Intra-seasonal and inter-annual patterns in the demographics of sand lance and response to environmental drivers in the North Pacific

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ABSTRACT: Sand lance and sand eels (*Ammodytes* spp.) are a critical component in all northern latitude pelagic ecosystems. They are primary forage species for marine birds and mammals, target stocks for commercial fisheries in Europe and Asia, and prey to nearly all commercial fishes in the North Atlantic and North Pacific oceans. Throughout their range, there are significant knowledge gaps in the status of populations, stock structure, and life history. Our analyses of Pacific sand lance *Ammodytes personatus* in the fall season provide insight to life history attributes, demographic patterns, intra-seasonal trends, and response to climate forcing. We document a seasonal shift from pelagic foraging to winter dormancy, coincident with reductions in light, temperature, and a shift from upwelling to downwelling. Intra-seasonal and inter-annual trends in relative abundance and body condition demonstrate a response to regional climate indices as well as local environmental conditions, particularly evident in the context of recent North Pacific anomalous warming. We provide new insights into life history patterns, including a shift from nearshore to deep water benthic habitats as a function of age. Inter-annual patterns in size structure and juvenile abundance suggest a regular pattern of biennial fluctuations in year-class strength. These results have implications for understanding annual recruitment and seasonal variation in availability of this important resource. Our findings expand knowledge of Pacific sand lance in the California Current and Gulf of Alaska ecosystems, with application to fisheries management, ecological interactions, and comparative analyses to other regions that host this important genus of small pelagic fishes.

KEY WORDS: *Ammodytes* spp. · Forage fish · Population structure · Abundance · Cyclic dynamics · Year-class strength · Age structure · Condition · Fall transition · Winter dormancy · Climate · Recruitment

1. INTRODUCTION

Sand lance and sand eels (*Ammodytes* spp.) are small, planktivorous, semi-demersal forage fishes that play a crucial role in the coastal pelagic ecosystems of the Northern Hemisphere. These fishes are important prey for more than 100 species of marine birds, mammals, and fishes (Furness 1990, Willson et al. 1999, Link & Garrison 2002, Haugland et al. 2006) and are an important target of commercial fisheries in Japan (Hamada 1985, Han et al. 2012) and the North Sea (Sherman et al. 1981, Furness 2002). Pacific sand lance *Ammodytes personatus* are distributed throughout the eastern North Pacific Ocean, Gulf of Alaska, Aleutian Islands, and eastern Bering Sea (Orr et al. 2015). Other related species include

A. hexapterus in the western North Pacific and North American Arctic, *A. japonicus* and *A. heian* in the western Pacific, *A. dubius* and *A. americanus* in the western Atlantic, and *A. marinus* and *A. tobianus* in the eastern Atlantic and North Sea. Despite their importance as forage and as commercial stocks, little is known about the biology, life history, and population dynamics of post-larval sand lance and sand eels (Nelson & Ross 1991, Robards et al. 1999a,b, Liedtke et al. 2013, Selleck et al. 2015).

Sand lances and sand eels are distinguished from other dominant northern latitude forage fish species, such as capelin *Mallotus villosus*, eulachon *Thaleichthys pacificus*, herring *Clupea pallasii*, shad *Alosa* spp., menhaden *Brevoortia tyrannus*, sardine *Sardina/ Sardinella* spp., and anchovies *Engraulidae* spp. in their remarkable ability to actively burrow into nearshore sand–gravel bottom sediments for refuge and rest (Bizzarro et al. 2016). This behavior is exhibited in both diurnal and seasonal cycles and time frames (Field 1988, Quinn 1999), such that *Ammodytes* spp. bury at night, for extended overwintering periods (Fisheries and Ocean Canada 2009, 2018, Pearson et al. 1984) and, in the case of *A. japonicus* and *A. heian*, for summer aestivation (Kishi et al. 1991). This highlights an important seasonal component to their life cycle. Following a winter dormant period, sand lance and sand eels emerge to forage in the spring and summer months when zooplankton are most abundant (Winslade 1974, Field 1988). In the fall, the majority of individuals cease feeding, bury, and remain dormant in benthic sediments for the duration of the winter (*A. personatus*, Robards et al. 1999a; *A. marinus*, Winslade 1974; *A. tobianus*, Reeves 1994, O'Connell & Fives 1995). While there is extensive documentation of these trends (Rindorf et al. 2017), most work to characterize this phenomenon is anecdotal. Our analyses focus on the critical autumn season and the fall transition from summer upwelling to winter downwelling conditions in the eastern North Pacific as these fish transition from summer foraging to winter dormancy.

There are apparent differences between *Ammodytes* spp. in life span, size-at-maturity, age-at-maturity, and spawning dynamics. Sexual maturation generally occurs towards the end of the second year of life (age-2) in *A. personatus* (Kitaguchi 1979), *A. americanus* (Richards 1982, Brethes 1992), and *A. tobianus* (O'Connell & Fives 1995, Bergstad et al. 2001); although there is evidence for maturity as early as age-1 in *A. dubius* (Nelson & Ross 1991). At the same time, there is considerable variation in age-at-maturity (Boulcott et al. 2006, Boulcott & Wright

2008), such that *A. dubius* (Scott 1968, Winters 1983) and *A. marinus* (Reay 1970, Bergstad et al. 2001, Boulcott et al. 2006) may mature at older ages. In *A. tobianus*, few individuals survive beyond age-3 or age-4 due to high natural mortality (van Deurs et al. 2009). Differences may also be evident within species across their geographic range. Better defining basic demographic traits and life history parameters is crucial to understand how these populations might respond to changing climate or environmental perturbation, determine implications for harvest conservation and management, and develop time scales for rebuilding stocks.

Pacific sand lance *A. personatus* appear to reach a length of 150 mm (Love et al. 2005) and are relatively short-lived, with an estimated maximum age of 6 yr (Robards et al. 2002). Adults spawn intertidally once per year on fine gravel or sandy beaches (Robards et al. 1999b, Penttila 1995). Larval surveys suggest that Pacific sand lance spawn from January–April in the Gulf of Alaska (Kendall et al. 1980, McGurk & Warburton 1992). Observations of captive fish collected from the northern California Current also indicate late winter spawning (Pinto 1984). Spawning occurs from November–February in Puget Sound and the Strait of Georgia (Penttila 1995, Thuringer & Truscott 2003), predominantly in the first half of that time period (Penttila 1995), and spawning sites appear to be used on a perennial basis (Penttila 2007).

Pacific sand lance transition between several ontogenetic stages in their first year of life. Demersal eggs attach to beach and intertidal substrates until emergence, with an incubation period of approximately 1 mo (Penttila 2007). Analyses of phenology and size-at-stage in the northern Gulf of Alaska indicate larval emergence at approximately 5 mm in February–March, yolk absorption and commencement of feeding at approximately 10 mm in March–April, flexion at approximately 15–20 mm in May, and complete transformation at approximately 50 mm in July (Doyle & Mier 2016). These life history traits may vary with latitude (Scott 1972). Planktonic sand lance larvae are common in the nearshore waters of the Puget Sound Basin in the late winter (Penttila 2007) and juvenile sand lance are common in the nearshore zone through their first summer of life (Penttila 2007). After metamorphosis, young-of-the-year juvenile fish descend to the bottom and settle in sandy substrates (Fisheries and Ocean Canada 2009, Washington Department of Fish and Wildlife 2018). Pacific sand lance may also be found burrowing at or below mean lower low water in the upper, oxygenated stratum of

intertidal sediments on Puget Sound beaches (Quinn & Schneider 1991, Quinn 1999). After settling, individuals show high site fidelity (Gauld 1990). Recruitment is traditionally defined as the number of post-settlement individuals in late spring.

Fish populations are highly sensitive to variation in recruitment (Cushing 1990). Forage fishes, in particular, have relatively short life spans, small body size, early maturation, and high fecundity. These traits often result in particularly large fluctuations in abundance in response to environmental conditions, susceptibility to predators, and availability of prey (Anderson & Piatt 1999). In general, predation and starvation mortality during early life stages of forage fishes is substantial but decreases rapidly with increasing size. More specifically for *Ammodytes* spp., it has been suggested that non-spawning (age-1) fish may have density-dependent effects that are not accounted for within spawning stock biomass-recruitment (SSB-R) relationships (Furness 1999, Arnott & Ruxton 2002, Arnott et al. 2002, van Deurs et al. 2009). Cyclic dominance in recruitment (e.g. divergent year-class strength in odd and even calendar years) has been suggested for several populations, including North Sea *A. marinus* and western Pacific *A. personatus* (Kishi et al. 1991, Kimura et al. 1992). This phenomenon may be the result of carrying capacity, competition for habitat and resources (Murdoch 1994), or density-dependent effects related to population-regulating mechanisms inherent to the species such as cannibalism (Ritzau Eigaard et al. 2014).

In addition to density-dependent constraints, environmental conditions may structure populations and influence relative survival and condition of individuals within a given period of time. Pelagic fishes are often subject to large-scale fluctuations in productivity related to variation in oceanographic conditions (Francis et al. 1998, Hollowed et al. 2001). Variability in near-surface temperatures in the North Pacific has been attributed to several large-scale modes of climate variability, including the El Niño-Southern Oscillation (ENSO; Zhang et al. 1997) and basin-scale drivers such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997). The condition of individual fish and the abundance of the population may also vary according to these changing oceanographic regimes. In particular, temperature may have direct effects on metabolic rates and indirect effects on growth related to the quantity, quality, composition, and availability (e.g. phenology of production) of planktonic prey available for consumption (Batten et al. 2016).

Understanding patterns and drivers in demographic trends requires baseline and time series data. We examined Pacific sand lance populations over a 6 yr period at 2 locations: (1) a known spawning site and nearshore rearing habitat; and (2) an offshore adult habitat. Our objectives were to explore dynamics related to foraging, condition, and winter dormancy as well as evidence for biennial patterns in year-class strength. To this end, we investigated several aspects of Pacific sand lance population structure, including their recruitment, relative abundance, condition, and age structure over intra-seasonal and inter-annual time scales. We also analyzed these trends in the context of seasonal environmental metrics and regional climate indices. This study represents one of the most extensive time series available for Pacific sand lance and provides insight into seasonal availability and size structure of sand lance populations in the eastern Pacific. Our results provide (1) evidence for distinct habitat use according to life stage; (2) new insights on fall seasonal dynamics related to foraging, winter dormancy, and winter reset; (3) preliminary evidence for biennial patterns in year-class strength and/or cyclical recruitment; and (4) evidence for a pronounced shift in condition across all age classes in response to recent anomalous warming in the North Pacific Ocean.

2. MATERIALS AND METHODS

2.1. Collection and handling of fish

Pacific sand lance were sampled from 2 distinct sites near San Juan Island, WA, USA: (1) Jackson Beach (JB), a known spawning and rearing habitat (Washington Department of Fish and Wildlife 2017), and (2) San Juan Channel (SJC), a recently discovered offshore deep-water (80 m) habitat (Greene et al. 2011, 2017) characterized by a prominent sand wave field that extends north to south a distance of approximately 2 km (Fig. 1). Both sites are within the San Juan Island Archipelago in the Salish Sea, at the US–Canadian border and confluence of the California Current and Gulf of Alaska large marine ecosystems.

