Trophic responses of juvenile Pacific salmon to warm and cool periods within inside marine waters of Southeast Alaska

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ABSTRACT

Marine growth and survival of juvenile Pacific salmon (*Oncorhynchus* spp.) have been linked to marine temperatures and feeding conditions during their first few months at sea. Therefore, understanding what salmon consume under varying environmental conditions is important to understanding how their growth and survival are affected by climate change. Here, we examined how warm/cool-phase variation in water temperature, salinity, wind speed, and pycnocline depth influenced the diet composition and quality of four species of juvenile Pacific salmon in Icy Strait (Southeast Alaska) from 2013 to 2017. During the five-year period, water temperatures shifted from a cool phase in 2013 to warm in 2014–2016, then back to cool in 2017. Overall, the diet composition and prey diversity varied among zooplanktivorous species (pink salmon *O. gorbuscha*, chum salmon *O. keta*, and sockeye salmon *O. nerka*) and piscivorous (coho salmon *O. kisutch*) species, with the exception of 2015, when euphausiids were the dominant prey for all four species. The summer of 2015 was notable for its deep pycnocline although it was not the warmest year in the study. Zooplankton nutritional quality was below average in 2015, but lipid intake by juvenile salmon appeared to be supplemented by the availability of larger euphausiid prey. Across years for all species, diet composition was weakly correlated with a combination of water temperature, salinity, and wind (Pearson correlation = 0.216). We conclude that while the marine heat wave altered the Gulf of Alaska ecosystem, within the range of variability observed during the study period, juvenile salmon were able to meet their energetic demands by switching to alternative prey.

1. Introduction

Ocean conditions, particularly temperature and food availability, have been linked to the early marine growth and survival of juvenile Pacific salmon (*Oncorhynchus* spp.) during the first few months in the ocean (Beamish and Mahnken, 2001; Beauchamp et al., 2007; Farley et al., 2007; Saito et al., 2009; Zavolokin et al., 2009; Fergusson et al., 2013). Changes in ocean conditions influence the feeding conditions of juvenile salmon through alterations in the zooplankton community composition, production timing, abundance, and nutritional quality (Duffy et al., 2010; Sturdevant et al., 2012), all of which are inherently connected. Understanding the relative importance of the prey community and nutritional condition to salmon condition and growth, and potential environmental drivers thereof, is therefore critical to uncovering mechanisms driving early marine survival of salmonids and anticipating population responses to climate change (Boldt and Haldorson, 2003; Brodeur et al., 2007; Sturdevant et al., 2012).

The Alaska Fisheries Science Center's Southeast Coastal Monitoring (SECM) project has conducted monthly summer monitoring surveys annually since 1997 (Fergusson et al., 2018). The surveys occur in the strait habitat of northern Southeast Alaska, a major migration corridor used by juvenile salmon as they migrate to the Gulf of Alaska (GOA) (Fergusson et al., 2018; Orsi et al., 2004). The survey is designed to identify potential relationships between year-class strength of juvenile salmon and biophysical parameters that influence their habitat use, marine growth, prey fields, predation, and stock interactions across years with varying environmental conditions (e.g., Kohan et al., 2017).

During 2014, a marine heat wave (the 'Blob'; Bond et al., 2015) developed in the GOA and was accompanied by a weak Aleutian Low, decreased winter storms, increased water column stratification, and low rates of heat loss from the marine environment into the atmosphere, which resulted in anomalously high water temperatures (Bond et al., 2015; Cavole et al., 2016; Peterson et al., 2016). The influence of the marine heat wave was amplified by an El Niño event that reached the

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GOA in 2016. The influences of these basin-scale forcing mechanisms resulted in reduced primary production (Leising et al., 2015; Whitney, 2015), reduced zooplankton abundance and an altered community structure (McKinstry and Campbell, 2018; Peterson et al., 2016), reduced abundance of adult Pacific salmon (Heinl et al., 2017; Peterson et al., 2016), and reduced survival of marine birds and mammals (Cavole et al., 2016; Savage, 2017). Clearly, climate forcing can alter trophic relationships and dominant energy pathways that drive survival of ecologically and commercially important species in the GOA, and understanding the driving mechanisms is critical in projecting effects of climate change for ecosystem-based fisheries management (Link, 2002).

