AGE AND GROWTH OF PACIFIC SAND LANCE (AMMODYTES PERSONATUS) AT THE LATITUDINAL EXTREMES OF THE GULF OF ALASKA LARGE MARINE ECOSYSTEM

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ABSTRACT—The Pacific Sand Lance (*Ammodytes personatus*) is a major component of the forage base for many species of marine birds, mammals, and fishes. Despite its ecological importance, relatively little is known regarding basic biology or life-history parameters for this species. Information on age and growth is particularly lacking for Pacific Sand Lance in the Salish Sea, an inland sea that encompasses the San Juan Archipelago in Washington State. Here, we present information on age and growth of Pacific Sand Lance from this region and then contrast it with a previous study based in Cook Inlet, Alaska. These 2 regions comprise the latitudinal extremes of the Gulf of Alaska large marine ecosystem. We found evidence for possible differences in growth of Pacific Sand Lance between the 2 regions, with San Juan Island fish generally being smaller at age than fish in Cook Inlet. We interpret these results with respect to regional and temporal differences in environmental conditions and resource availability linked to duration and magnitude of seasonal production, which we hypothesize affects the period of winter dormancy employed by this species as a strategy to cope with resource limitation.

Key words: age, *Ammodytes*, forage fish, growth, otolith, sand lance, Salish Sea

Sand lances, sometimes referred to as sand eels, are members of the family Ammodytidae, and are found throughout the world's oceans. These key forage fishes comprise a significant portion of the diet of many species of marine birds, mammals, and fishes in various ecosystems. In particular, the Pacific Sand Lance, *Ammodytes personatus*, is an important forage resource throughout the Gulf of Alaska (GOA) large marine ecosystem (LME). This species is distributed from California to the northern GOA, through the Aleutian Islands, and into the eastern Bering Sea (Orr and others 2015), and is an important constituent of the diets of predatory groundfishes and pelagic fishes (Field 1988; Wilson and others 1999) as well as many marine birds and mammals (Wilson and others 1999; Beaubier and Hipfner 2013; Sydeman and others 2017) in the GOA LME. The GOA LME is a highly productive ecosystem that supports numerous economically valuable fisheries (Za-

dor and Yasumiishi 2016; McDowell Group 2017) and encompasses the southern coast of Alaska and western coast of the Pacific Northwest, extending from the Strait of Juan de Fuca in the Salish Sea to Unimak Pass in the Aleutian Islands (Baker and Smith 2018; Fig. 1). This productive system, defined largely by circulation of major ocean currents (Royer 1998; Mundy and others 2010), covers a vast area of approximately 1.5 million km^2 (Aquarone and Adams 2010; TWAP 2015), and is extremely heterogeneous in oceanography as well as species composition and richness (Mundy 2005; Spies 2007; Zador and Yasumiishi 2016).

In the North Pacific, 4 species of *Ammodytes* are currently recognized, with 1 species, *A. personatus*, identified in the northeast Pacific (Orr and others 2015). Although most earlier publications on "Pacific Sand Lance" have used the scientific name *A. hexapterus* for populations in the northeast Pacific Ocean, *A. hexapterus* (the
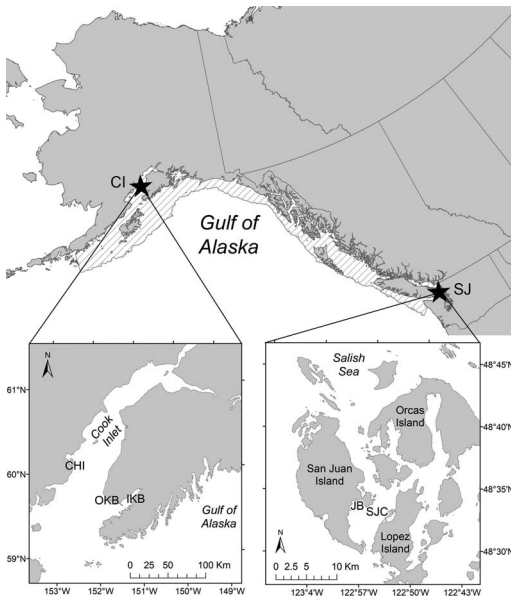
FIGURE 1. Pacific Sand Lance (*Ammodytes personatus*) sampling regions in the Gulf of Alaska (GOA) continental shelf large marine ecosystem (LME) (hatched area). Cook Inlet (CI) sampling sites (CHI = Chisik Island, OKB = outer Kachemak Bay, IKB = inner Kachemak Bay) are from Robards and others (2002). San Juan Archipelago (SJ) sampling sites (JB = Jackson Beach, SJC = San Juan Channel) are from the present study. Note the difference in scale between insets. GOA LME map shapefile adapted from the University of Rhode Island and NOAA Fisheries Large Marine Ecosystem Program (http://lme.edc.uri.edu/).

Arctic Sand Lance) is a northwest Pacific and Arctic species, only overlapping with *A. personatus* in the eastern Bering Sea (Orr and others 2015). Therefore, all mentions of Pacific Sand Lance hereafter refer solely to *A. personatus*, even if the old scientific name was used in the literature (for example, Robards and others 2002).

Pacific Sand Lance are commonly found in the shallow nearshore waters of the GOA LME to depths of 100 m (Field 1988; Robards and others 1999a; Johnson and others 2008). Pacific Sand Lance spawn on sandy intertidal beaches in late September through February, with peak hatch occurring in March; the pelagic larval stage lasts through June, after which young sand lance (≥25-mm standard length) settle in nearshore benthic habitats (Robards and others 1999b; Matarese and others 2003; Doyle and others

2009). Calanoid copepods and other mesozooplankton are an important component of their diet (Blackburn and Anderson 1997; Sisson and Baker 2017). Similar to other members of the genus *Ammodytes* (Winslade 1974; Robards and others 1999a), Pacific Sand Lance employ a strategy of winter dormancy buried in bottom sediments to avoid predation risk and conserve energy in months when prey is in short supply (Ciannelli 1997; Robards 2000; van Deurs and others 2010). Adults briefly interrupt dormancy to spawn, but return thereafter to the protection of sediments, emerging at the start of the spring production cycle. Adaptations that are likely to increase the odds of overwinter survival in this species are long-gut evacuation times and slow digestion rates to accumulate fat reserves prior to dormancy (Ciannelli 1997), coupled with reduced oxygen-consumption demands during dormancy (Quinn and Schneider 1991).