Relative abundance (catch per unit effort, CPUE) was recorded at JB and at the SJC wave field throughout the fall. Fish at JB were sampled via beach seines performed approximately twice per week at dawn or dusk between 28 September (day of the year 271) and 10 November (day of the year 314) from 2010–2015. Timing was designed to target apparent crepuscular feeding behaviors. In total, 127 seines were conducted
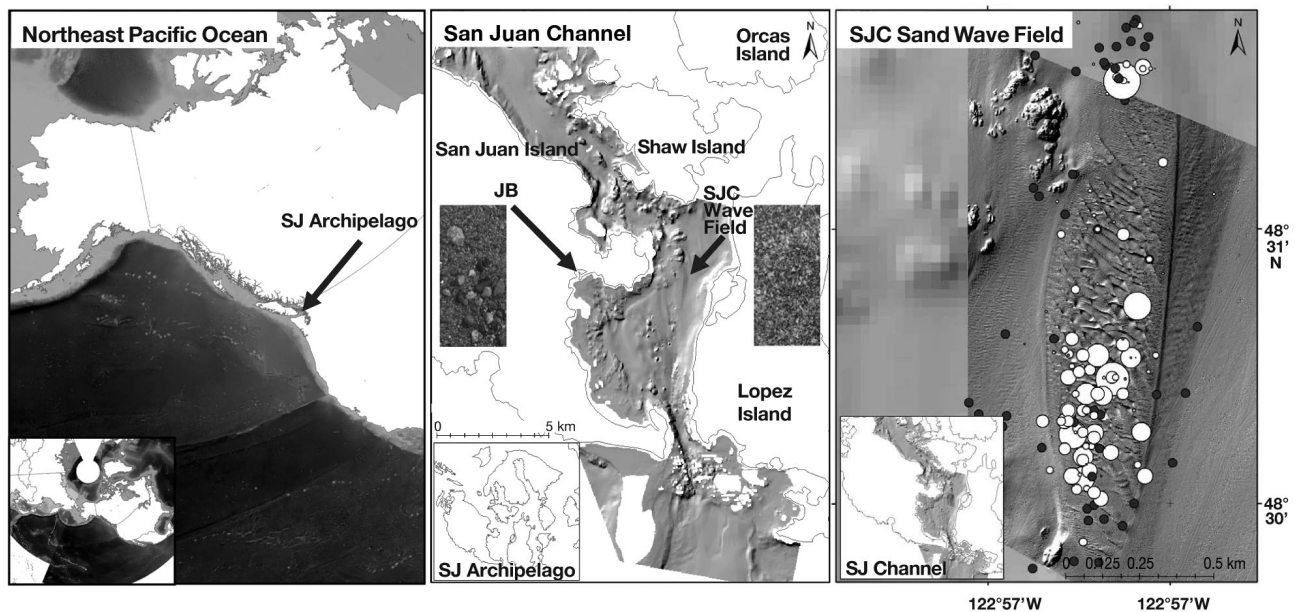
Fig. 1. Pacific sand lance *Ammodytes personatus* sample sites in the San Juan Island archipelago in the Salish Sea (left panel): spawning area Jackson Beach (JB), and offshore deep-water sand wave field in San Juan Channel (SJC) (center panel). A high-resolution multibeam bathymetry contour is provided for the full extent of the San Juan Channel (center panel) as well as for the SJC sand wave field (right panel) (multibeam data courtesy of G. Greene and J. Aschoff, Moss Landing Marine Laboratories, Tombolo Mapping Team). Sites of Van Veen grabs are displayed, with empty grabs represented by dark points and grabs with fish represented by white points, each scaled proportionally to catch per unit effort (right panel). Inset photographs (center panel) display sediments typical of each site. A larger proportion of coarse grain sand and shell hash was present at SJC and greater proportion of fine grain sand and pebbles was present at JB

over 35 sampling events, using a knotless nylon mesh with dimensions 36.6 m (width) × 3.7 m (depth). The net was set parallel to the beach at a distance of 25 m as described by Cailliet et al. (1986). A total of 127 seines (12–47 yr^{-1}) were conducted at JB (Table 1). A Van Veen grab sample (Høines & Bergstad 2001) was deployed from the University of Washington R/V 'Centennial' or R/V 'Auklet' to sample fish in sediments in the SJC sand wave field between 15 September (day of the year 258) and 28 November (day of the year 332). The Van Veen samples a maximum sediment volume of 0.026 m^3 over a surface area of 0.12 m^2. A total of 282 grabs (28–84 yr^{-1}) were successfully deployed (i.e. Van Veen completely closed on retrieval) in the SJC wave field (Table 1). Sampling also occurred in the area spanning the distance between these sites to assess whether there was potential benthic habitat between them (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m617p221 _supp.pdf); no fish were found in this area.

2.2. Fish processing and measurements

All live fish brought back to the laboratory were handled as described under the University of Wash-

ington Institutional Animal Care and Use Committee (IACUC) Protocol 4238-03. Fish were administered a lethal dose of the anesthetic tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate (1:1 ratio), in accordance with IACUC guidelines. Most samples were stored in a 1:1 solution of 10% formalin (formaldehyde supersaturated with Borax) and saltwater (except for fish collected for otolith analysis, described below). Fish were blotted dry, and fork length (FL), total length (TL), and girth measurements were taken. Length measurements were taken to the nearest 1 mm. FL was used in analyses of length–weight regressions, length frequency distributions, and length-at-age analyses. Wet weight was measured to the nearest 0.01 g using an OHAUS Scout Pro 400 g × 0.01 g scale. A total of 5499 fish were measured for length and weight between 2010 and 2015 (SJC, n = 2597; JB, n = 2902; Table 2).

2.3. Otolith measurement and analysis

Sampling for age occurred from September– November 2015. Sagittal otoliths were removed from the sacculus after making a transverse incision

Table 1. Pacific sand lance sampling events from 2010–2015 in Jackson Beach (JB) and San Juan Channel (SJC) with zero (empty) and non-zero (positive) catch. Sampling in off-shore wave fields with Van Veen grabs occurred from 15 September to 28 November. Sampling in the nearshore site with beach seines occurred from 25 September until fish were no longer caught in beach seines on 2 consecutive sampling occasions. Fish were not observed in the water column after 15 November in any year

Location (gear type)	Year	Sample days	Total samples	Fish present	No fish
JB	2010	4	12	4	8
(beach seines)	2011	–	–	–	–
	2012	9	19	5	14
	2013	9	19	16	3
	2014	9	47	36	11
	2015	9	30	21	9
SJC	2010	4	28	26	2
(Van Veen	2011	2	36	31	5
grabs)	2012	11	44	42	2
	2013	6	37	30	7
	2014	8	84	72	12
	2015	9	53	50	3

behind the skull. Otoliths were dissected from fresh fish or fish preserved in ethanol and frozen. Otoliths were cleaned of soft tissue and placed in Eppendorf tubes containing ethanol. One otolith from each pair was affixed to a glass slide sulcus-side down using Loctite UV-curing adhesive. Otoliths were viewed using a Leica MZ95 dissecting microscope and re-flected light. Mineral oil was applied to the surfaces of mounted otoliths to enhance contrast between growth zones. The surfaces of some otoliths were very faint or opaque in appearance; to improve clar-ity, they were polished by hand using 320 grit fol-lowed by 1200 grit Buehler wet–dry abrasive paper. In some cases, the unmounted otolith was sectioned

transversely through the core to further aid identifi-cation of growth zones.

Standard methods (Matta & Kimura 2012) were used to estimate fish age. Otoliths were read 2 times blindly and independently by a single age reader; if age estimates did not agree, otoliths were read a third time to reach a consensus age. Precision between age estimates was estimated by calculating the percent agreement (PA), average percent error (APE; Beamish & Fournier 1981), and coefficient of variation (CV; Chang 1982). PA between age estimates was 84%, APE was 4.31%, and CV was 6.09%.

In agreement with other studies in the Atlantic and Pacific oceans (Nelson & Ross 1991, Robards et al. 1999a), no significant differences in length–weight relationships were observed between sexes. There-fore all data were pooled in subsequent analyses. On the basis of analyses of sagittal otoliths removed in 2015, Pacific sand lance with FLs 0–60 mm were con-sidered young-of-the-year (YOY; age-0), fork lengths 60–80 mm corresponded to age-1, fork lengths 80–100 mm corresponded to age-2, and fork lengths 100–120 mm corresponded to age-3 (Fig. 2). Using these data, known maturation cycles (van Deurs et al. 2009), and approaches used in other studies (Robards et al. 1999b), fish were assigned as juveniles (age-0 and age-1; immature) or adults (age-2+; mature), as per the age–length key (Table 3).

2.4. Environmental measurements

Local environmental conditions and broad-scale climate regime indices were evaluated to determine correlation with seasonal and inter-annual trends in fish condition and abundance. Photosynthetically

Table 2. Relative percentage and absolute numbers (n) of Pacific sand lance by length (age-class) in Jackson Beach (JB) and San Juan Channel (SJC)

| Location (gear type)	Year	0–60 mm (age-0)		60–80 mm (age-1)		80–100 mm (age-2)		100–120 mm (age-3)		120 mm+	
		%	n	%	n	%	n	%	n	%	n
JB	2010	6.16	9	79.45	116	14.22	21	–		–	
(beach seines)	2011	–		–		–		–		–	
	2012	21.81	190	73.25	638	4.94	43	–		–	
	2013	7.05	9	76.31	979	22.68	291	0.00	4	–	
	2014	2.42	4	64.85	107	32.72	54	–		–	
	2015	2.29	10	90.85	397	6.86	30	–		–	
SJC	2010	0.01	2	71.28	144	27.27	55	0.00	1	–	
(Van Veen	2011	–		49.11	139	31.80	90	18.02	51	1.06	3
grabs)	2012	–		60.41	595	35.64	351	2.44	24	1.42	14
	2013	–		–		17.00	17	71.00	71	12.00	12
	2014	–		36.00	175	58.64	285	3.91	19	1.44	7
	2015	–		19.04	103	63.22	342	14.05	76	3.70	20
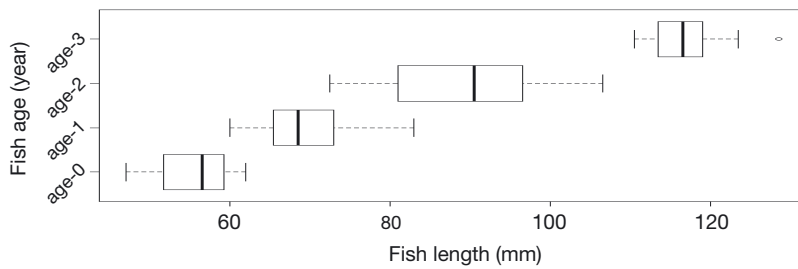
Fig. 2. Lengths associated with Pacific sand lance *Ammodytes personatus* age-0 to age-3+ yr, as assessed by analysis of growth zones within sagittal otoliths (Age and Growth Program, Alaska Fisheries Science Center, NOAA). Boxplots display the range of length values; shaded box: inter-quartile range or middle 50% of the data; vertical black line: median value; whiskers: 5th and 95th percentiles; points: outliers

active radiation (PAR) and sea surface temperature (SST) measurements were collected on-site at the NOAA Friday Harbor Station FRDW1-9449880 at 48° 32′ 43″ N, 123° 0′ 44″ W (http://wx.fhl.washington. edu/vdv/VV_Frame.php) and were referenced to the NASA Aqua MODIS, NPP 1-day composite at 45° 32′ 42″ N, 123° 0′ 43″ W (http://coastwatch.pfeg.noaa. gov/erddap/griddap/erdMWpar01day_LonPM180.h tml), approximately 4.5 km from SJC and 2.8 km from JB. Upwelling indices (UI) were daily averages of wind-driven, cross-shore transports computed from the Fleet Numerical Meteorology and Oceanography Center and National Data Buoy Center 6-hourly surface pressure analyses in units of $m^3 s^{-1}$ along each 100 m of coastline, developed from NOAA Bakun Index Values at 48° N, 125° W (www.pfel.noaa.gov/ products/PFELData/upwell/daily/p06dayac.all), marking the transition from summer upwelling conditions to winter downwelling conditions. Indices for broadscale climate regimes, including ENSO, the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008), and PDO (Mantua et al. 1997, Zhang et al.

1997) were derived from the Northwest Association of Networked Ocean Observing Systems (NANOOS) database (http://nvs.nanoos.org/Climatology).

2.5. Statistical data analysis

Condition factor (K) was calculated for fish collected at both sampling sites using the following formula (Bagenal & Ricker 1978):

$$K = m \times 10^7 \times l^{-3} \tag{1}$$

where m is mass (in g) and l is FL (in mm).