This study examined the feeding ecology of juvenile salmon in the inside waters of northern Southeast Alaska over cool and warm stanzas encompassing the 2014 marine heat wave and the El Niño event of 2016. Specifically, our objectives were to (1) quantify the diets of juvenile salmon over five years (2013–2017); (2) examine the relationship between diet variation and environmental factors; and (3) assess the relationship between prey quality and feeding habits across temporal shifts in ocean conditions to characterize trophic mechanisms driving early marine growth and survival.

2. Methods

2.1. Field sampling

Monthly field sampling was conducted in summer in the northern region of Southeast Alaska from May to August 2013 to 2017. Oceanographic, zooplankton, and surface (upper 20 m) trawl sampling was conducted during daylight hours at four stations in Icy Strait each month using a chartered fishing vessel (Fig. 1; Kahle and Wickham, 2013).

Oceanographic and zooplankton data were collected monthly at each sampling station. Hydrographic data was collected using a conductivity-temperature-depth (CTD) profiler (SBE 19plus V2 SeaCAT Profiler; Seabird Scientific) towed from the surface to 200 m depth or within 10 m of the bottom. Water temperature, salinity, and density were derived from the CTD data. Zooplankton samples were

Fig. 1. Sampling and weather station locations and in the strait habitat of the northern region of Southeast Alaska from June to August 2013–2017. The Sisters Islands weather station is run by the National Data Buoy Center.

opportunistically collected with a bongo net monthly at one of the four Icy Strait stations to provide zooplankton for lipid analyses. The bongo net was towed obliquely from the surface to 200 m, or within 20 m of the bottom, and back to the surface along a V-shaped path. The bongo had a 60-cm diameter tandem frame with 333- and 505-μm meshes. A VEMCO ML-08-TDR time-depth recorder was attached to the bongo frame to record the maximum sampling depth of each haul. General Oceanics Model 2031 flow meters were placed inside the bongo nets for calculation of water volume filtered. Zooplankton were immediately sorted by species and stage, and depending on size, between 2 and 20 individuals were combined in vials and frozen.

Fish were collected using a rope trawl towed at the surface (upper 20 m) directly astern the vessel. For each haul, the trawl was towed across a station for 20 min at approximately 1.5 m/sec (3 knots) to cover 1.9 km (1.0 nautical mile) with station coordinates targeted as the midpoint of the trawl haul. After each haul, juvenile salmon were identified by species and subsamples of up to 50 of each species were measured (fork length, ±1.0 mm), individually bagged, and frozen for later processing and laboratory analyses.

2.2. Environmental data

The physical environment was categorized by monthly measures of water temperature and salinity, pycnocline depth, and wind speed. Water temperature was summarized as the average water temperature of the entire water column (°C) and temperature above and below the pycnocline at each station in Icy Strait. Water salinity was summarized as the mean salinity of the entire water column (PSU) and salinity above and below the pycnocline at each station in Icy Strait. Pycnocline depth was calculated as the depth where density (σ_t) was 0.1 kg/m^3 greater than σ_t at 5 m depth at each station in Icy Strait (Danielson et al., 2011). Wind speed data were obtained from the National Data Buoy Center, Sisters Islands weather station (58.177 N, 135.259 W). To describe water column and wind mixing just prior to and during the sampling period, mean monthly wind speeds (m/s) from April to August were calculated for each year.