Forage fishes, including sand lances, are increasingly recognized as critical to ecosystem structure, function, and energy transfer to higher trophic levels, and are becoming a greater priority to management agencies because of their vital role in marine ecosystems (Pikitch and others 2012, 2014; Essington and others 2015). However, most of these species, including Pacific Sand Lance, are considered extremely data poor, with information lacking even on basic biological metrics and attributes such as age, growth, reproduction, and mortality. Very little is known regarding the life history of *A. personatus*, especially in the Salish Sea, a biologically rich inland sea extending from southwestern British Columbia, Canada, to northwestern Washington State, USA (Pietsch and Orr 2019). Reliable published age and growth information is currently limited to Alaska waters (Robards and others 2002; Johnson and others 2008; von Biela and others 2019). Therefore, the main objective of our study was to characterize the age and growth of a stock of Pacific Sand Lance from the San Juan Archipelago, Washington, in the Salish Sea, the southern end of the GOA LME. We contrast growth (length at age) of this stock with 3 previously studied Cook Inlet stocks (Robards and others 2002) at the northernmost extreme of the GOA LME, and discuss differences between the stocks with respect to regional and temporal observations on temperature and productivity.

Fish Sampling

Fish were collected from 2 sites near San Juan Island in the San Juan Archipelago: Jackson Beach and San Juan Channel (Fig. 1). Jackson Beach is a known nearshore spawning site and nursery habitat for young-of-year Pacific Sand Lance (Penttila 1999; Selleck and others 2015). Following maturation, young (age-1+) fish are thought to move from this nursery habitat into a sand-wave field in the middle of the San Juan Channel (80 m depth), where they burrow into the bottom sediments, likely as a refuge from predators during non-feeding and overwintering periods (Ciannelli 1997; Bizzarro and others 2016; Baker and others 2019). The 2 sampling sites are considered to represent a single stock (Sisson and Baker 2017; Baker and others 2019). Therefore, all data were pooled in age and growth analyses.

Fish were collected using 2 different methods: (1) beach seines at Jackson Beach; and (2) Van Veen benthic sampling in the San Juan Channel at 80 m depth. The 2 different sampling methods were employed to obtain Pacific Sand Lance during periods when they occupy different habitat types (that is, shallow nearshore areas for spawning and nursery habitat, and deep-water sediment refugia during non-feeding periods and winter dormancy). Fish were collected at both locations in autumn (October to November) 2015, in the San Juan Channel in winter (February) 2016, and at Jackson Beach in spring (May) 2016. Beach seining was performed with a knotless nylon 3-mm mesh net (36.3 m by 3.7 m) set parallel to the beach at a distance of 10 m. During each set, the beach seine was actively dragged for a total of 2 min at a steady pace. At least 5 sets were made during each sampling occasion. The Van Veen sampling instrument resembles a large clamshell and is used to sample underwater sediments; its design also makes it quite effective at sampling buried sand lances (Hoines and Bergstad 2001; Sisson and Baker 2017; Baker and others 2019). The Van Veen sampler was deployed from a small vessel during slack tides using a hydraulic winch to allow rapid deployment and sampled a maximum sediment volume of 0.026 m^3 over a surface area of 0.12 m^2. At least 5 grabs were taken during each sampling occasion.

Sample Preparation, Age Determination, and Quality Control

After returning to the laboratory, fish were euthanized using MS-222 in accordance with University of Washington IACUC guidelines. Most fish were then measured for fork length (FL) to the nearest millimeter. Otoliths were dissected from fresh fish whenever possible. Owing to time limitations following field sampling, some otoliths were dissected from fish that had previously been preserved in ethanol and frozen. Otoliths were placed in Eppendorf tubes containing ethanol for at least 1 mo to "clear" them, as hydration helps improve the contrast between growth zones.

Otolith age determinations were made by the Age and Growth Program at the National Oceanic Atmospheric Administration (NOAA) Alaska Fisheries Science Center in Seattle, WA. To maintain consistency with methods of Robards and others (2002), otoliths were aged by surface examination whenever possible. However, growth zones were not always sufficiently clear using this method, and some otoliths had surfaces that were opaque. Therefore, to improve clarity in these specimens, 1 otolith from each pair was affixed to a glass slide sulcus-side down using Loctite UV-curing adhesive and hand polished using 320-grit followed by 1200-grit Buehler wet-dry abrasive paper. Whether read whole or polished, otoliths were placed against a dark background and viewed using a Leica MZ95 dissecting microscope and reflected light. Mineral oil was applied to surfaces of mounted otoliths to enhance contrast of banding patterns. Otoliths were imaged using a Leica DFC420 camera and measured across the longest axis (length of whole otolith from the anterior to posterior tip).

Age determination criteria were developed by examining clear (Fig. 2) and unclear specimens prior to making age estimates. During development of age determination criteria, the average length of the 1st annulus ($\bar{x} = 1.063$ mm, $s = 0.099$, $n = 8$) was estimated from the clearest otoliths and compared to unclear otoliths to help guide identification of the 1st annulus in particularly difficult specimens. In some cases the unmounted otolith was sectioned transversely through the core to confirm identification of translucent zones.
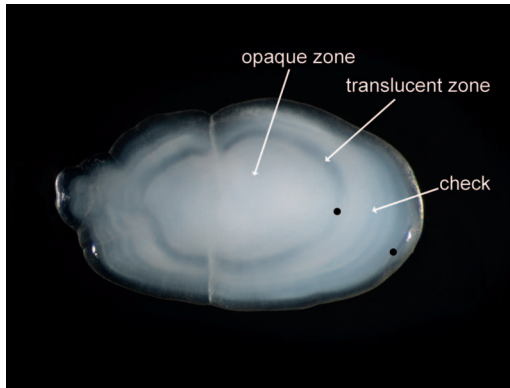
FIGURE 2. Image of a whole otolith from an 88-mm Pacific Sand Lance (*Ammodytes personatus*) collected in the San Juan Channel in February 2016, viewed with reflected light. Opaque (light) and translucent (dark) growth zones, and a growth "check" (false annulus), are indicated by arrows. Putative annuli are indicated by black dots to arrive at an age estimate of 2 y for this individual.

