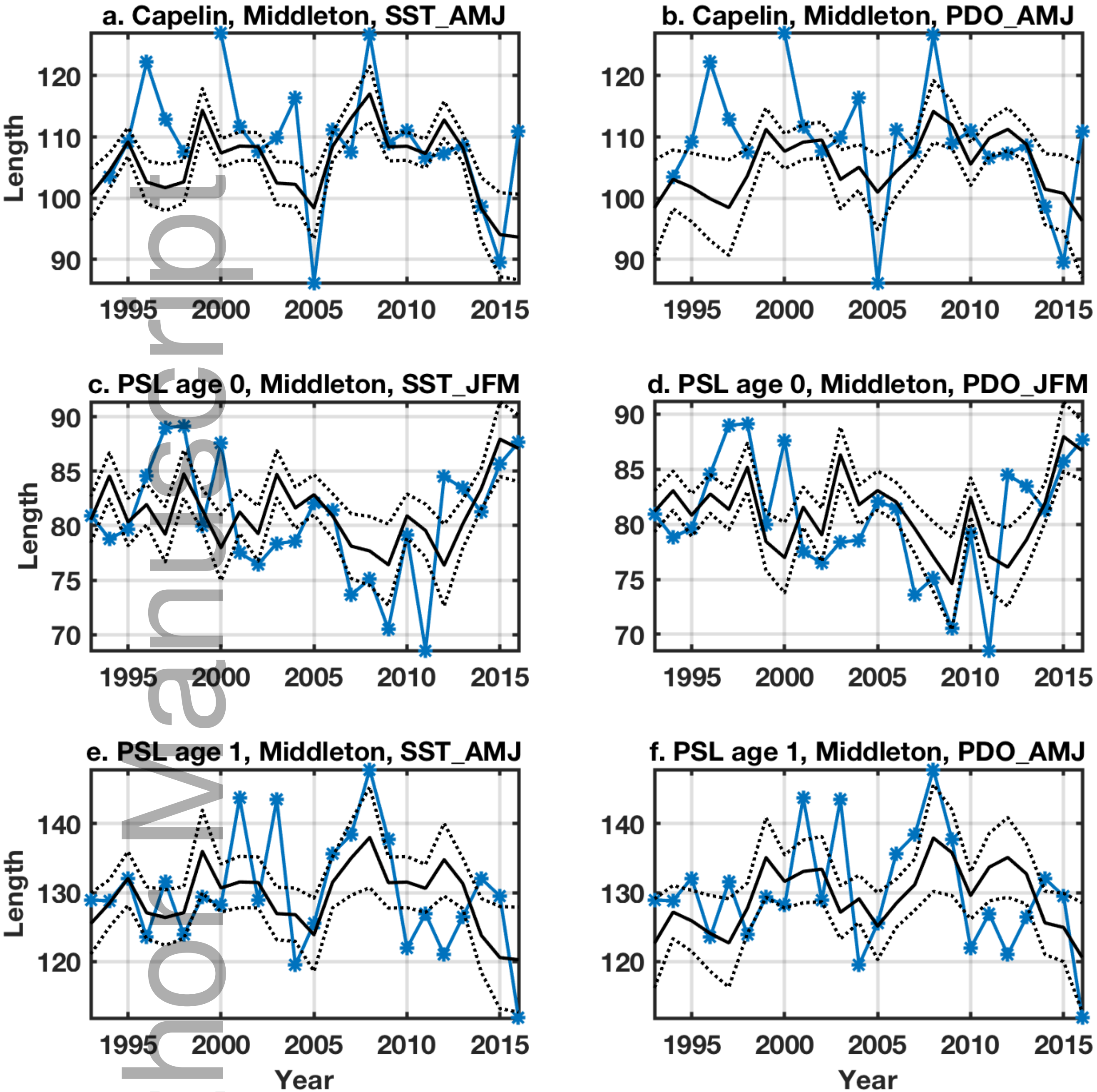

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