2.3. Biological data

Lipid content of the zooplankton was determined in the lab using a modified colorimetric method (Van Handel, 1985) within one month of collection. Samples were stored at −80 °C prior to processing. In brief, 1 mL of 2:1 (v/v) chloroform:methanol was added to each sample, the vials were capped, and placed in a sonicating water bath for 30 min. One hundred μL of supernatant was added to a glass 96-well plate, with each sample run in triplicate. Solvent was evaporated from the 96-well plate at 100 °C for 10 min. Twenty μL of concentrated sulfuric acid was added to each well and incubated at 100 °C for an additional 10 min, after which the plate was allowed to cool to room temperature. 280 μL of sulfo-phospho-vanillin (SPV) reagent (6.8 mM vanillin, 2.6 M phosphoric acid) was added to each sample followed by incubation at room temperature with gentle shaking for 30 min. The absorbance at 490 nm was recorded and the triplicates were averaged. Percent of total lipid was calculated by comparison of the absorbance values to a calibration curve generated using menhaden oil.

Fish species identification was verified, and lengths (frozen fork, ±1.0 mm) and weights (frozen, mg) were measured. Up to 10 fish of each species, within one standard deviation of the mean length of that species in each month and year was selected for diet analyses. For these samples, stomachs were excised, contents were removed and weighed (±0.1 mg), and the empty stomach was returned to the fish for subsequent energetic analyses. Stomach contents were examined under a dissecting microscope with prey items identified to lowest taxa possible, grouped, and weighed (±1.0 mg) for each fish. Prey groups were pooled by major taxa categories: euphausiids (furcillia and juveniles, < ~12 mm), amphipods (primarily hyperiids), gastropods (primarily
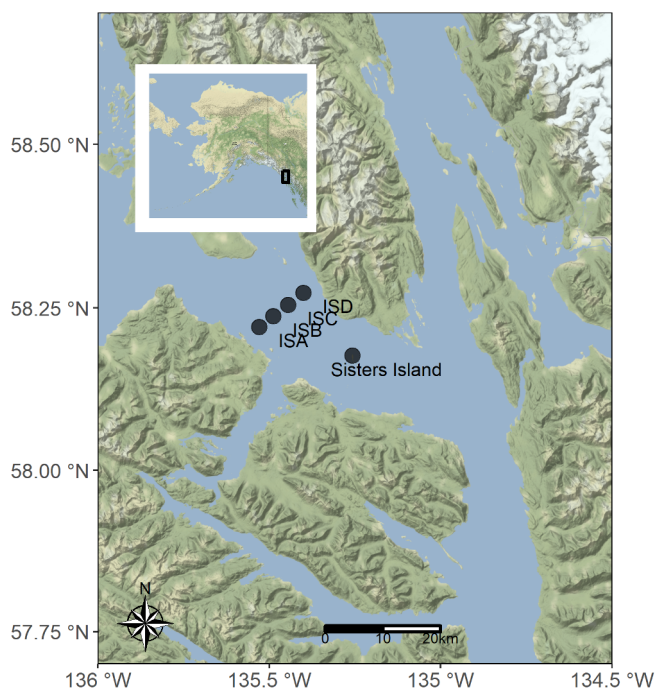
Limacina helicina), gelatinous-prey (primarily oikopleurans), decapods (zoea and megalopae), copepods (large [> 2.5 mm] and small [< 2.5 mm] calanoids), fish (larvae), and 'other'. The other category contained barnacle larvae, cephalopods, chaetognaths, insects, mala-costraca, and unidentified digested tissue (Appendix A). Percent diet composition was calculated as (weight of prey category/weight of all prey categories) * 100.

To examine the influence of prey quality on the caloric intake by juvenile salmon, we calculated 'lipid intake', defined as the average total mass of lipid ingested. Total lipid was calculated for each individual included in the diet analysis then averaged for each year and species. To correct for the differing sizes of individual salmon, prey weight was calculated as a percent of fish body weight (% BW). To calculate lipid intake, the % BW for each prey item was multiplied by the percent lipid value for that prey item. When possible, year- and month-specific average lipid values for the prey items were used, estimated as described previously. If a lipid value for a prey item was not available for a specific month, either the annual average was used or literature values were used for prey items that were absent from our source list (Appendix B). Annual lipid intake values were graphically summarized for each juvenile salmon species.