Standard methods (Matta and Kimura 2012) were used to estimate fish age. Translucent growth zones were counted to determine age, and were only considered to represent annuli if they were strong and completely encircled the otolith (Fig. 2). False rings, or "checks", were noted in some otoliths (Fig. 2). Birthdate was considered to be 1 January by international convention (Williams and Bedford 1974; CARE 2006), and any new growth observed on the otolith edge in autumn-caught fish was not included in the age estimate, as it was presumed to have been deposited during the year of capture (Robards and others 2002; Matta and Kimura 2012). This practice maintains consistency with Robards and others (2002), is appropriate given the known hatching period of Pacific Sand Lance, and allows for fish to be assigned to the correct cohort (Chilton and Beamish 1982; Fig. 3).

Otoliths were independently read 2 times by a single reader. If age estimates did not agree, otoliths were read a 3rd time to reach a consensus age. Precision between age estimates (a measure of reproducibility) was estimated by calculating the percent agreement, average percent error (Beamish and Fournier 1981), and coefficient of variation (Chang 1982). Precision statistics were not calculated for larval otoliths to avoid inflation of age-estimate reproducibility.

Data Analysis

Linear regression analysis between otolith size and fish length was used to estimate fork length for fish that were not measured in the laboratory. Otolith length was treated as the independent variable and fish fork length was treated as the dependent variable.

Wilcoxon rank sum tests (Zar 1999) were used to assess whether length and age distributions differed between collections in autumn 2015 and winter 2016. Tests were 1-tailed, where the alternative hypothesis was that length or age was greater in winter 2016 than in autumn 2015.

Fish length-at-age data were fit with the von Bertalanffy growth function, parameterized as $L_t = L_\infty(1 - e^{-K(t-t_0)})$, where L_t (mm FL) is length at age t, L_∞ (mm FL) is the theoretical asymptotic length, K (y^{-1}) is the growth rate coefficient, and t_0 (y) is the theoretical age at zero length. The von Bertalanffy growth function was fit to the data using nonlinear least squares parameter estimation (nls function) in R statistical computing software (R Development Core Team 2016).

Growth (length at age) of Pacific Sand Lance was compared between San Juan Island and a previous study on the same species based in Cook Inlet, Alaska (Fig. 1). The Cook Inlet fish were collected by Robards and others (2002) in 1996 and 1997 from 3 sites representing separate stocks: Chisik Island, inner Kachemak Bay, and outer Kachemak Bay (Fig. 1). Using an analysis of residual sum of squares (Chen and others 1992), Robards and others (2002) were able to demonstrate that von Bertalanffy growth functions differed among all 3 of the Cook Inlet stocks. Von Bertalanffy parameters and standard errors of parameter estimates reported in Robards and others (2002) for each Cook Inlet stock are presented here for comparison with those estimated for fish from San Juan Island.

Comparison of Regional Environmental Conditions

To determine typical seasonal patterns in abiotic and biotic factors in Cook Inlet and the San Juan Archipelago, we drew from a variety of data sources that might relate to Pacific Sand Lance growth. Unfortunately, environmental datasets are scant for the time period when the fish collected by Robards and others (2002) were alive. Therefore, we performed 2 separate analyses. The 1st was an analysis of monthly sea-surface temperatures (SST; °C) produced by
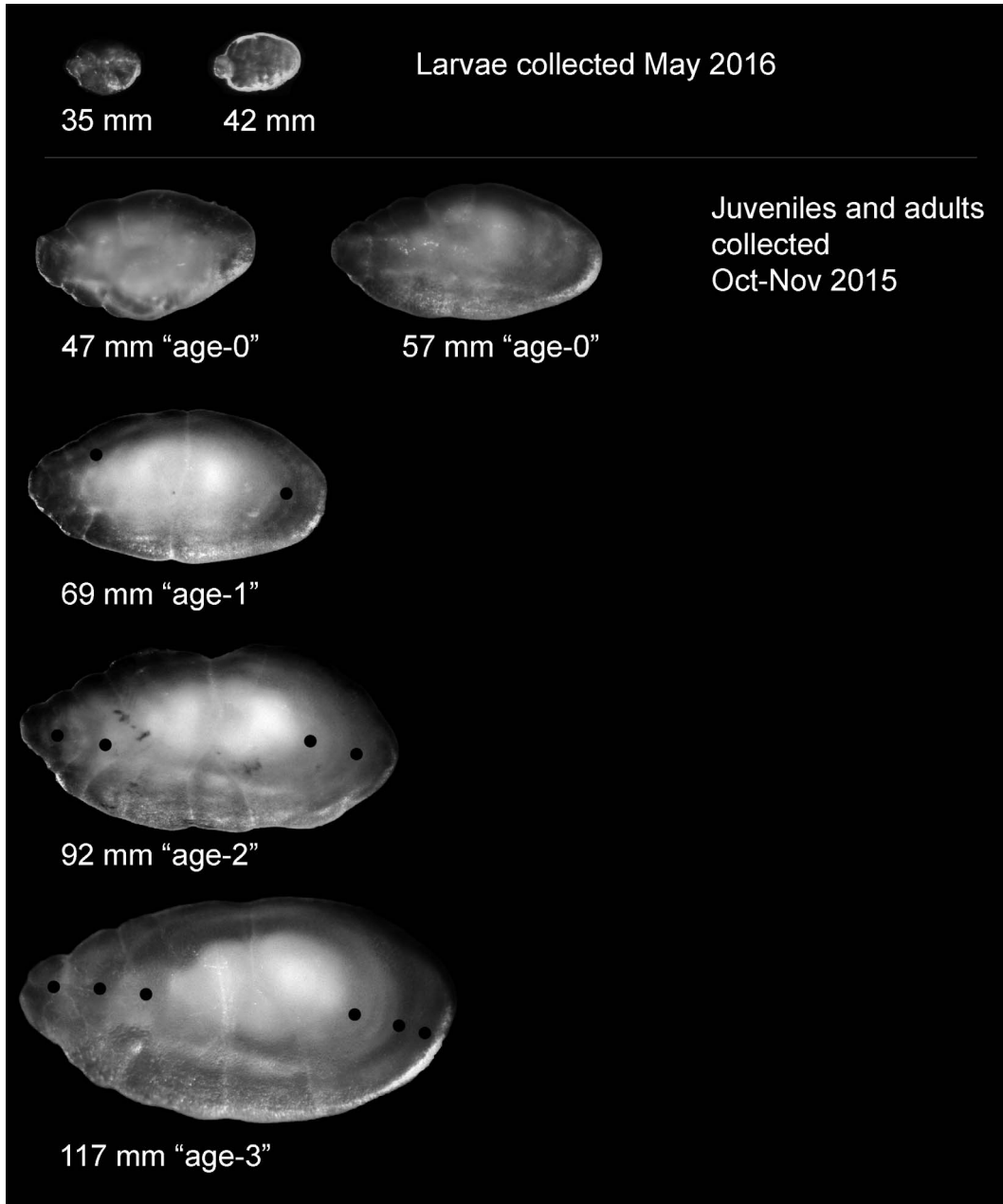
FIGURE 3.   Images of Pacific Sand Lance (*Ammodytes personatus*) otoliths of various age classes, with fish fork length (mm) and estimated age (years), all taken at the same magnification and marked with age annotations (black dots). Top row shows otoliths from late larvae (age 0) collected in spring (May) 2016; all other otoliths are from fish collected in autumn (October to November) 2015. Because of the lateness in the year of the autumn collections, any annuli present on the otolith edge were not counted in the growth estimate (following a 1 January birthdate convention; see text).