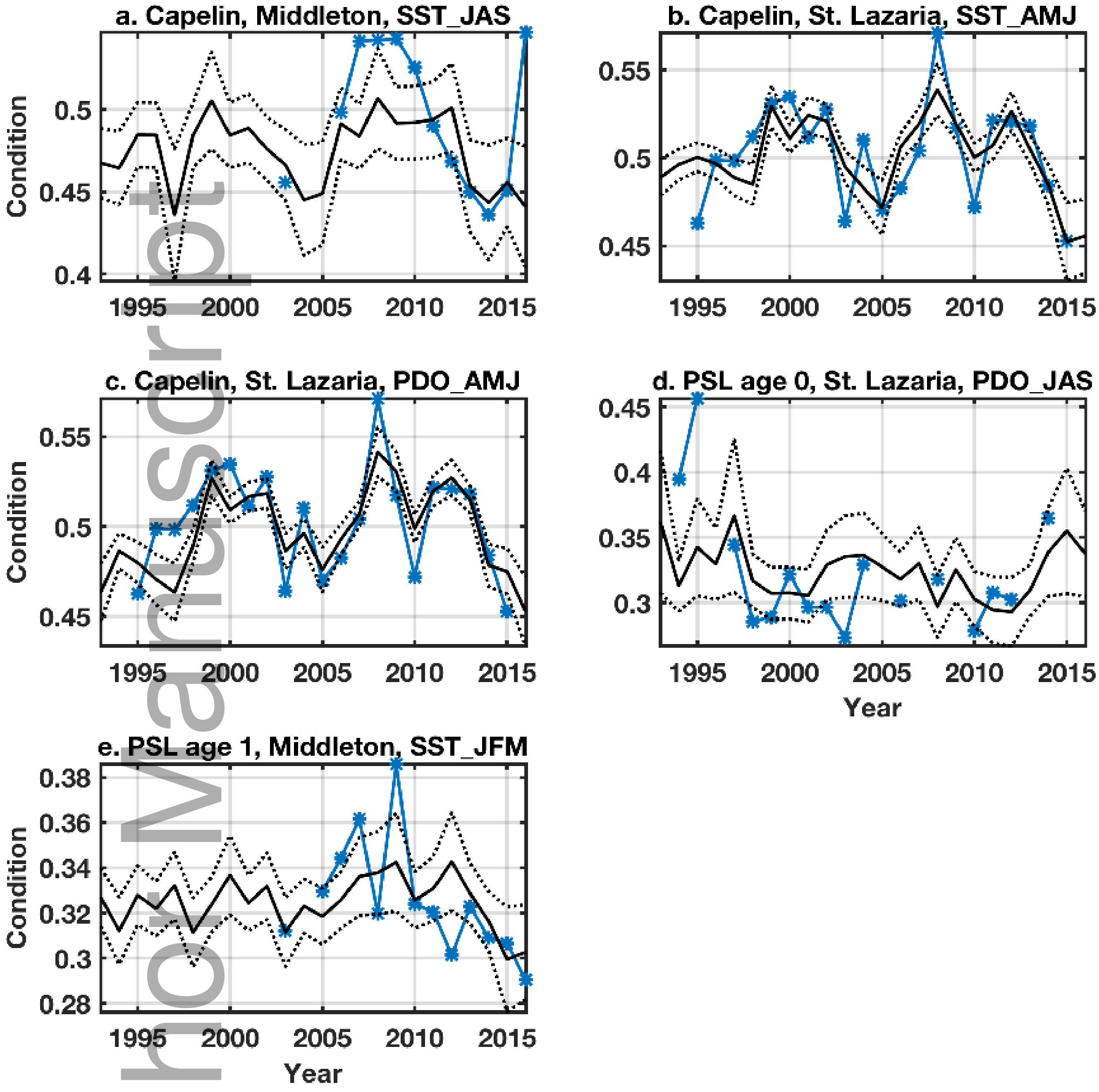

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