2.4. Data analyses

Percent diet composition was summarized by month and year for each species. The annual percent composition of these taxa groups was graphically summarized for each juvenile salmon species across the time series. All multivariate data analyses were conducted in PRIMER v. 7 (Clarke and Gorley, 2015). The data matrix was based on average monthly diets of each species, with a potential of 3 values per year. We used a two-way crossed analysis of similarity (ANOSIM) procedure, with year and species as factors, to test for differences in diet composition among year or species pairs ($\alpha = 0.01$). When differences between groups were found, pairwise comparisons were used to identify which groups were significantly different. Finally, we used the Similarity Percentages (SIMPER; Clarke, 1993) procedure to classify the species that contributed most to the dissimilarity between each of the significant pairwise groups.

We examined relationships between average monthly juvenile salmon diets and water temperature, salinity, pycnocline depth, and wind speed by comparing dissimilarity matrices of salmon diets to dissimilarity matrices of all possible combinations of environmental variables (Clarke and Ainsworth, 1993). The BEST routine in PRIMER was used to calculate Spearman rank correlation between diet and environmental matrices to determine which set of environmental variables best predicted salmon diet. The data were permuted 99 times (Global BEST test; Clarke and Warwick, 1998) to test the null hypothesis of no relationship between the selected set of environmental variables and the diet data ($\alpha = 0.01$).

We used an analysis of variance (ANOVA), with year as a factor, to test for differences in percent lipid of each zooplankton taxa ($\alpha = 0.01$). When differences between the years were found, Tukey's pairwise comparisons were used to identify which years were significantly different ($\alpha = 0.05$). We used Pearson's product moment correlation to test for relationships between the percent lipid of each zooplankton taxa and the environmental variables ($\alpha = 0.05$).

3. Results

A total of 441 juvenile pink, chum, sockeye, and coho salmon were examined from June to August of 2013–2017 (Table 1). Due to budget limitations, only oceanographic surveys were conducted in August 2017; no fish sampling occurred.

3.1. Diets by year and species

Overall, diets of juvenile salmon were significantly different by year (ANOSIM, global R = 0.332, p < 0.001; Fig. 2) and species (ANOSIM, global R = 0.281, p < 0.001). Pairwise tests showed that: (1) 2015 was the only year that was significantly different from all other years (ANOSIM, p < 0.002), and (2) diets of the juvenile salmon were significantly different among species, except between chum and pink salmon and between sockeye and pink salmon (ANOSIM, p < 0.006). Euphausiids contributed 30–33% to the dissimilarity between diets in 2015 and the other years. Gelatinous prey and fish larvae contributed 27% and 21% to the dissimilarity between diets of juvenile chum and coho salmon (SIMPER analyses; Table 2). Decapods and fish larvae contributed 19–22% and 21–24%, respectively, to the dissimilarity between juvenile coho salmon diets and juvenile pink and sockeye salmon diets. Empty stomachs were rare in all years and species (Table 1). The highest frequency of occurrence of empty stomachs was observed for juvenile coho salmon in June of 2017 (4 of 10 fish analyzed).

3.2. Diet trends in relation to environmental factors

Environmental parameters varied over the 5 years examined (Fig. 3). Water temperature rose steadily from 2013 through 2016, and then dropped in 2017 to the lowest value observed in the 5-year time period. Salinity above the pycnocline was similar for all years, averaging 27.7 PSU. Wind speed decreased slightly from 2013 to 2014, increased markedly from 2014 to 2015, and dropped sequentially in 2016 and 2017. Except for 2015, when pycnocline depth was approximately 8 m, pycnocline depths in the other years were similar at approximately 6.5 m.

Of the environmental parameters examined, the combination of water temperature, salinity above the pycnocline, and wind described the highest proportion of interannual variation in the juvenile salmon diets (r = 0.22, p < 0.001, Global BEST); values of r for the remaining environmental parameters were ≤ 0.20.