TABLE 1. Specimen information for Pacific Sand Lance (*Ammodytes personatus*) collected from San Juan Island in 2015 and 2016. JB = Jackson Beach, SJC = San Juan Channel (see Figure 1 for collection locations).

Year	Season	Site	*n*	Length range (mm)	Age range (y)
2015	Autumn (October to November)	JB	44	47–118	0–3
		SJC	20	70–129	1–3
2016	Winter (February)	SJC	57	68–120	2–4
2016	Spring (May)	JB	8	29–42	0

the Met Office Hadley Centre Sea Ice and Sea Surface Temperature dataset (HadISST) and obtained from the NOAA Coastal and Oceanic Plankton Ecology Production & Observation Database Interactive Time-series Explorer (CO-PEPODITE) Toolkit (available at https://www.st.nmfs.noaa.gov/copepod/toolkit/). We graphed region-specific monthly point values of SST from a broad, 30-y period (1989–2018) in tandem with the average monthly SST experienced by fish extant in both the Robards and others (2002) study (1993–1997) and that experienced by fish extant in the present study (2012–2016). The purpose of this analysis was to describe the general range of temperatures experienced by Pacific Sand Lance stocks in Cook Inlet and the San Juan Archipelago, and to determine whether fish in each study were alive during typical thermal conditions within each region.

The 2nd analysis explored other potential factors to explain general differences in productivity between Cook Inlet and the San Juan Archipelago. Measurements of these indices do not extend as far back in time as those for SST. Therefore, because of limitations in the lengths of these time series, data were extracted from a common period corresponding to the years 2003–2017. Although these indices do not reflect the exact conditions experienced by the fish in each region, we present them here to compare general patterns in the seasonality of daylight and primary productivity between regions. We obtained the following data from COPEPODITE and the NOAA CoastWatch website (available at https://coastwatch.pfeg. noaa.gov/): (1) Photosynthetically Available Radiation (PAR; einstein units m^{-2} day^{-1}) measured by the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument aboard the Aqua satellite; (2) chlorophyll-*a* (mg m^{-3}) data from the NASA combined-satellite dataset; and (3) net primary productivity (mg C m^{-2} day^{-1}) measured by

MODIS. Chlorophyll-*a* and net primary productivity values were natural log-transformed. Boxplots of monthly values for each variable were produced to identify regional differences in general seasonal patterns of oceanography and productivity related to differences in fish growth between the 2 regions.

All environmental data were retrieved from locations as close as possible to the Pacific Sand Lance sampling sites in both studies (48.3°N, 123.0°W, in the Strait of Juan de Fuca about 23 km south of the San Juan Island site, and 60.2°N, 152.0°W, in the middle of Cook Inlet about 30–60 km from the Chisik Island and Kachemak Bay sites) to approximate average monthly conditions experienced in each region. Data were assessed for normality and equality of variances via residual plot examination, Shapiro-Wilk tests, and Levene's tests; none of the datasets met assumptions required to run parametric statistical tests. Therefore, to determine the effects of region and month (including their interaction) on mean environmental values, we performed nonparametric aligned rank transform analysis of variance (Wobbrock and others 2011) using the package ARTool in R statistical computing software.

Results

A total of 129 Pacific Sand Lance were collected near San Juan Island from October 2015 to May 2016 (Table 1). These included 64 fish collected in autumn 2015, 57 fish collected in winter 2016, and 8 late larvae collected in spring 2016. The late larvae ranged in length from 29 to 42 mm, and were confirmed to be in the post-flexion and transformation stages through microscopic inspection by an independent larval fish expert.

Age was determined for 123 individuals (otoliths were not collected for 6 fish in winter 2016). Approximately 50% of the otoliths were clear and aged solely by surface examination; the
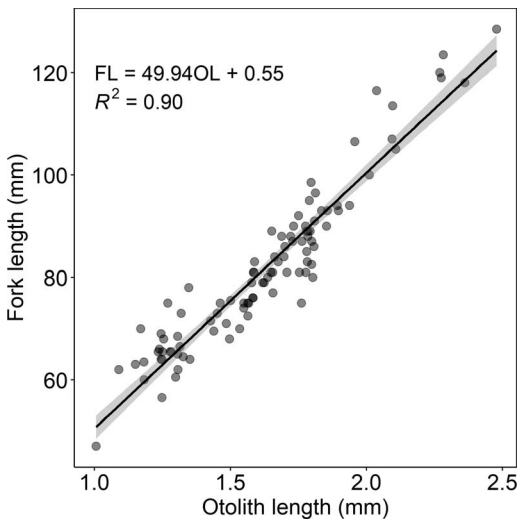
FIGURE 4. The relationship between otolith length (OL) and fish fork length (FL) for juvenile and adult Pacific Sand Lance (*Ammodytes personatus*) from San Juan Island (points), fitted with a linear relationship (black line, with 95% confidence interval in light gray).

other 50% were aged using the hand-polishing method. Despite being from young fish, otoliths were somewhat difficult to interpret. Some otoliths were quite clear, whereas others contained checks in the growth pattern (Fig. 2). Difficulties in age estimation were also often associated with interpretation of growth observed at the otolith edge. This was particularly true for fish caught in autumn (Fig. 3). Polishing helped improve clarity and enabled differentiation between growth zones in some of these cases. Despite these difficulties, agreement between readings was high, with an overall percent agreement of 84%. The average percent error was 4.31% and the coefficient of variation was 6.09%, within the range considered acceptable for age determination studies (Campana 2001). A reference library of annotated otolith images was created and is available upon request from the Alaska Fisheries Science Center (contact 1st author for details).