Relative abundance (i.e. CPUE) for each date was calculated by dividing the total number of fish caught on that day by the number of seines or Van Veen grabs performed that day. Regression analyses were run in SigmaPlot (Systat Software). All other statistical applications were applied in R statistical computing software (R Development Core Team 2016).

Seasonal trends were assessed using linear or logistic regression functions. Differences in K and FL values between the JB and SJC populations were assessed using analysis of variance (ANOVA) and Tukey's HSD test. Differences in length distributions were analyzed with Kolmogorov-Smirnov (KS) tests. Shifts in the mean length distribution between years were evaluated with the Wilcoxon rank sum test, and unimodality was evaluated with the Hartigan dip test statistic. Pearson correlations were calculated between annual mean condition and physical environmental variables (i.e. SST) and climate indices (ENSO, PDO, NPGO).

Wilcoxon rank sum test with continuity correction was used to evaluate differences in occurrence (presence or absence at JB) as a function of odd and even years. Kruskal-Wallis rank sum with pairwise comparisons and year as factor was used to evaluate abundance (mean CPUE, JB) as a function of year. Pooled mean and standard deviation for abundance (mean CPUE, JB) in even vs. odd years was calculated as:

$$\overline{X}_p = \frac{(n_1 \cdot \overline{X}_1) + (n_2 \cdot \overline{X}_2)}{n_1 + n_2} \tag{2}$$

$$s_p^2 = \frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2} \tag{3}$$

To further explore shifts in relative abundance over the season, while accounting for inter-annual shifts in abundance, individual catch per haul results (in

Table 3. Age–length key of Pacific sand lance. Estimated age-associated lengths based on analysis of lengths of known-age fish sampled in the fall season of 2015 (September–December 2015, n = 64). No fish were aged in other years. Differences in annual growth between years may mean that length–age estimates based on 2015 samples are not applicable to other years

Estimated length (mm) (age class)	Known-age observed length (mm)	
	Mean	Range
0–60 (age-0)	55.1 ± 7.59	47–62
60–80 (age-1)	69.1 ± 5.36	60–83
80–100 (age-2)	89.4 ± 10.26	81–106
100–120 (age-3)	114.3 ± 13.04	110–129

every day and year, including hauls with no fish) were analyzed using a generalized linear model (GLM, negative binomial distribution). Since variances in catch within each year were often higher than the mean difference between years, a negative binomial regression was used to account for over-dispersion (Venables & Ripley 2002). The zero-augmented models extend the mean function by modifying the likelihood of zero counts (Chambers & Hastie 1992) and allow for associated methods for diagnostics and inference (https://stats.idre.ucla.edu/r/dae/negative-binomial-regression/). The GLM was developed in R using the 'stats' package and 'glm.nb' in the 'MASS' package (R Development Core Team 2016; https://stat.ethz.ch/R-manual/R-devel/library/MASS/html/glm.nb.html). Standardization to the annual mean was implemented by including year as a factor.

A similar model framework (GLM, negative binomial distribution) was applied to analyze trends in relative condition of mature Pacific sand lance (offshore population, SJC) over the course of the fall season. A correlation matrix was also developed to compare the decline in condition and decline in seasonal environmental variables associated with summer production (e.g. SST, PAR, and UI). Correlations between physical indices (SST, PAR, UI) within and among years were analyzed in R using the packages 'PerformanceAnalytics', 'Hmisc', and 'corrplot'; 'hclust.method' was used for hierarchical clustering and the agglomeration of values.

A model (GLM, gamma distribution) was also applied to analyze annual trends condition in both the offshore (SJC) and nearshore (JB) populations as a function of annual SST, annual PAR, year-specific date of fall transition, and the predominant regional climatic indices (ENSO, PDO, NPGO). Data on climate indices (ENSO, PDO, NPGO) were aggregated into annual mean values. Data on environmental variables (SST, PAR) were year-specific mean values calculated over the dates of sampling (15 September–15 December 2015). The annual date of fall transition was determined at the following site: www.cbr.washington.edu/status/trans.

3. RESULTS

3.1. Length-at-age and size and age structure

FL distribution data were compiled from 2010 through 2015 for the JB and SJC populations (Fig. 3). While the JB population length frequency distribution differed slightly in all years (KS test, p < 0.005), this nearshore population was consistently composed of age-0 and age-1 fish. It was characterized by a similar range in FL across all years (mean ± SD = 74.88 ± 8.19 mm, range = 49–106 mm), with the exception of 2012 (66.84 ± 7.93 mm), for which the population had a slightly smaller distribution (Fig. 3, Table 2). The SJC population distribution was much more variable from year to year (KS test, p < 0.001), and included fish that were age-1 to age-3+. The mean (±1 SD) length of the SJC population was 84.40 ± 12.20 mm (range = 61–144 mm) and was significantly higher than that of the JB fish ($F_{1,2640}$ = 1040, p < 0.001). In the SJC, most years were dominated by fish corresponding to lengths associated with age-1 and age-2 fish. A bimodal trend was notable in odd years, such that a pulse of larger fish appeared in a relatively higher proportion in 2011, 2013, and 2015. The same phenomenon was noted in 2017 (Fig. S2 in the Supplement). This was not apparent in even years, including in the analysis of even-year data in a previous study (Blaine 2006, Fig. S3 in the Supplement). The 2013 SJC population was almost entirely comprised of this larger, presumably age-3, cohort. Histograms and boxplots (Fig. 3, inset) of FL distribution in SJC fish have a distributional skew towards larger fish in the 2011 and 2015 SJC populations (KS test, p < 0.001; Fig. 3, Table 2). At both sites (JB and SJC), significant shifts in distribution were noted between all years (JB all years, Wilcoxon test, p < 0.004; SJC all years, Wilcoxon test, p < 0.001). At both locations, distributions in all years were non-unimodal (i.e. at least bimodal; Hartigan dip test, JB all years, p > 0.629; SJC all years, p > 0.497), presumably reflecting the presence of multiple year classes at both locations (JB = age-0 to age-1; SJC = age-1 to age-3+). No variation in FL over the fall season was detected at either site (Fig. S4 in the Supplement).

3.2. Temporal trends in relative abundance

At JB, the mean (±SD) annual CPUE was 55.73 ± 41.58 fish seine^{-1} (range in annual mean = 14.91–287.33). At SJC, mean annual CPUE was 12.04 ± 6.98 fish per Van Veen grab (range in annual mean = 4.61–23.17). Data from all available years were plotted together initially without standardization to visualize in-season trends. Sampling occasions where no fish were caught were removed from seasonal analyses to reduce zero inflation. For the nearshore JB sand lance population (2013–2015 inclusive), CPUE showed a decreasing but not significant trend (R^2 = 0.06, p = 0.215; Fig. 4A). For the offshore SJC popula-
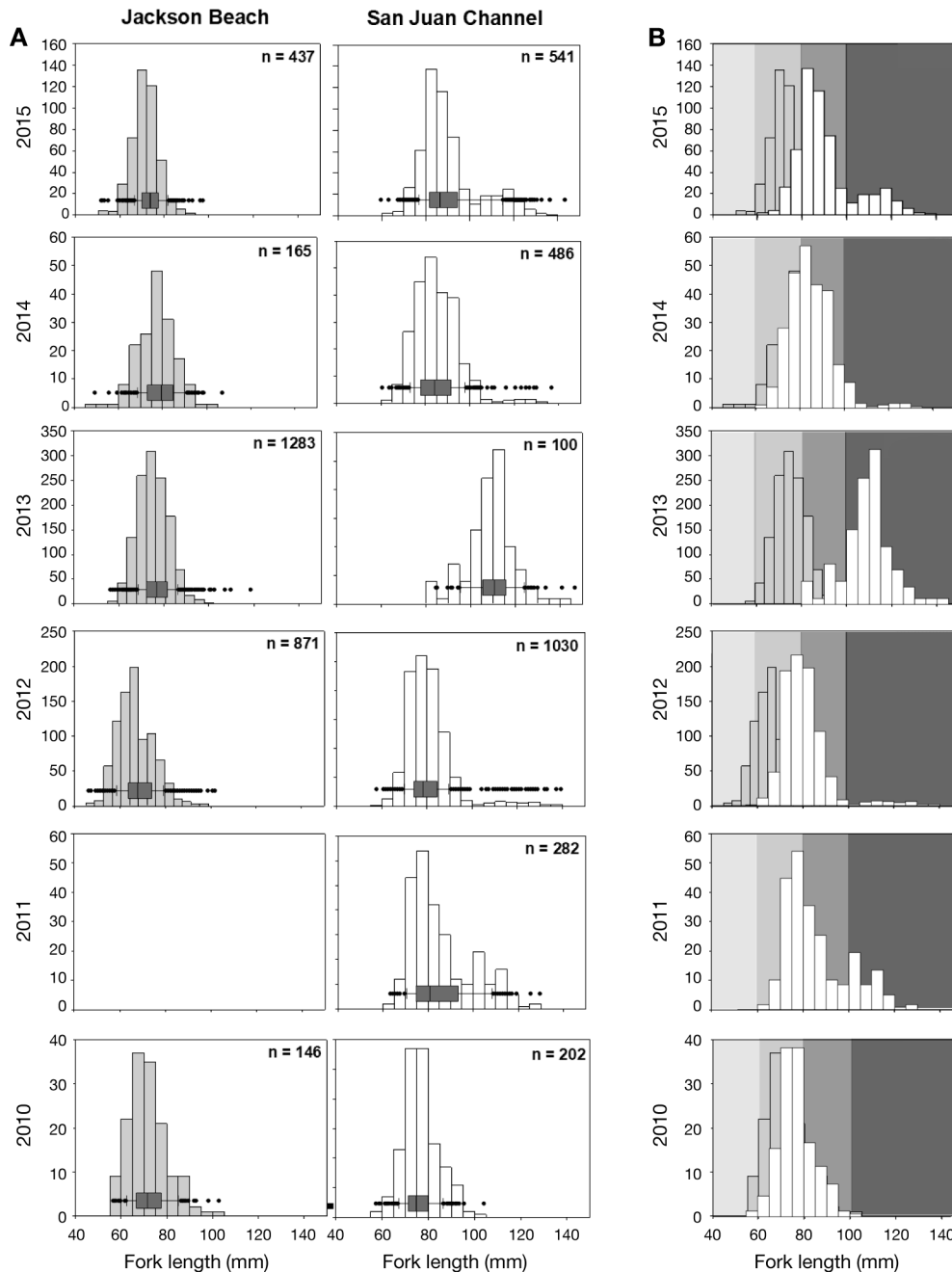
Fig. 3. (A) Pacific sand lance *Ammodytes personatus* length histograms at nearshore (Jackson Beach) and offshore (San Juan Channel) sites. Boxplots (box: interquartile range; line: median; whiskers: 95 % CI) are overlaid on histograms for comparison of distributional spread. Length distributions were distinct in each habitat, suggesting immature fish nearshore and mature adults offshore. Inter-annual patterns in age structure were evident in the bimodal distribution in the offshore adult population, pronounced in odd years, suggesting pulsed year-class strength. (B) Length histograms overlaid for distributional comparison and background shading used to indicate expected age classes (age-0: off-white; age-1: light gray; age-2: medium gray; age-3+: dark gray)