3.3. Prey quality and diet trends

The overall annual trends in zooplankton lipid content fluctuated concomitantly among taxa (Fig. 4, Appendix B). Lipid content of the large calanoid copepod *Calanus marshallae* increased significantly (p < 0.01) from 2015 to 2016 then decreased significantly (p < 0.01) to the lowest observed value from 2016 to 2017. Lipid content of the small calanoid copepod *Pseudocalanus* spp. increased significantly from 2013 to 2014 (p < 0.01). Lipid contents of *Pseudocalanus* spp., *T. pacifica*, and euphausiid (furcillia and juveniles) decreased significantly from 2014 to 2015 (p < 0.04). Temperature was significantly and positively correlated with lipid content of *C. marshallae* (r = 0.49, p < 0.01), while wind speed was significantly and negatively related to the lipid content of euphausiids and *Pseudocalanus* spp. (r = −0.38, p = 0.02 and r = −0.47, p < 0.01, respectively).

The total lipid ingested varied by year and species (Fig. 5). Lipid consumption was highest in 2014 for juvenile pink, chum, and sockeye salmon and 2017 for juvenile coho salmon. The high 2014 lipid values occurred in conjunction with above-average lipid values for many of the individual prey items in 2014 (Appendix B).

4. Discussion

This study described the diets of juvenile pink, chum, sockeye, and coho salmon in inside waters of Southeast Alaska over a time of extreme environmental shifts and provided an assessment of prey quality for juvenile salmon during a critical time in their life cycle. We observed marked shifts in the diet composition of juvenile salmon corresponding with warming water temperatures and high winds. The convergence of

Table 1

Diet composition summary of juvenile pink, chum, sockeye, and coho salmon including the number of diets examined (#fish), number of empty stomachs (#empty), and percent composition (weight) by major prey taxa of feeding fish. Juvenile salmon were captured by rope trawl at the surface (upper 20 m) in the marine waters of Northern Southeast Alaska from 2013 to 2017. Dashes indicate no samples were available for analysis. Prey categories that were not present in stomach contents are blank. See Appendix A for details of the Other category.