The relationship between fish fork length (*FL*) and otolith length (*OL*) was well described in juveniles and adults by a linear function of the form: $FL = 49.94OL + 0.55$ ($P < 0.0001$; $R^2 = 0.90$; Fig. 4). This relationship was used to estimate fork lengths of 9 fish that were not measured prior to otolith analysis.

Mean fish size was 78 mm in autumn 2015 and 87 mm in winter 2016, although we observed a larger range of lengths in autumn (47–129 mm) than in winter (68–120 mm). The largest fish captured during the course of the study was 129 mm (an individual captured in the San Juan Channel in autumn 2015). In autumn 2015, age 1 was the dominant year class. In winter 2016, ages 2 and 3 were the largest age classes, and we did not observe any age-0 or age-1 individuals. Two of the fish collected in autumn 2015 at Jackson Beach were in a spawning state (milt was present). These individuals had fork lengths of 116 mm and 118 mm; both were estimated as age 3.

A general progression in length and age was observed between fish caught in autumn 2015 and several months later in winter 2016 (Fig. 5). The 1st clear length mode of autumn-caught fish was centered at approximately 70 mm, and the center of the largest length mode of winter-caught fish (about 4 mo later) was at approximately 85–90 mm (Fig. 5A). These strong length modes likely correspond to fish that were assigned as age 1 in 2015 (median length of age-1 fish in 2015 = 68.5 mm) and as age 2 in 2016 (median length of age-2 fish in 2016 = 81.0 mm). Indeed, visual examination of the age frequencies of fish caught in late 2015 and early 2016 supports the modal progression of this 2014 cohort through time (Fig. 5B). Length (Wilcoxon rank sum test: $W = 2451.5$, $P < 0.001$) and age (Wilcoxon rank sum test: $W: 2772.5$, $P < 0.001$) were statistically greater in winter 2016 than in autumn 2015, lending further credence to this progression.

Comparison of Pacific Sand Lance length-at-age data from our study with that reported by Robards and others (2002) revealed differences among San Juan Island and Cook Inlet stocks. Pacific Sand Lance collected near San Juan Island were generally smaller at age than fish from Cook Inlet, especially those from both Kachemak Bay stocks (Fig. 6). However, examination of standard errors of von Bertalanffy parameter estimates suggest some statistical overlap in growth between the San Juan Island and Chisik Island stocks (Table 2). Differences in maximum age estimates were observed between San Juan Island and Cook Inlet. The oldest fish observed at San Juan Island was age 4, but Robards and others (2002) observed age-5 fish at Chisik Island and fish up to age 6 in both Kachemak Bay stocks.
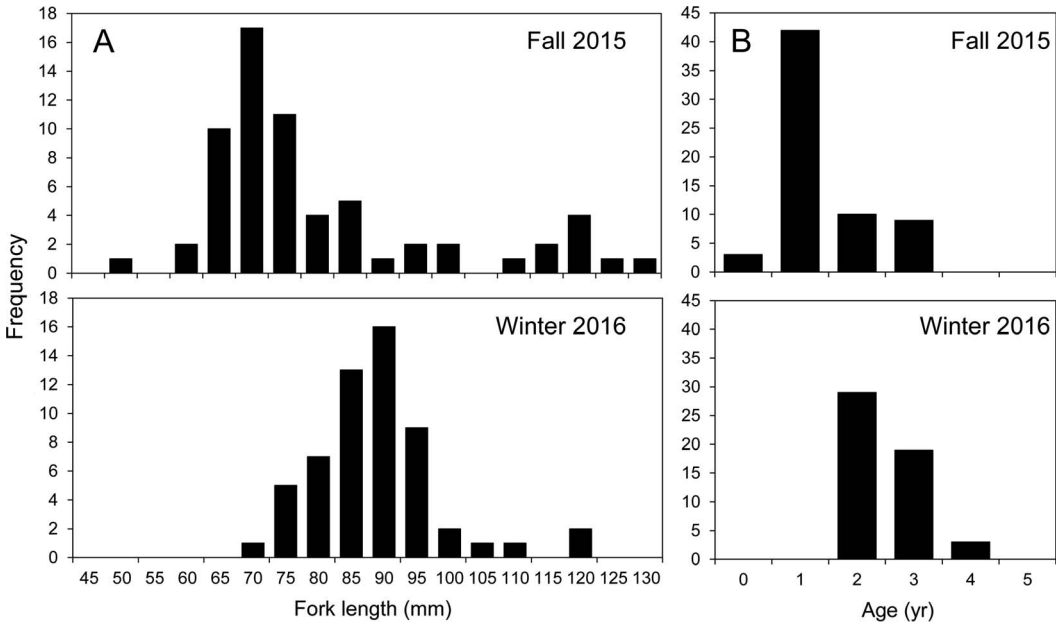
FIGURE 5.　Pacific Sand Lance (*Ammodytes personatus*) (A) length and (B) age frequencies from San Juan Island in autumn (October to November) 2015 and winter (late February) 2016.

Comparison of monthly oceanographic and productivity indices between the San Juan Archipelago and Cook Inlet illustrated some general differences in environmental conditions
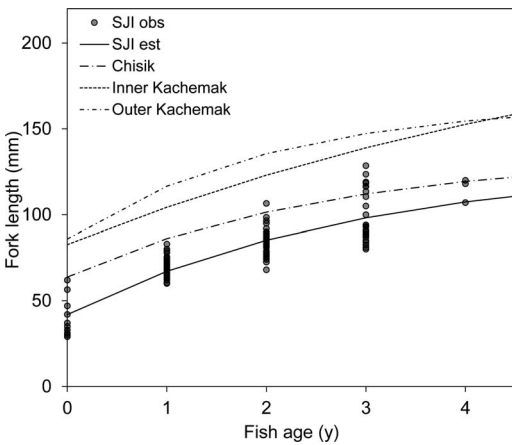

FIGURE 6.　Pacific Sand Lance (*Ammodytes personatus*) length-at-age data and fitted von Bertalanffy growth functions for Cook Inlet, Alaska (Chisik Island, Inner Kachemak Bay, and Outer Kachemak Bay stocks) and San Juan Island (SJI, observed and estimated). Observed point data are not available for Alaskan fish; von Bertalanffy growth functions for Alaskan fish are reproduced from Robards and others (2002).