tion (2012–2015 inclusive) CPUE showed an increasing trend over the fall season ($R^2 = 0.11$, p = 0.052; Fig. 4C). Data from all studies were also standardized for relative abundance within each year to a mean of 0.0 and SD of 1.0 to reduce noise caused by variation between years. Using standardized data, the trend at JB remained nonsignificant ($R^2 = 0.02$, p = 0.488; Fig. 4B). Using the standardized data strengthened the increasing trend in CPUE at SJC over fall ($R^2 = 0.13$, p = 0.043; Fig. 4D), indicating that more
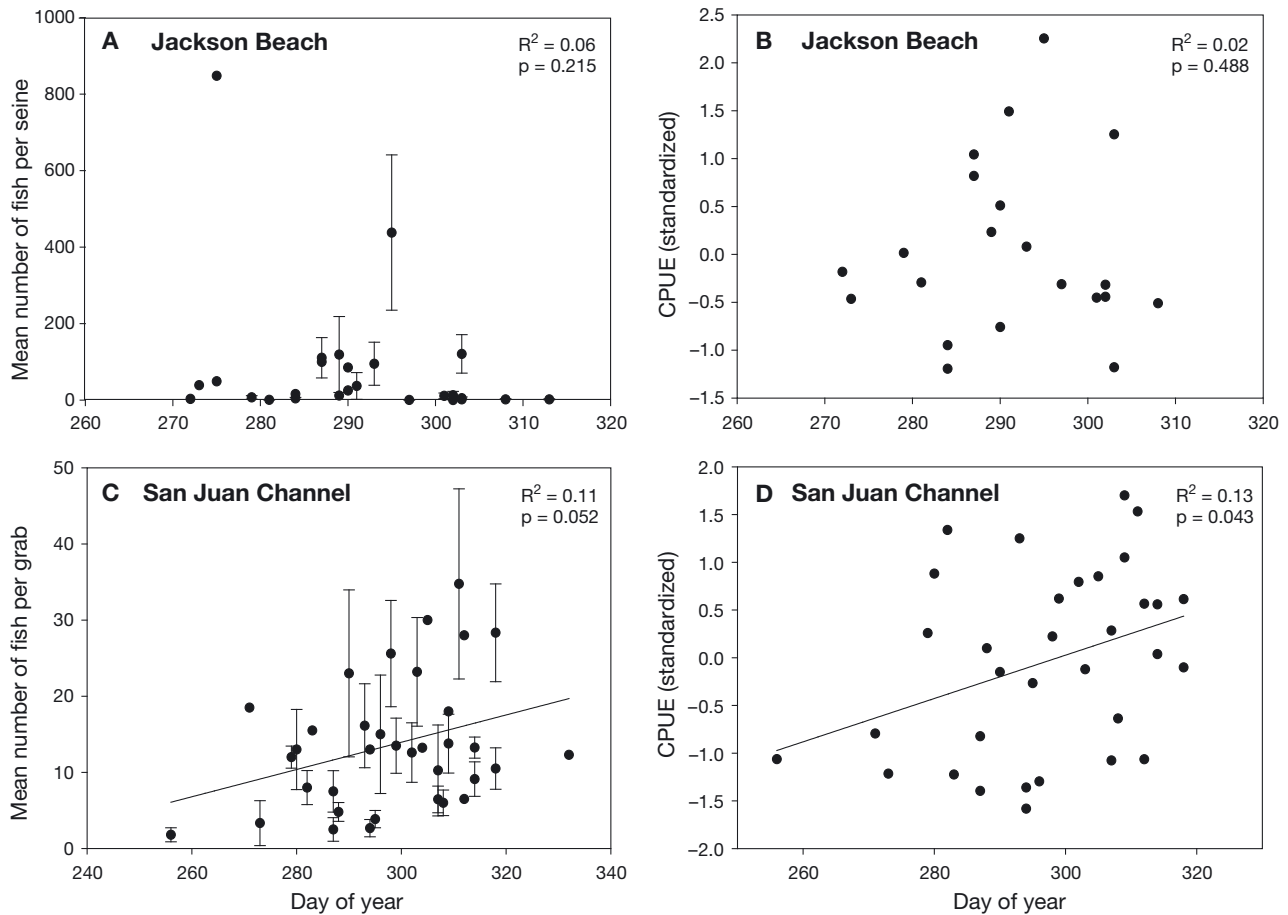
Fig. 4. Trends in Pacific sand lance *Ammodytes personatus* abundance (catch per unit effort, CPUE) at (A,B) Jackson Beach and (C,D) San Juan Channel over the fall season (by day of the year), using (A,C) all data (error bars: SE) 2013–2015 and (B,D) data standardized for mean annual condition

sand lance were present in the benthic substrates as the fall season progressed. A GLM examining CPUE as a function of day of the year (inclusive of all sampling occasions, including zero catch) found a significant increase of abundance over the season at SJC (GLM = negative binomal, link = log, year as factor; $z_{288,1} = 2.58$, p = 0.009) and a significant decrease in abundance at JB ($z_{106,1} = 2.99$, p = 0.003). A comparison of models with and without a year effect determined year to be an important factor in each case (likelihood ratio test of negative binomial models: SJC $F_{1,286} = 59.96$, p < 0.001; JB $F_{1,04} = 6.81$, p = 0.009).

3.3. Temporal trends in the environment and condition

Variation in condition was also assessed across the fall season. At JB, based on data pooled from 2012–2015, no significant increase or decrease in condition in this juvenile population was noted over

the progression of the fall season ($R^2 = 0.04$, p = 0.311; Fig. 5A). When these data were standardized to control for year effects, the same trend was observed ($R^2 = 0.02$, p = 0.462; Fig. 5B). Data from SJC were available from 2010 and 2012–2015. In this adult population, there was a significant decline in condition over the fall ($R^2 = 0.20$, p = 0.009; Fig. 5C). A similar trend was observed in the standardized SJC data ($R^2 = 0.17$, p = 0.013; Fig. 5D). Trends in environmental variables over the course of the fall season indicated a pronounced shift in oceanographic regime (i.e. a transition from upwelling to downwelling), and a marked reduction in light and temperature (Fig. 6).

Results of correlation analysis of seasonal indices (SST, PAR, UI) demonstrated high positive correlation between SST and PAR for all years (2010–2015; Fig. 7). Within-year correlation between PAR and SST was consistently high (mean = 0.70, range = 0.56–0.82) and significant in all years from 2010–2015 (p < 0.001). UI and PAR were weakly positively correlated (mean = 0.24, range = 0.00–0.44) in most years and
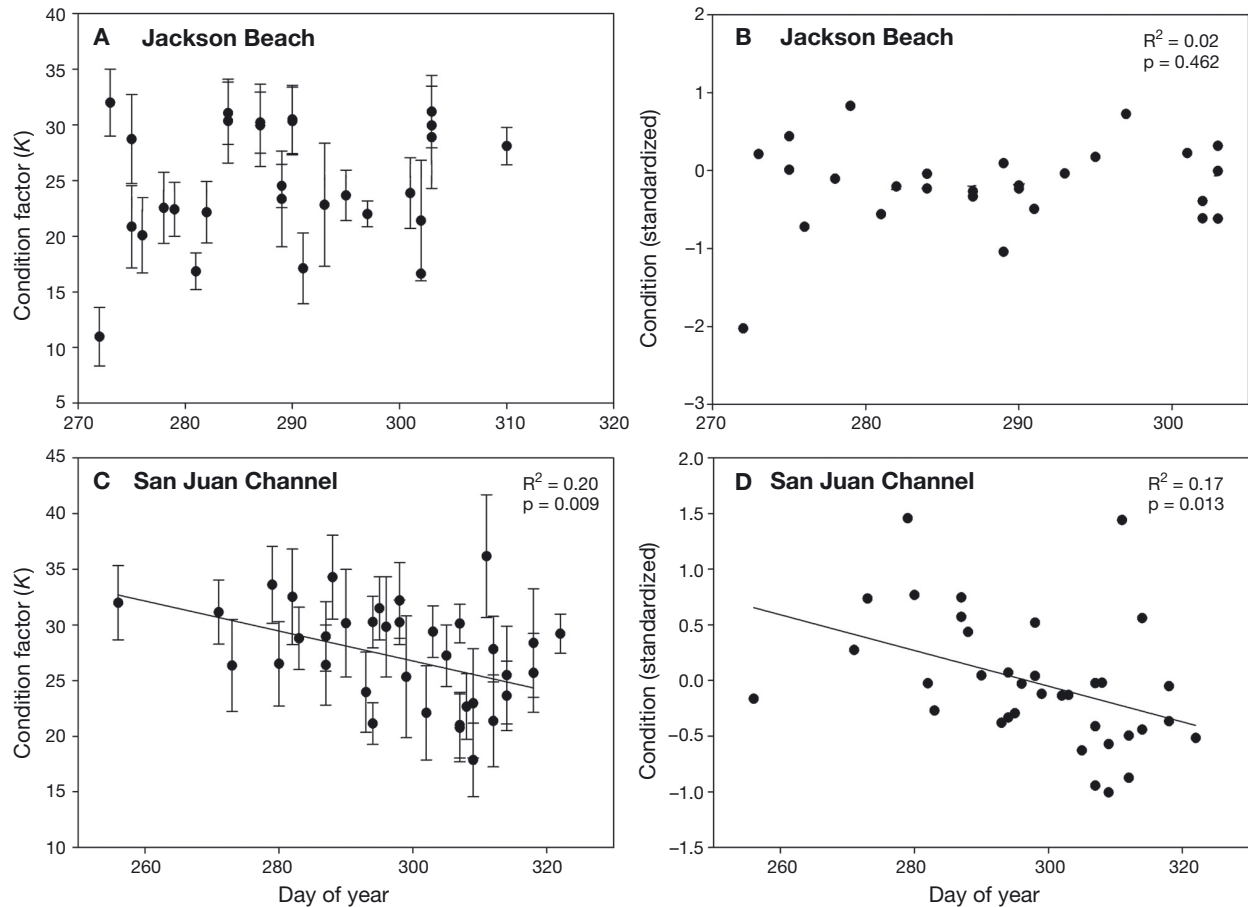
Fig. 5. Trends in Pacific sand lance *Ammodytes personatus* condition factor (*K*) in the (A,B) Jackson Beach and (C,D) San Juan Channel populations over the fall season (by day of the year), using (A,C) all data (error bars: SE) 2012–2015 and (B,D) data standardized for mean annual condition

nonsignificant in 2011 and 2013. UI and SST were weakly positively correlated (mean = 0.24, range = −0.03 to 0.46) in most years, negative in 2010, and nonsignificant in 2011 and 2013.

A GLM examining condition as a function of day of the year found a significant decrease in condition over the season at SJC (GLM = negative binomial, link = log, year as factor; $z_{1623,1} = 3.88$, p < 0.001). A comparison of models evaluating all combinations of environmental variables, day, and year effects determined the best explanatory model to include all environmental variables (PAR, SST, UI), day of the year, and year (Table 4).

3.4. Inter-annual patterns in abundance and year-class strength

Our sampling efforts provided a crude index for abundance and we noted substantially higher (13.1×) relative abundance in juvenile fish sampled at JB

(age-1) in odd (pooled mean ± SD = 131.02 ± 231.74, n = 2) relative to even years (10.01 ± 24.81, n = 4; Fig. 8). We also noted an increase in occurrence (non-zero catches, JB beach seines) in odd years (Wilcoxon test, $W = 1312$, p < 0.001) and an increase in abundance in odd years (Kruskal-Wallis rank sum test, $\chi_4^2 = 34.10$, p < 0.001). This pattern was significant in pairwise comparisons of years, such that differences were noted between all even and odd years (Kruskal-Wallis pairwise comparisons, p < 0.015), but no differences were noted between odd (p = 0.612) or between even years (p > 0.222). An examination of the bimodal length distribution in the SJC population also indicated a relatively larger proportion of fish in lengths associated with age-3 fish in odd years (Fig. 3, Figs. S2 & S3).