| Year	Month	# fish	# empty	Amphipod	Copepod	Decapod	Euphausiid	Fish	Gastropod	Gelatinous prey	Other
Pink salmon											
2013	Jun	7	0						48.5		51.5
2013	Jul	9	0	1.8	0.1	6.3			83.9		7.9
2013	Aug	10	0	19.7		3.3	16.8		6.8	53.0	0.4
2014	Jun	10	0		13.7		32.4				53.9
2014	Jul	10	1	<0.1	0.4		15.6	10.9			73.1
2014	Aug	10	0	44.4	2.1	5.5	25.7			16.4	5.9
2015	Jun	10	0	0.3	0.8	0.2	87.8	0.1			10.8
2015	Jul	10	0	9.4	0.1	0.4	82.4		1.7		6.0
2015	Aug	10	0				90.9		9.1		
2016	Jun	10	1	9.3	2.3	31.9	16.5	0.6	22.3	4.9	12.2
2016	Jul	10	0	0.1	0.4	0.1	24.1		4.7	70.0	0.6
2016	Aug	10	0					2.5	96.0		1.5
2017	Jun	–	–	–	–	–	–	–	–	–	–
2017	Jul	10	0	77.8	6.2		<0.1			15.6	0.4
2017	Aug	–	–	–	–	–	–	–	–	–	–
Chum salmon											
2013	Jun	5	0		20.5		0.3	12.8	22.8	19.6	24.0
2013	Jul	10	0	3.6	8.5	4.6	9.1		70.6	2.2	1.4
2013	Aug	10	0	3.7		43.1		2.5		49.3	1.4
2014	Jun	10	0			8.3	23.6	1.4		66.6	0.1
2014	Jul	10	2	9.9		0.1				90.0	
2014	Aug	10	0	27.2	0.2	13.9	0.3			54.4	4.0
2015	Jun	10	0				67.7	3.5		28.8	
2015	Jul	10	0	0.6		0.1	86.6			6.8	5.9
2015	Aug	7	0	<0.1			99.9		0.1		
2016	Jun	10	0	5.8	2.3	21.6	6.3	0.5	6.3	26.1	31.1
2016	Jul	10	0		0.1		1.0		6.7	92.0	0.2
2016	Aug	10	0	0.4	0.2		1.3		35.2	62.9	
2017	Jun	10	1	5.2	5.5	6.8			4.6	31.1	46.8
2017	Jul	10	0	71.5	4.0	0.9	3.4	1.7	<0.1	18.5	
2017	Aug	–	–	–	–	–	–	–	–	–	–
Sockeye salmon											
2013	Jun	10	0				1.6	24.7	70.3		3.4
2013	Jul	10	0	15.9		21.5	36.5		4.9		21.2
2013	Aug	10	0	10.7			62.6			20.0	6.7
2014	Jun	10	0				1.2	41.1			57.7
2014	Jul	10	0	27.7		3.5	26.2	28.6			14.0
2014	Aug	10	0	87.4		6.6	4.6				1.4
2015	Jun	10	0				100				
2015	Jul	10	0	0.1	4.9		78.5				16.5
2015	Aug	9	0				100				
2016	Jun	10	0	24.6	4.0	58.2	2.0	2.5	0.4		8.3
2016	Jul	10	0	0.9	0.5	9.0	5.0			28.7	55.9
2016	Aug	10	0		0.4	0.9	22.6		65.4	10.4	0.3
2017	Jun	10	0	3.5	15.9	27.8		32.6	1.2		19.0
2017	Jul	10	0	65.4	16.5	11.2			2.9		4.0
2017	Aug	–	–	–	–	–	–	–	–	–	–
Coho salmon											
2013	Jun	–	–	–	–	–	–	–	–	–	–
2013	Jul	10	0	1.3		84.1	0.1	6.1	<0.1		8.4
2013	Aug	–	–	–	–	–	–	–	–	–	–
2014	Jun	10	1	<0.1		5.7	12.2	79.8	<0.1		2.3
2014	Jul	10	0	<0.1		49.5	2.5	10.2	<0.1		37.8
2014	Aug	10	0	0.4		83.1	0.1	16.3	0.1		<0.1
2015	Jun	10	1	0.2		17.2	4.6	64.3	<0.1		13.7
2015	Jul	10	0	0.8		3.6	93.8	1.8	<0.1		<0.1
2015	Aug	10	0	<0.1		<0.1	98.3	<0.1	1.7		<0.1
2016	Jun	10	4	<0.1		57.5	0.8	39.9	1.8		<0.1
2016	Jul	10		0.6		65.6	4.5	29.3	<0.1		<0.1
2016	Aug	10	0	<0.1		17.4	1.3	78.3	0.6		2.4
2017	Jun	10	4	<0.1		27.3	<0.1	60.3	<0.1		12.4
2017	Jul	10	0	24.5		44.5	5.8	24.7	<0.1		0.5
2017	Aug	–	–	–	–	–	–	–	–	–	–