that may partially explain differences in fish growth between the 2 regions. Over the past 30 y (1989–2018), SST values were generally higher in the vicinity of San Juan Island (overall mean = 11.0°C) than in Cook Inlet (overall mean = 7.8°C) (Fig. 7). Mean SST values in each month were dependent on region, as evidenced by a significant interaction effect between month and region in the aligned rank transform analysis of variance ($F_{11,667} = 50.41$, $P < 0.001$). Temperatures during this 30-y period ranged from 7.1–16.8°C near San Juan Island and 3.5–14.1°C in Cook Inlet. Mean temperatures during the periods fish were alive in both regions (11.3°C near San Juan Island during 2012–2016 and 7.9°C in Cook Inlet during 1993–1997) were similar to the 30-y averages, and did not fall at either extreme of temperatures observed over that broader period, suggesting that study fish were not experiencing anomalous conditions in either region (Fig. 7). Temperature ranges during these shorter time periods were narrower, from 8.1–14.7°C in 2012–2016 near San Juan Island, and from 4.6–12.7°C in 1993–1997 in Cook Inlet, than those during the longer period. Similar to the 30-y period, there was a significant interaction effect between month and region on mean SST

TABLE 2. Estimated von Bertalanffy growth parameters (L_∞, K, t_0) and standard errors (in parentheses) for Pacific Sand Lance (*Ammodytes personatus*) collected from San Juan Island, WA, and Cook Inlet, AK (Chisik Island, Inner Kachemak Bay, and Outer Kachemak Bay). Von Bertalanffy growth parameters for Cook Inlet fish are reproduced from Robards and others (2002).

Location	L_∞ (mm FL)	K (y^{-1})	t_0 (y)
San Juan Island (WA)	130.73 (14.91)	0.33 (0.09)	−1.16 (0.25)
Inner Kachemak Bay (AK)	235.74 (18.10)	0.15 (0.02)	−2.83 (0.30)
Outer Kachemak Bay (AK)	166.33 (1.61)	0.48 (0.02)	−1.51 (0.07)
Chisik Island (AK)	135.61 (3.81)	0.37 (0.04)	−1.71 (0.17)

during the time fish were extant ($F_{11,88} = 50.41$, $P < 0.001$).

Fish near San Juan Island generally experienced a longer photoperiod, with higher maximum PAR levels extended over more of the growing season than fish in Cook Inlet (Fig. 8A). There was a significant interaction effect between month and region on mean PAR values ($F_{11,314} = 21.21$, $P < 0.001$). Regional differences in monthly PAR may be partially responsible for differences in chlorophyll-*a* observed in each region. Chlorophyll-*a* was generally higher near San Juan Island during the spring and summer months, as hours of daylight and water temperatures increased; however, the observed values were far more variable in that region, suggesting greater interannual variability in production (Fig. 8B). There was a significant interaction effect between month and region on mean chlorophyll-*a* values ($F_{8,265} = 13.34$, $P < 0.001$). Values of net primary productivity were also slightly higher in spring (April to June) near San Juan Island, but generally more variable throughout the year than in Cook Inlet (Fig. 8C). There was a significant interaction effect between month and region on mean net primary productivity values ($F_{6,183} = 6.08$, $P < 0.001$).

DISCUSSION

In the present study, we compared Pacific Sand Lance stocks across a latitudinal gradient
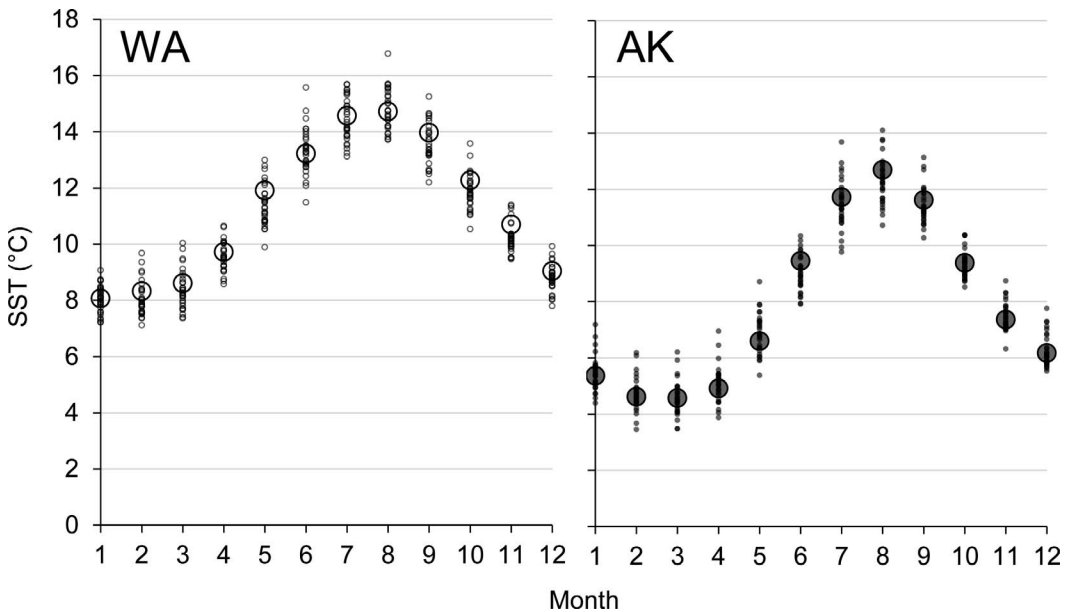