3.5. Environmental indices and inter-annual response

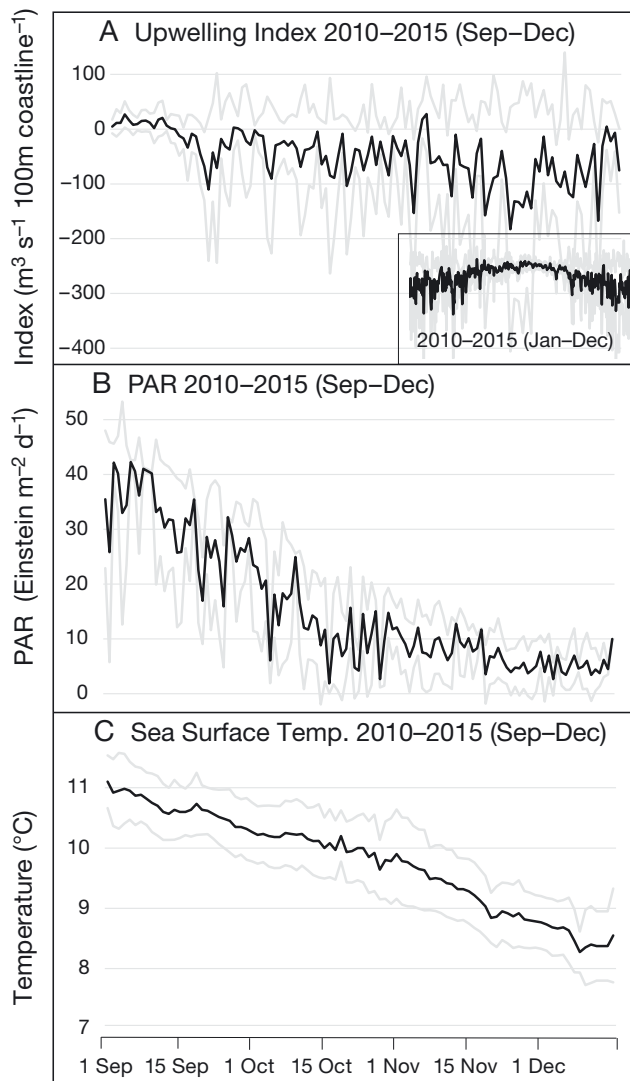Condition was also compared between years. Pacific sand lance at JB had a mean (±SD) *K* of

Fig. 6. Indices for seasonal shifts in (A) oceanographic patterns (upwelling index: Bakun Index Values, 48° N, 125° W), (B) light availability (photosynthetically active radiation [PAR]: NOAA Station FRDW1-9449880, Friday Harbor, WA, 48° 32′ 43″ N, 123° 0′ 44″ W), and (C) temperature (sea surface temperature: NOAA Station FRDW1-9449880) over the time frame of analysis (2010–2015). Black lines: mean; grey lines: SD. The mean annual cycle 2010–2015 of the upwelling index is shown (inset) to provide a reference for summer and winter dynamics and the timing of the spring and fall transition between upwelling and downwelling regimes

26.16 ± 4.98, while sand lance in SJC had a mean K of 28.29 ± 3.91 (Fig. 9). In each year from 2012–2015, K values for sand lance at SJC were consistently higher than those of JB fish (ANOVA, $F_{1,2640} = 66.91$, p < 0.001; Fig. 9), suggesting that older, mature fish in the SJC generally had a higher proportion of stored energy relative to juveniles. The breadth of

distribution of K for the SJC population was also distinguished from the JB population (KS test, $D = 0.44$, p < 0.001), indicating that the amount of stored energy was more variable among mature (SJC) fish than immature (JB) fish.

Interestingly, the inter-annual pattern in relative condition between years was mirrored at the 2 sites (ANCOVA, $R^2 = 0.23$, $F_{2,3967} = 589.80$, p < 0.001) with strong correlation between mean values across the time series (Pearson's r = 0.997, df = 4, p < 0.001). Condition was relatively high in 2012 and 2013 for both study sites and notably lower at both in 2014 and 2015. Tukey's HSD test was run on K values to determine if any year was significantly different from each of the others. Condition for JB fish in years 2010–2013 was not significantly different (p > 0.175), while significant pairwise differences were noted in years 2014 and 2015, distinguishing these years from all others (p < 0.001). Condition for SJC fish in years 2010–2012 was not significantly different (p > 0.175), while significant pairwise differences were noted in years 2013–2015, distinguishing these years from all others (p < 0.001). An examination of climate indices over the time frame of the study indicates a shift in early 2014 to the negative phase of the NPGO and a positive phase of the ENSO and PDO (Fig. 10). This corresponds to the marked decline in mean condition for juvenile and adult fish (2014–2015) in contrast to previous years. Significant correlations were noted between JB condition, some environmental metrics and climate indices, particularly the PDO (Table 5). An overlay of fish condition, relative to environmental climate indices is provided for reference (Fig. 11).

A GLM examining mean annual condition as a function of annual environmental conditions (SST, PAR, UI) and climate indices (ENSO, PDO, NPGO) found all 6 explanatory variables were influential on mean annual condition in both juvenile (nearshore population, JB) and mature fish (offshore population, SJC). The limited number of years (n = 5) of data available was a constraint, and model comparisons were not able to consider all combinations of the explanatory variables. Instead, all combinations including 3 or fewer explanatory variables were evaluated. The 2 most robust models each included 3 independent combinations of these predictors, such that, in reviewing both models, all predictive variables were determined significant. This was true for both SJC and JB data. In the JB data, the best model included the variables PDO ($t_{4,1} = -88.00$, p = 0.007), ENSO ($t_{4,1} = 26.84$, p = 0.024) and the date of fall transition ($t_{4,1} = -27.23$, p = 0.023). The next best model included the variables mean SST ($t_{4,1} = -24.98$, p =
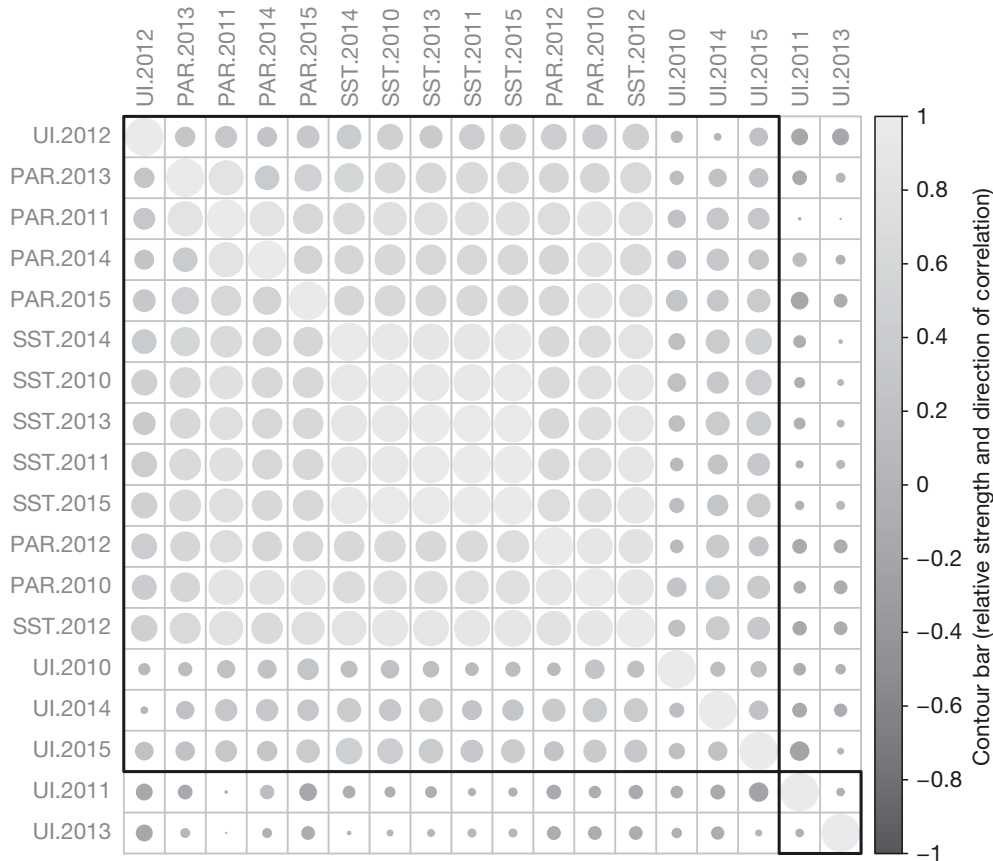
Fig. 7. Correlation matrix for sea surface temperature (SST), photosynthetically active radiation (PAR) and the regional upwelling index (UI), ordered according to the relative strength of the correlation coefficient to identify hidden structure and pattern in the matrix. Color intensity and the size of the circle are proportional to the correlation coefficients (larger symbols: higher correlation coefficients; lighter colors: positive correlations; darker colors: negative correlation). Contour bar (right margin): direction and relative strength of correlation

0.026), mean PAR ($t_{4,1} = -5.25$, p = 0.119), and the NPGO ($t_{4,1} = 11.82$, p = 0.054). Similarly, in the SJC data the best model included mean SST ($t_{4,1} =$

-256.94, p = 0.002), mean PAR ($t_{4,1} = -48.95$, p = 0.013), and the NPGO ($t_{4,1} = 130.96$, p = 0.005). The next best model included the remaining variables PDO ($t_{4,1} = -25.64$, p = 0.025), ENSO ($t_{4,1} = 9.17$, p = 0.069), and the date of fall transition ($t_{4,1} = -9.68$, p = 0.066).

Table 4. Generalized linear model (GLM) of Pacific sand lance condition factor (K) as a function of day-of-year (DoY), year, and environmental variables. AIC: Akaike's information criterion; UI: upwelling index; SST: sea surface temperature; PAR: photosynthetically active radiation. Asterisks indicate significance at ***p < 0.001

Best model ———————————ΔAIC———————					
$K \sim$ DoY + UI + SST + PAR + Year					
Parameter estimates (coefficients)					
	Estimate	SE	t	p	
(Intercept)	1.051×10^3	2.706×10^2	3.882	0.0001	***
DoY	2.362×10^1	1.299×10^2	-18.181	<0.0001	***
UI	9.799×10^3	1.491×10^3	6.574	<0.0001	***
SST	-3.598	3.466×10^1	-10.379	<0.0001	***
PAR	-5.910×10^2	1.162×10^2	-5.086	<0.0001	***
Year	-4.547×10^1	1.366×10^1	-3.329	0.0009	***

4. DISCUSSION

This study provides insight into seasonal abundance and demographics of Pacific sand lance populations, including their relative abundance, condition, and size structure over intra-seasonal and inter-annual time scales. The results indicate important considerations related to shifts in habitat use by life stage (e.g. nearshore vs. offshore), seasonal shifts in distribution and availability (e.g. pelagic vs. benthic), seasonal shifts in relative condition, and inter-annual fluctuations in abundance and condition.
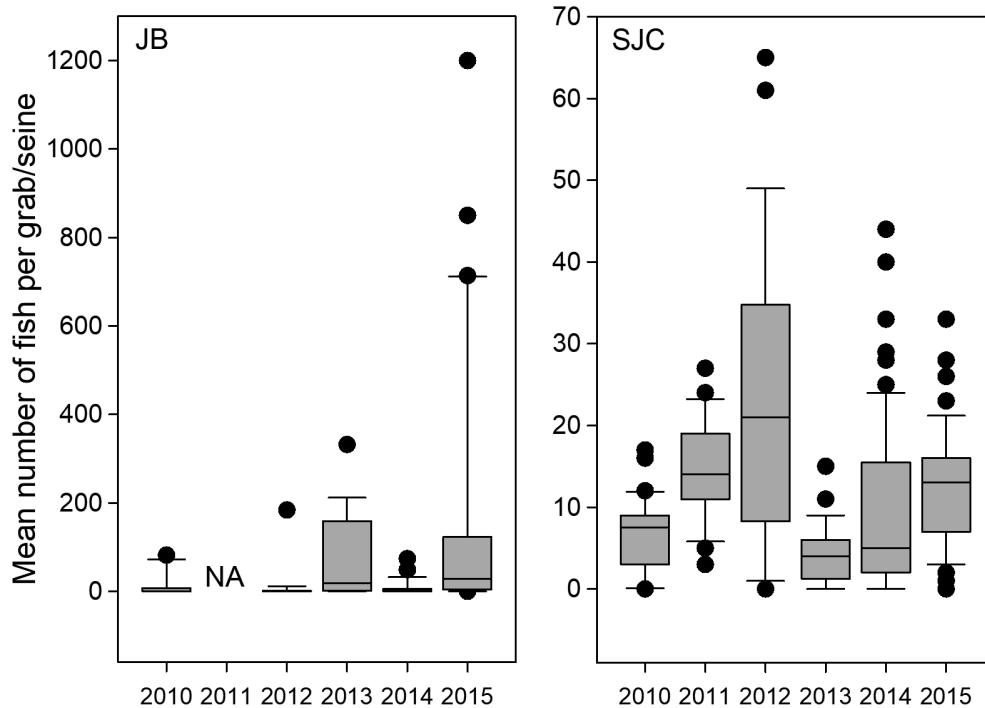
Fig. 8. Comparison of relative abundance of Pacific sand lance *Ammodytes personatus* resulting from targeted sampling effort at Jackson Beach (JB, beach seine) and San Juan Channel (SJC, Van Veen grab) from 2010–2015. Shaded box: interquartile range; line: median; whiskers: 10th and 90th percentiles; points: outliers. There was no available (NA) data at JB in 2011

4.1. Habitat use and population structure

Our analyses of 2 sites within the San Juan Archipelago, WA, provide further evidence that Pacific sand lance may exhibit a profound onto-genetic shift in their use of habitat, such that juvenile fish forage inshore and move to offshore habitat at maturity or in response to declines in system productivity, as the autumn season progresses. There are known differences in habitat use between age-0 fish and adults (Chikilev & Datskii 2000). Mature Pacific sand lance appear in high numbers in the nearshore region (intertidal and subtidal) in the early summer, followed later by the appearance of age-0 in late summer as they recruit from the larval stage (Dick & Warner 1982). As the summer progresses, older sand lance become less abundant in nearshore waters, which become dominated by the age-0 and age-1 year class (Robards et al. 1999b). This also corresponds with studies on western Atlantic stocks (i.e. *Ammodytes dubius*) that have demonstrated fish moving offshore as a function of age (Scott 1968, 1972, Nelson & Ross 1991) as well as abundance shifts from coastal to offshore waters during the summer (Winters 1983, Nelson & Ross 1991).
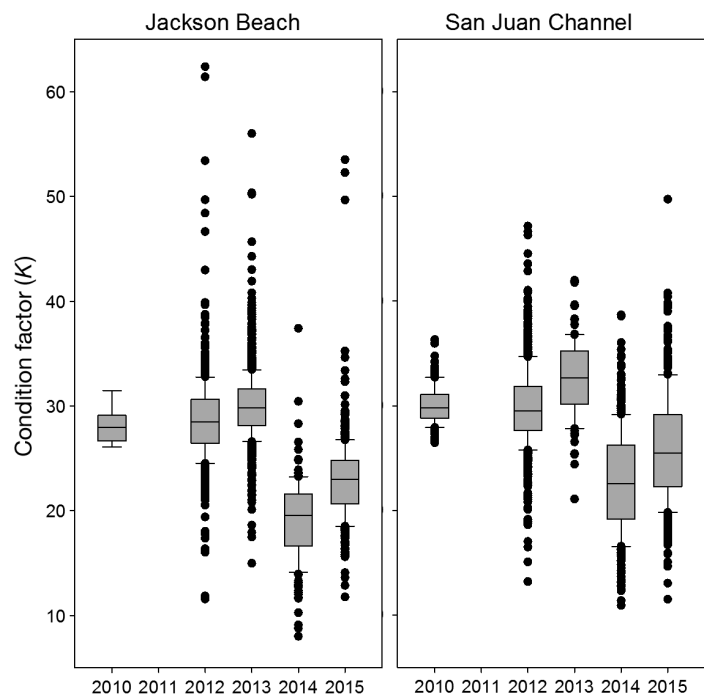

Fig. 9. Condition factor (*K*) for Pacific sand lance *Ammodytes personatus* at each site during 2010–2015. *K* was significantly lower in the period of anomalous warming in the North Pacific (i.e. 'The Blob') in 2014–2015 relative to baseline data from 2010–2013. Box-plots display the range of *K* values: shaded box: interquartile range; line: median; whiskers: 10th and 90th percentiles; points: outliers
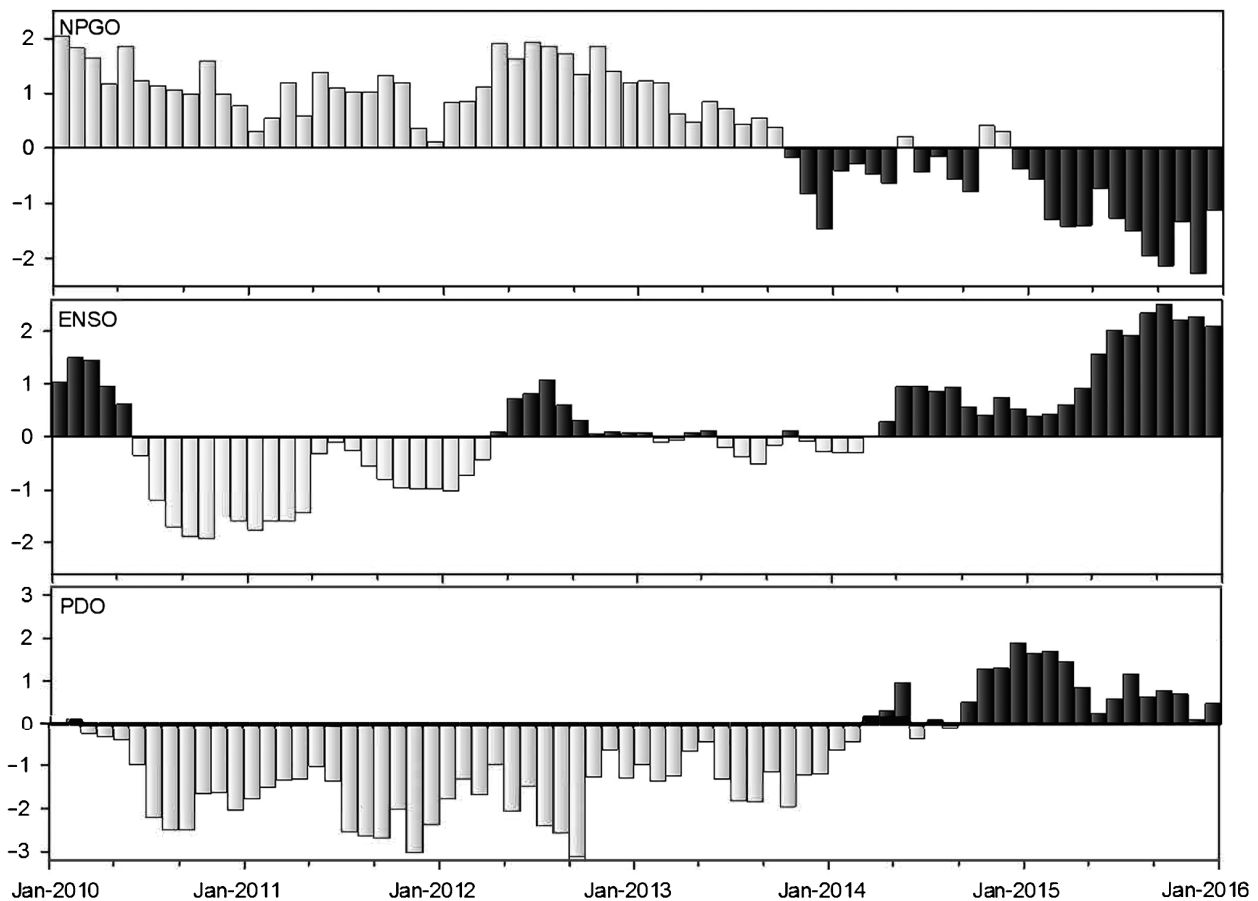
Fig. 10. Indices of climate regimes relevant to the study area (light gray bars: values less than the mean of the time series [negative anomaly]; dark gray bars: values greater than the mean of the time series [positive anomaly]). The North Pacific Gyre Oscillation (NPGO) is a climate pattern that emerges as the second dominant mode of sea surface height variability in the North Pacific. This index is significantly correlated to fluctuations in salinity, nutrients, and chlorophyll *a* as measured in long-term data sets in the California Current and Gulf of Alaska. The multivariate El Niño-Southern Oscillation (ENSO) Index (MEI) is the dominant ocean–atmosphere driver of climate variability on inter-annual time scales. The Pacific Decadal Oscillation (PDO) is a climate index based on patterns of variation in sea surface temperature in the North Pacific and is highly correlated with precipitation and freshwater input into the eastern North Pacific. Climate indices were derived from the Northwest Ocean Observing System database (http://nvs.nanoos.org/Climatology)

It is likely that JB and SJC are life-stage specific habitats for a common stock. Evidence from studies on *A. dubius* and *A. americanus* (Scott 1972) as well *A. personatus* (Robards et al. 1999b) suggest that these species exhibit site fidelity and exhibit only limited movement along coastlines. Kühlmann & Karst (1967) and van der Kooij et al. (2008) suggest daily horizontal movements for mature *Ammodytes* spp. to be limited to 1–5 km. While the intertidal is thought to be important habitat (Robards et al. 1999b, Quinn 1999, Haynes et al. 2007), Pacific sand lance use of the intertidal and subtidal nearshore environment is not well understood. It is also unknown to what extent Pacific sand lance partition habitat by life stage (Haynes et al. 2007). Our results characterized habitat partitioning between immature and mature stages of fish

Table 5. Influence of climate and environmental conditions on Pacific sand lance condition in Jackson Beach (JB) and San Juan Channel (SJC). Asterisks indicate significant correlation (*p < 0.100; **p < 0.050). ENSO: El Niño-Southern Oscillation; NPGO: North Pacific Gyre Oscillation; PDO: Pacific Decadal Oscillation; SST: sea surface temperature

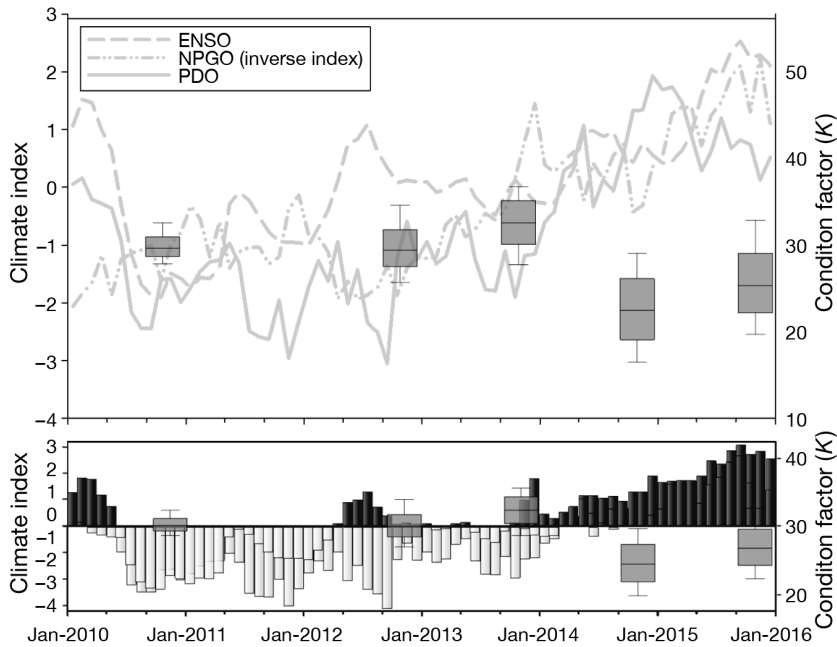| Loca-tion	Environ-mental index	Pearson correlation		
		r (95% CI)	t_4	p
JB	ENSO	−0.57 (−0.94 to 0.45)	−1.37	0.242
	NPGO	0.62 (−0.18 to 0.95)	−1.98	0.088*
	PDO	−0.75 (−0.97 to 0.17)	−2.28	0.085*
	SST	−0.57 (−0.94 to 0.45)	−1.37	0.241
SJC	ENSO	−0.53 (−0.94 to 0.49)	−1.26	0.277
	NPGO	0.57 (−0.45 to 0.94)	−1.38	0.240
	PDO	−0.71 (−0.97 to −0.24)	−2.41	0.014**
	SST	−0.54 (−0.94 to 0.49)	−1.28	0.271

Fig. 11. Overlay of mean annual condition factor (K; box-plots in both panels, right y-axis) of Pacific sand lance in San Juan Channel (SJC) and climate regime (annual deviations, El Niño-Southern Oscillation [ENSO], Pacific Decadal Oscillation [PDO], North Pacific Gyre Oscillation [NPGO]) displayed as trend lines (top panel) and as deviation from the mean (bottom panel; positive anomalies in dark gray, negative anomalies in light gray; see aslo Fig. 10). The inverse index of the NPGO is used to simplify the display and to demonstrate correlation in the climatic indices. Shaded box: interquartile range; line: median; whiskers: 10th and 90th percentiles; points: outliers

in the fall and suggest that nearshore sites (e.g. known beach spawning sites) may serve as important juvenile rearing habitats. Presumably many discrete nearshore sites might serve as source populations to larger offshore sites of the type identified in this study. More research is needed to examine whether this apparent life history pattern is evident in other seasons (e.g. late winter, spring, early summer), determine the consistency of this pattern at various temporal and spatial scales, investigate potential connectivity between nearshore and offshore habitats, investigate evidence for site fidelity, and determine whether there is evidence for phenotypic and genetic differentiation across discrete nearshore and offshore sites and phenotypic and genetic connectivity between linked nearshore and offshore sites.