FIGURE 7. Monthly sea surface temperatures (SST) near San Juan Island, WA, and Cook Inlet, AK, Pacific Sand Lance (*Ammodytes personatus*) collection locations. Small circles represent within-month averages for each year from 1989 to 2018. Large circles represent mean monthly SSTs during the time fish were extant in each region (San Juan Island: 2012–2016; Cook Inlet: 1993–1997).
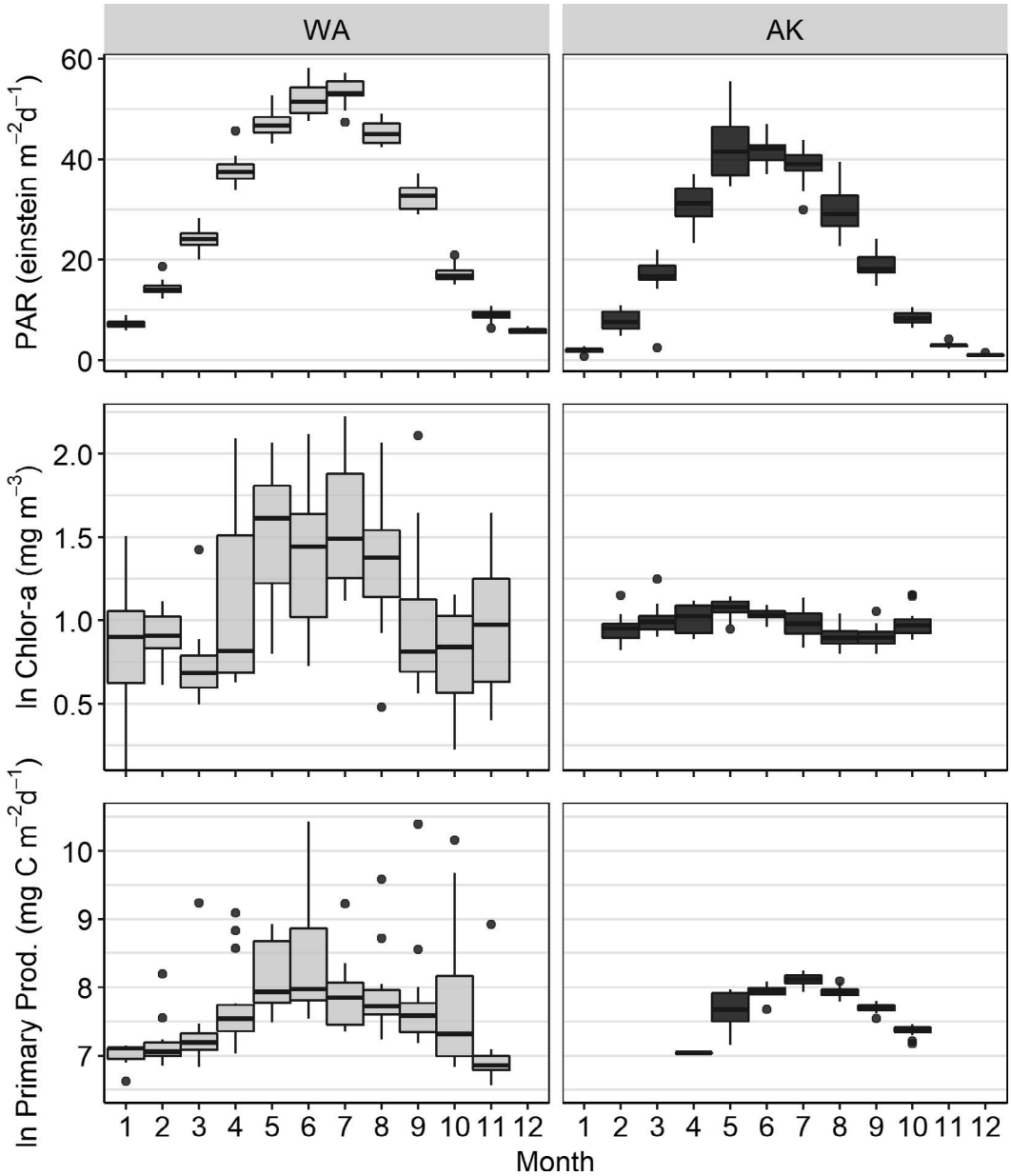
FIGURE 8. Monthly values of environmental conditions measured from 2003 to 2017 proximate to Pacific Sand Lance (*Ammodytes personatus*) collection sites at San Juan Island, WA, and Cook Inlet, AK: (A) photosynthetically available radiation (PAR), (B) chlorophyll-*a* (ln-transformed), and (C) primary productivity (ln-transformed). The horizontal lines within each box are median monthly values, the bottom and top of each box represent the 25th and 75th percentiles, respectively, the whiskers represent values within 1.5 times the interquartile range and points represent outliers.

of 11.5° in the highly dynamic GOA LME. There were large differences in growth between the San Juan Island, Washington, stock and 2 of the Cook Inlet, Alaska, stocks of Pacific Sand Lance, which may be at least partially attributable to general differences in environmental conditions between the 2 regions. For example, fish in Cook Inlet tend to experience greater seasonal temperature fluctuations and a shorter photoperiod than fish near San Juan Island. Although water temperatures are colder in Cook Inlet overall, the difference in temperatures between the 2 regions is greater in winter than summer. This leads to similar thermal conditions in the summer, when increased temperatures facilitate accelerated growth, and divergent conditions in winter, when colder temperatures in Cook Inlet allow greater energy conservation in winter dormancy.

Latitudinal variation in the phenology and magnitude of lower-trophic-level productivity also likely affect growth of Pacific Sand Lance differentially across its range. Many mobile taxa migrate to polar latitudes, including to Alaska waters, in spring and summer months to capitalize on the intense productivity related to seasonal plankton blooms (Baker and others 1985; Phillips and others 2018). Indices of productivity (chlorophyll-*a* and net primary productivity) were more variable from year to year near San Juan Island than in Cook Inlet. San Juan Island fish have increased metabolic demands because they experience higher mean temperatures, possibly reducing their capability for fast growth in conditions of resource limitation. Conversely, Pacific Sand Lance in Cook Inlet may have more rapid growth coinciding with the productivity window when conditions are favorable (Conover and others 1997; Varpe 2017). This capability for fast growth may be particularly important for fish in their 1st year. Pacific Sand Lance in Cook Inlet grow extremely quickly in their 1st year, from 20–50 mm in June to 80–90 mm by October, with most of that growth occurring in August and September when temperatures are highest (Blackburn and Anderson 1997); Robards and others (2002) observed similar growth rates. Additional studies describing region-specific primary and secondary productivity, most importantly the abundance and size composition of common Pacific Sand Lance prey such as calanoid copepods and euphausiids, may further clarify these potential effects on growth.

Latitudinal variation in the duration and timing of the winter dormancy period with respect to energy storage and expenditure could also explain observed differences in size at age of Pacific Sand Lance. Catch, diet, and energetics data from Cook Inlet (Blackburn and Anderson 1997; Robards 2000) and the San Juan Archipelago (Sisson and Baker 2017; Baker and others 2019) suggest that the dormancy period of adult fish is longer in Cook Inlet (October through April) than at San Juan Island (November through March). The length of the dormancy period also appears to be somewhat dependent on life stage. Diet and catch data from San Juan Island suggest that adults enter winter dormancy earlier than juveniles, presumably owing to their greater ability to leverage energy stores (Sisson and Baker 2017; Baker and others 2019). Juveniles likely need to continue foraging in marginal conditions in autumn to accumulate sufficient reserves for overwinter survival (Baker and others 2019). In Cook Inlet, somatic energy content of adults peaks in spring and early summer, and then starts declining with gonad development, in preparation for spawning in the autumn and winter (Robards and others 1999c). The need for increased starvation resistance may be more pronounced at higher latitudes with an extended winter season, such as in Alaska. A longer period of winter dormancy at these higher latitudes would require larger initial body sizes and additional starting energy reserves. By the same token, an extended period of dormancy allows high-latitude Pacific Sand Lance to conserve energy by lowering metabolic demands in winter (Quinn and Schneider 1991) while taking advantage of higher temperatures in summer to increase overall growth.