4.2. Trends in abundance and mechanisms to explain cyclical patterns in recruitment

This apparent biennial trend in year-class strength may indicate a pulse in recruitment in alternating years. Sampling in subsequent years (2016–2017)

suggests the persistence of this biennial pattern (Figs. S2 & S3), though the limited time series precludes any definitive conclusion. In an examination of spawning stock biomass and recruitment trends in *Ammodytes* spp. throughout the Northern Hemisphere, biennial patterns in alternating year-class strength do not appear evident nor consistent outside of select stocks in the North Pacific. While this pattern appears evident in several (n = 4) short time series of recruitment (3–8 yr) in the Gulf of Alaska, Sea of Okhotsk, and northern Sea of Japan, this pattern is not emergent in recruitment time series in the northeast and northwest Atlantic and central and southern Sea of Japan (n = 9), except at limited time intervals (mean ± SD = 6.11 ± 2.32 yr, range = 3–11 yr), or in less than half of the available time series in each case (Fig. 12).

High-magnitude, high-frequency inter-annual fluctuations in recruitment are common in forage fishes. Low-frequency trends at decadal scales are also often evident (Somarakis 2017). It is important to distinguish between fluctuations in stock abundance versus pulses in year-class strength. Overall stock abundance may be a reflection of predation, winter mortality, or environmental conditions affecting all age classes within a population. Pulses in year-class strength, in contrast, reflect patterns of recruitment. While we expect fluctuations in both stock abundance and recruitment, the apparent alternating inter-annual year-class strength suggested here may indicate regular biennial patterns in recruitment. Various factors that may affect recruitment include (1) the abundance of spawners (influenced by fisheries exploitation, predation, population age, and size structure); (2) the number and viability of eggs (influenced by population age structure and energy reserves); (3) the timing of spawning and emergence (influenced by life history and physical conditions); (4) mortality in early life history stages (influenced by physical and trophodynamic factors, density-dependent competition for resources, and vulnerability to predation); and (5) adult survival and growth (influenced by physical conditions, food resources, and inter- and intra-specific competition and densities). While the
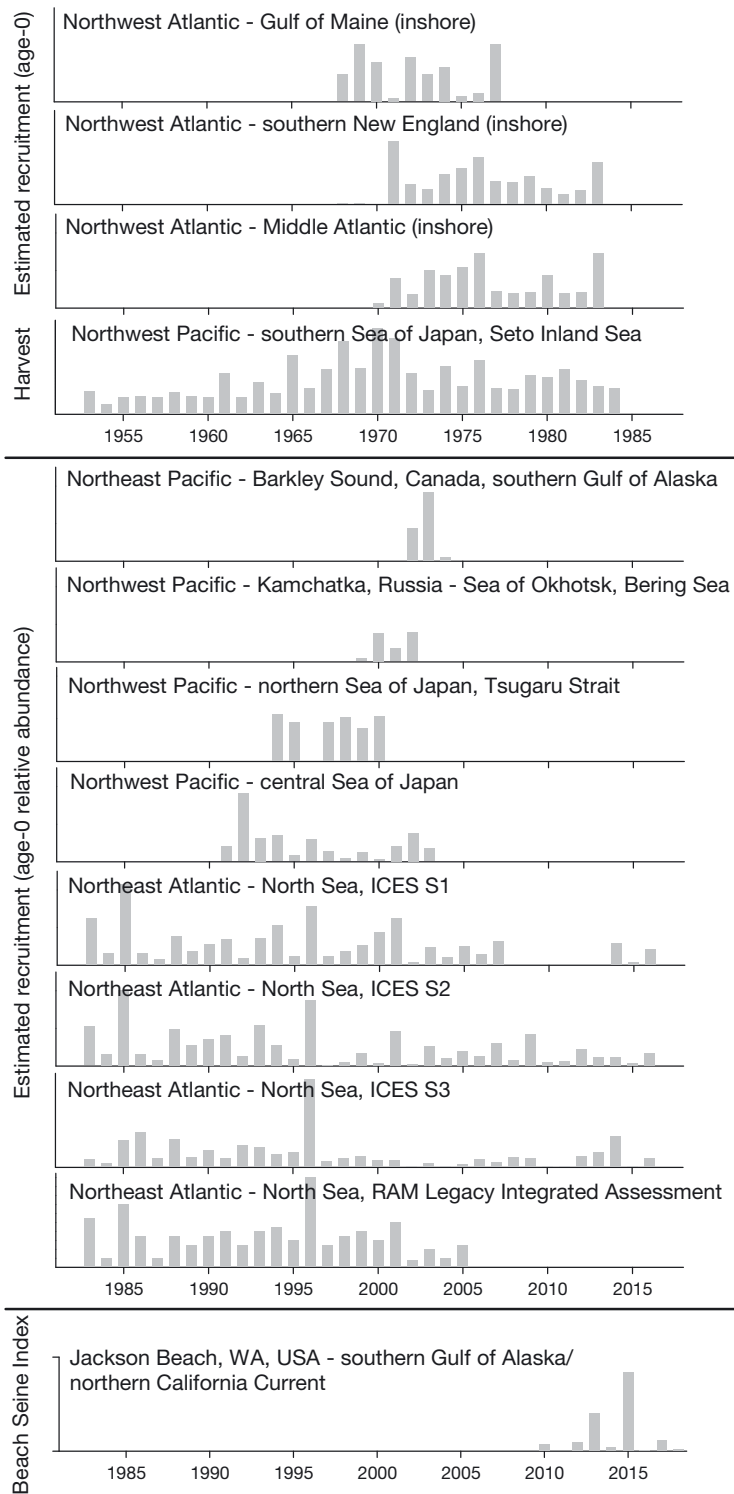
Fig. 12. Patterns in recruitment for 12 discrete stocks of *Ammodytes* spp. throughout the Northern Hemisphere (1980–2018). Vertical bars: standardized indices of estimated recruitment (age-0 abundance or inshore abundance, relative to survey mean catch per unit effort, CPUE). Each graph is unitless as annual estimates within each time series are relative to the mean of the time series. Data includes time series of stocks of *A. dubius* in the northwest Atlantic (Gulf of Maine, southern New England, Middle Atlantic: Nelson & Ross 1991), *A. heian* and *A. japonicus* in the northwest Pacific (Seto Sea: Hamada 1966, 1967, Kishi et al. 1991; central Sea of Japan: Yamada 2009; northern Sea of Japan: Nanjo et al. 2017), *A. hexapterus* in the northwest Pacific (Kamchatka: Tokanov 2007), *A. personatus* in the northeast Pacific (Barkley Sound: Haynes & Robinson 2011); and *A. marinus* in the North Atlantic (Arnott & Ruxton 2002, van Deurs et al. 2011; RAM Legacy Stock Assessment Database: Ricard et al. 2012; North Sea S1–S3, stock aggregate: ICES 2016). These time series are compared to our observations of relative abundance (mean CPUE = 2–139) of juvenile *A. personatus* in the San Juan Archipelago (Salish Sea) at the confluence of the southern Gulf of Alaska and northern California Current

4.2.1. Spawning stock size

Despite notoriously weak correlations in stock–recruitment relationships, spawning stock biomass is ultimately a critical factor in informing recruitment (Ricker 1954, Beverton & Holt 1957, Cushing 1981, Hilborn & Walters 1992). Large year classes may perpetuate large recruitments in subsequent years as a reflection of their abundance relative to other year classes. Alternatively, several studies in small pelagic fishes have provided evidence for density-dependent larval mortality (Somarakis & Nikolioudakis 2007), density-dependent habitat use (Fréon et al. 2005, Barange et al. 2009), age/size effects in annual fecundity (Parrish et al. 1986), and habitat constraints on spawning and recruitment (Yatsu & Kaeriyama 2005, Planque et al. 2007).

size structure of the JB population appears relatively constant interannually, the size structure of the SJC population appears to fluctuate from year to year, possibly reflecting inter-annual pulses in year-class strength, which may indicate density-dependent processes. Possible mechanisms are explored below.

4.2.2. Stock energetics, reproductive potential, and skip spawning

Stock reproductive potential is another mechanism worth further exploration. Similar to Pacific herring, Pacific sand lance spawn demersal eggs in a single

wave rather than batch spawning as in other small pelagics (e.g. anchovies *Engraulis* spp., sardines *Sardina* spp., sardinella *Sardinella* spp., sprat *Sprattus* spp.; McBride et al. 2015). Moreover, like Pacific herring, Pacific sand lance may skip spawning in some years (Rideout & Tomkiewicz 2011). Pulses in year-class strength might be related to skip spawning in the second reproductive season (Engelhard & Heino 2005) or in alternate years. Female nutritional energy reserves may also determine relative energy expenditure in spawning in a given year. Density-dependent effects from high previous year-class abundance might reinforce relative female condition in a cyclical pattern (Skjæraasen et al. 2012).

4.2.3. Density-dependence

Population-level compensation. Density-dependence is evident even in small pelagic forage species (Ricard et al. 2012, Somarakis 2017). Persistent patterns in year-class strength have been demonstrated in other fish, including sockeye salmon *Oncorhynchus nerka* (Cass & Wood 1994) and walleye pollock *Gadus chalcogrammus* (Bailey et al. 1999), 2 well-studied species. Evidence for a 2 yr periodic fluctuation in relative abundance have been suggested in other *Ammodytes* stocks, including *A. marinus* in the North Sea (Arnott & Ruxton 2002, van Deurs et al. 2009), *A. personatus* in East Asia (Hamada 1966, 1967, Kishi et al. 1991, Kimura et al. 1992), and *A. personatus* in the Gulf of Alaska (Haynes & Robinson 2011). These studies noted alternating years of high and low recruitment and attributed this to density-dependent recruitment. It has also been noted that adults may compete with juveniles for resources in the nearshore area (*A. personatus*; summarized in Field 1988). Sand lance and sand eels are non-migratory residential species associated with defined habitat areas, where the spatial distribution of adults and juveniles may overlap. These characteristics increase the likelihood of density-dependence and decoupling of the spawning stock–recruitment relationship when population size approaches carrying capacity (van Deurs et al. 2009).

Cannibalism of larvae. Larval survival may also be subject to density-dependent pressures from other age classes. Kimura et al. (1992) developed a numerical model of population dynamics of sand lance in the eastern Seto Inland Sea that successfully simulated an observed 2 yr periodic fluctuation as a function of adult cannibalism on larvae. Both Arnott & Ruxton (2002) and van Deurs et al. (2009) provide evidence that *A. marinus* recruitment (age-0) in the

North Sea is under density-dependent regulation, related to the relative abundance of the age-1 population. Specifically, these recruitment analyses suggest the main driver of density-dependence is not spawning stock size, but the quantitatively dominant premature age-1 population, where age-0 abundance may be negatively related to age-1. While the exact mechanism is uncertain, this negative relationship may reflect egg and larval mortality via disturbance of sediments by age-1 fish, cannibalism (e.g. intraspecific predation on eggs and larvae), or indirect mortality and/or reduced growth via competition for prey resources or benthic refuge (habitat). In the case of age-0 fish, reduced growth might prolong foraging in the marginal seasons, necessitate foraging in areas further from the refuge of benthic substrates, and/or postpone and abbreviate the relatively low-risk winter dormancy period (Bergstad et al. 2002).