Even across relatively small spatial and temporal scales, Pacific Sand Lance appear to display high variability in growth. Robards and others (2002) found statistically significant differences in length at age among the 3 Cook Inlet stocks described herein. Furthermore, they determined that temperature was positively correlated with growth within stocks, but among stocks, fish in the warmest site (Chisik Island) were smaller and grew slower than fish in the coolest site (outer Kachemak Bay). Robards and others (2002) concluded that small-scale differences in productivity and sand lance abundance among their study sites were likely responsible for the observed differences in growth. In the

present study, it is possible that localized conditions experienced by the San Juan Island stock were relatively limiting to growth, and that variation in growth at small spatial scales may obscure any broader latitudinal patterns across the range of Pacific Sand Lance. Further sampling of heterogeneous habitats across a greater portion of the Salish Sea may better elucidate regional fine-scale spatio-temporal variation in growth or other life-history attributes of Pacific Sand Lance.

A question that deserves further investigation is the effect of recent climate warming on Pacific Sand Lance in the Salish Sea, Washington, and therefore on our comparison between the San Juan Island and Cook Inlet stocks. Sampling limitations precluded direct regional comparisons within the same timeframe; the Cook Inlet stocks were sampled during the mid-1990s, and the San Juan Island stock was sampled during "The Blob," a marine heatwave event documented in the North Pacific Ocean in 2014–2016 (Bond and others 2015; Hu and others 2017). Marine heatwaves such as The Blob have had profound and widespread effects on multiple trophic levels, resulting in reduced productivity, lower fishery catches, altered species distributions, and seabird die-offs (Peterson and others 2014; Jones and others 2018; Yang and others 2019). Despite the fact that the San Juan Island stock was sampled during The Blob, the SSTs measured during that period were not at the extreme of the 30-y range, which suggests that the relatively low size at age at San Juan Island may not be directly attributable to anomalous temperatures in that region. However, recent studies have described other negative effects of the Blob on Pacific Sand Lance in the GOA LME. For example, age-1 Pacific Sand Lance in Prince William Sound, Alaska, had lower growth and lipid accumulation during The Blob compared to cooler periods (von Biela and others 2019), and a recent study at our sampling sites in the San Juan Islands showed that Pacific Sand Lance had generally lower body condition during the 2014–2015 Blob years compared to 2010, 2012, and 2013 (Baker and others 2019). Possible negative effects imposed by The Blob on growth of Pacific Sand Lance could be direct (for example, increased metabolic demands cause lower growth) or indirect (for example, changes in prey distribution, abundance, or quality affect consumption rates and lipid storage). In particular, lipid-rich cold-water copepods, preferred food items of Pacific Sand Lance, have been shown to be negatively affected by anomalously warm temperatures in the North Pacific (Mackas and others 2007). Long-term data on copepod community composition and abundance from the San Juan Archipelago is currently limited, making it difficult to test this possibility directly. Contemporaneous otolith collections of Pacific Sand Lance throughout its range in timeframes spanning warm and cool periods, in tandem with measurements of local ambient environmental conditions and productivity indices, may allow us to further differentiate among climate-change mediated effects and latitudinal effects on annual growth.

The growth parameter estimates presented here provide an important baseline for comparisons with other regions and stocks of Pacific Sand Lance. This represents the 1st peer-reviewed study describing otolith-based age and growth estimates of Pacific Sand Lance in the Salish Sea, near the southern extreme of the GOA LME, and is among the 1st robust analyses of age for this species anywhere in its range. Although we cannot rule out the potential for age determination bias between our study and Robards and others (2002), to reduce this possibility we employed similar methods and applied similar criteria to define annuli. Both studies also used independent methods to support the validity of age estimates: ours through the observed annual progression of age classes, and Robards and others (2002) through the seasonal progression of growth zones on the otolith edge. Regardless, age estimates from both studies should be considered preliminary until additional repeated sampling is undertaken to identify strong year classes or other stronger forms of validation can be used to verify age determination accuracy in this species (Campana 2001; Kimura and others 2006).

Our study aligns with routine monitoring of Pacific Sand Lance in the San Juan Channel that has been ongoing since 2010 (Sisson and Baker 2017; Baker and others 2019). The maximum length of Pacific Sand Lance in the present study is only 10 mm less than the maximum length of 139-mm FL observed over the entire monitoring program, during which over 7000 individual fish collected using Van Veen and beach-seine sampling methods have been measured (MB,

unpubl. data). Length distributions obtained from Van Veen benthic grabs are also similar to those obtained from submersible stereocamera surveys (MB, unpubl. data). Although we are not certain that either method is fully sampling the true length distribution of the population, these results suggest that the Van Veen method is not biased relative to more passive sampling methods. Beach seines are also considered to be a non-size selective sampling method (Cailliet and others 1986; Robards and others 2002).

Despite the ecological importance of Pacific Sand Lance to the GOA LME, few investigations have focused on the basic biology and life-history variability of this species across its range. In this study, we provide new age information for this key forage species, identifying clear geographic patterns in growth that are likely related to external factors including climate forcing and prey availability. Pacific Sand Lance is 1 of the 2 dominant forage species (together with Pacific Herring, *Clupea pallasii*) in the inner waters of the Pacific Northwest and Alaska (Abookire and others 2000; Penttila 2007; Therriault and others 2009) and is among the most energy-dense fish in this trophic niche (Van Pelt and others 1997; Anthony and others 2000). Although this species is not the subject of a target fishery in the GOA LME, it is an important forage species, supporting many commercially exploited groundfish species as well as most piscivorous marine birds and mammals throughout its range. Therefore, the establishment of baseline biological information and continued monitoring, particularly as the climate warms, is critical. Evaluating spatial and temporal variation in Pacific Sand Lance life-history parameters is crucial to understanding relative abundance, recruitment dynamics, and distribution of this species and its role in the ecosystem.

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