4.2.4. Inter-species interactions

Alternatively, this signal in recruitment and year-class strength might be indicative of interspecific interaction. In the North Pacific, pink salmon *Oncorhynchus gorbuscha* differ significantly in abundance in odd- and even-numbered years (Heard 1991, Ruggerone & Nielsen 2004). Since 1976, annual returns of pink salmon in the Salish Sea have averaged 17.8 ± 1.8 million fish in odd years and 0.4 ± 0.1 million in even years (Ruggerone & Irvine 2018). These large odd-year runs produce hundreds of millions of juvenile pink salmon that enter marine waters in even-numbered years; in odd-numbered years there are very few juvenile pink salmon (Beamish et al. 2010). Research elsewhere in the North Pacific has demonstrated ecosystem effects of biennial patterns in pink salmon recruitment (Sugimoto & Tadokoro 1997, Shiomoto et al. 1997, Ruggerone & Connors 2015, Ruggerone et al. 2016, Ward et al. 2018). Biennial patterns in pink salmon abundance correlate with the biennial patterns we observed in Pacific sand lance (e.g. lower recruitment in even years). Recent work has suggested a potential mechanism, where pink salmon exert top-down pressures on plankton resources (Batten et al. 2018, Springer et al. 2018).

4.2.5. Need for continued monitoring and research

While our sampling time frame was too limited to provide definitive insight into patterns in absolute or

relative recruitment, the apparent differences in relative year-class strength in even and odd years and the biennial patterns in juvenile abundance suggest that patterns in recruitment in this region may mirror similar trends noted elsewhere in the North Pacific, may be influenced by the same mechanisms, and warrant further study.

4.3. Differential foraging, in-season condition, and winter dormancy in adults and juveniles

Dramatic seasonal variations in energetics and proximate composition have been documented in various forage species (e.g. herring and capelin; Montevecchi & Piatt 1984, Smith et al. 1990, Lawson et al. 1998). Contrasting interspecific life histories may result in markedly different cycles of feeding and energy storage. *Ammodytes* spp. exhibit a winter dormant period, timed to coincide with periods of low food availability (Field 1988). As the summer season ends and the fall season progresses, sand lance reduce pelagic feeding, as evidenced by late summer declines in CPUE and frequency-of-capture (Winslade 1974, Robards et al. 1999b) and increases in the prevalence of empty stomachs (Sisson & Baker 2017). With reduced production in the water column (Damkaer 1977), sand lance remain dormant in substrates through the winter, reduce metabolic rates (Quinn & Schneider 1991), and prolong gut evacuation times (Ciannelli 1997).

4.3.1. Onset of winter dormancy

Understanding the transition from an active state to winter dormancy is crucial to understanding seasonal changes in sand lance abundance and energetics over the fall season. Two opposing pressures play a role in determining the timing of this transition. The first is the need to secure adequate energy reserves to survive the winter. As primary productivity in the system decreases with decreasing light over the fall season, there is less available prey. Continued feeding later in the season provides diminishing returns. The second factor is the increased risk of predation. Active foraging means leaving the safety of the sand and risking exposure in the water column. There is a basic ecological tradeoff between foraging profitability and predation risk. If the risk of predation outweighs the benefits of feeding, it is no longer profitable to continue feeding (Walters & Juanes 1993, Ahrens et al. 2012, van Deurs et al. 2010).

Young-of-the-year fish direct energy in their first year towards growth in length, rather than in weight, in an attempt to outgrow a predation window (Robards et al. 1999a) and have less protein to buffer against starvation than adults (Robards et al. 1999a). Limited stored energy reserves may therefore mean that there is no choice but to continue feeding in this lower production environment, to ensure maintenance and survival.

For relative abundance, the transition to winter dormancy was expected to reduce CPUE in the water column (JB) and increase CPUE in sediments (SJC). We expected and observed an increase in CPUE in SJC sediments, as more fish entered a dormant state late in the season. At JB, we expected mean CPUE to decrease as the season progressed, as fewer fish emerged from the sand to forage at dawn and dusk. A decreasing logistic trend was observed in some years but had a poor fit. This expected decline in prevalence in the water column from summer to fall might be better captured with increased sampling activity in late summer. Some of the high variability in CPUE during the fall at Jackson Beach might also result from the variable nature of beach seining. Catch per seine is highly punctuated, in contrast to sampling discrete sediments with the Van Veen.

4.3.2. In-season condition and energy reserves

For relative condition, we expected and observed mean condition to remain constant in fish that continued to feed (JB) and decrease in fish that initiated dormancy (SJC) and began to expend their energy reserves (Robards et al. 1999a). At SJC we observed a significant decrease in condition over the fall, consistent with the expectation that mature fish had already entered dormancy and were expending stored energy. For this adult population of fish, marginal feeding opportunities later in the fall season may not be worth the continued risk of predation in the water column. The trend in constant condition at JB indicates that younger fish need to continue foraging later in the season to secure sufficient reserves to survive the winter. That young sand lance may postpone overwintering to extend opportunities for growth or to maintain energy reserves is consistent with other studies, including observations of *A. marinus*, where large quantities of age-0 individuals were observed in the water column in fall (Winslade 1974, Reeves 1994) and mechanistic explanations for alternate year-class strength (van Deurs et al. 2009).

These results provide new insights about seasonal energetics and seasonal availability of Pacific sand lance as a forage resource for predators. No adults were caught in the water column during our sampling (September–December). This is consistent with sampling of *Ammodytes* spp. in winter months (November–March) in other systems, including the Gulf of Alaska (Robards et al. 1999b, Haynes et al. 2007) and the North Sea (Macer 1966). Immature fish (age-0 and age-1), however, were present in the water column. Studies of *A. marinus* have also noted older or high-condition fish burying earlier than smaller and younger individuals (Bergstad et al. 2002, Wanless et al. 2005, van Deurs et al. 2011).

4.4. Inter-annual condition and winter reset

Condition increases in most fishes as a function of length (Robards et al. 1999a). As expected, we noted higher condition values for adults than juveniles. While adult condition was always greater than juvenile condition, the inter-annual patterns in relative condition in juvenile and adult populations were synchronous. The striking parallel between the JB and SJC populations each year suggests that a winter reset in condition may occur, similar to the reset observed in nutrient and production dynamics in the region (Khangaonkar et al. 2012) and in ecological systems more generally (Hastings 2001). Fish may expend all or most accessible stored energy reserves during the winter dormant period and rebuild energy reserves each spring with limited carry-over between years. The implication is that condition in each year may be highly dependent on environmental conditions in that specific year.

4.5. Response to environmental conditions and climate patterns

Seasonal and inter-annual differences in length–weight relationships may be attributed to variation in abiotic (e.g. light, temperature, latitude) and biotic (e.g. production, competition, predation) factors (Nelson & Ross 1991). Increased temperature will increase metabolic rates and energetic demands. If that increase is not matched with a coincident increase in food availability, quality, or improved foraging conditions, increases in temperature will lead to decreased condition (Pörtner et al. 2001). Arnott & Ruxton (2002) found that warmer sea temperatures correlated with poorer than average recruitment in

A. marinus, and recent sampling of *A. personatus* in the northern Gulf of Alaska demonstrated a marked decrease in condition in *A. personatus* sampled in 2012–2013 compared to 2014–2015 (Arimitsu & Piatt 2018), similar to our results. Further exploration of the influence of recent North Pacific anomalous warming (Bond et al. 2015) is needed.

Environmental effects may also influence recruitment. Historical data suggest large fluctuations in abundance of *Ammodytes* spp. (Winters 1983). The reasons for such fluctuations remain unresolved. Smith et al. (1978) suggested that favorable water circulation and bottom temperatures enhanced survivorship, while Sherman et al. (1981) dismissed environmental conditions as factors that regulate sand lance abundance and suggested that shifts in abundance were in response to competitive release, citing fishery-induced collapses in Atlantic mackerel *Scomber scombrus* and herring. Match–mismatch dynamics due to environmental effects on phenology and seasonal timing may influence prey availability during larval stages (Haldorsen et al. 1993, Fortier et al. 1995). More recent studies have demonstrated effects of large-scale oceanographic processes on recruitment. Arnott & Ruxton (2002) detected a negative relationship between recruitment and the winter index of the North Atlantic Oscillation (e.g. SST and egg and larval period). Robards et al. (2002) found marked mesoscale differences in Pacific sand lance abundance, growth, and mortality associated with differing oceanic regimes, and van Deurs et al. (2009) found a climate/temperature effect in models of recruitment, particularly a significant effect of the mean winter North Atlantic Oscillation index.

In the analysis of seasonal trends in environmental metrics (SST, PAR, UI), a significantly weaker (and occasionally negative) correlation between the UI and SST and PAR was noted, particularly in 2010, 2011, and 2013 relative to other years. This was expected. While SST and PAR represent daily measures illustrating seasonal trends, the UI indicates a threshold shift from upwelling to downwelling. This also suggests notable inter-annual differences in the synchrony and the timing of nutrient cycling and movement (advective surface velocities) of offshore and nearshore water masses (i.e. the onset of fall transition from upwelling to downwelling) relative to background environmental conditions (i.e. light, temperature). Still, all 3 seasonal variables were significant in explaining intra-seasonal and inter-annual trends in condition.

In contrast to the seasonal environmental metrics, the climate indices (ENSO, PDO, NPGO) indicate

broader regional patterns in environmental conditions and ecological response. The ENSO reflects periodic variation in wind and SST. The NPGO reflects sea surface height variability in the Northeast Pacific and is correlated with salinity, nutrients, and chlorophyll *a* (chl *a*) in the California Current and Gulf of Alaska; it provides a strong indicator of fluctuations in the mechanisms driving planktonic productivity (Di Lorenzo et al. 2008). The PDO reflects variability of North Pacific SST anomalies (Mantua et al. 1997, Zhang et al. 1997); its temporal patterns are linked to several biological and ecosystem variables in the ocean (Hare & Mantua 2000). In our time series, patterns in mean annual condition were explained as a function of both annual environmental conditions (SST, PAR, UI) and climate indices (ENSO, PDO, NPGO). This was true for both SJC and JB. These trends should be monitored, particularly in the context of recent anomalous warming (Bond et al. 2015) and expectations for continued increases in temperature.

It should be noted that annual values for condition were evaluated for only one period in the year (fall) and compared to environmental indices that encompass the full year. The rationale to include the full year is that these environmental variables influence growth and condition throughout the annual life cycle of these fish. Environmental conditions in the spring and summer influence annual growth and accumulation of energy reserves, while fall and winter conditions influence the rate of energy retention and expenditure. In our analysis, we used a single consistent reference period for annual condition, at the conclusion of the summer growing season (end point for energy accumulation), and at the onset of winter dormancy (initiation of expenditure of stored energy reserves). While information on fish condition in alternate seasons is currently not available, it would be valuable to collect these data to better define annual cycles in energy accumulation and expenditure and contrast trends in condition between seasons.

4.6. Implications and further research

We identified trends in Pacific sand lance abundance, condition, and age structure over intraseasonal and inter-annual time scales. Our findings suggest that Pacific sand lance may segregate according to age, with an ontogenetic shift from nearshore to offshore habitats following maturity. Our findings also suggest that relative body condition is influenced by environmental conditions within the year and that body condition may be subject to winter reset. This study also strengthens evidence for pronounced inter-annual cyclic fluctuations in population structure that reflect either density-dependent recruitment or a pulsed response to interspecific competition. These results have expanded our ecological knowledge and may be used to inform management of this important forage species, while underscoring the necessity of long-term studies to monitor its population dynamics.

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