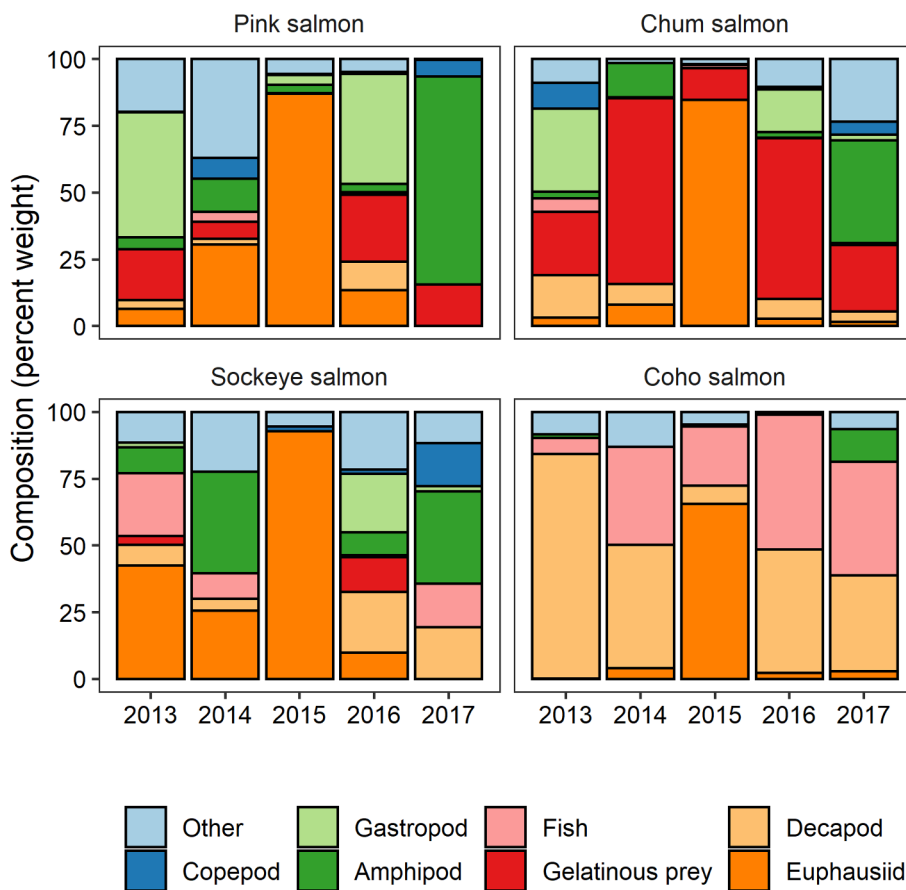
Fig. 2. Diet composition by major prey taxa of juvenile pink, chum, sockeye, and coho salmon captured in surface marine waters of northern Southeast Alaska, 2013 to 2017. Annual values are averaged over June, July, and August. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diets among the four juvenile salmon species in 2015 was the most pronounced observed over the duration of the SECM project (E. Fergusson, unpubl. data). Although 2015 was not the warmest year in our study period, the lipid content of prominent zooplankton taxa was anomalously low, as was the estimated lipid intake for all juvenile salmon species but chum salmon. Juvenile salmon, even the trophically distinct coho salmon, appeared to respond to these poor feeding conditions by switching to euphausiids in 2015. In the two years following 2015, feeding conditions (expressed as estimated lipid intake) appeared to improve substantially for coho salmon and decline for chum salmon and showed a mixed response for sockeye and pink salmon. Although we lacked marine survival estimates for these populations, low lipid intake of the juvenile pink salmon in 2017 was followed by record low returns of adult pink salmon to SEAK in 2018 (A. Piston, Alaska Department of Fish and Game unpubl. data), supporting a link between early marine feeding conditions and recruitment.

4.1. Anomalous salmon diets in 2015

The diets of all juvenile salmon in our study expressed a marked increase in the contribution of euphausiids throughout the months surveyed in 2015 (Fig. 2), suggesting the prevalence of this prey group within the inside waters of Icy Strait at this time. In the other years of the study, dominant prey items varied among the species in ways consistent with other diet studies of juvenile Pacific salmon. Juvenile coho salmon are typically more piscivorous, with other major prey being decapod larvae and to a lesser extent euphausiids (Weitkamp & Sturdevant, 2008). Juvenile pink, chum, and sockeye salmon are more zooplantivorous, with dominant prey within nearshore waters being

hyperiid amphipods, appendicularians (*Oikopleura* sp.), decapod larvae, and euphausiids (e.g. Healey, 1991; Boldt & Haldorson 2003; Beamish et al. 2004; Preikshot et al. 2010). In a regional comparison of juvenile salmon diets across several years, however, Brodeur et al. (2007) observed similarly high levels of euphausiids contributing to the diets of pink, chum, and sockeye salmon from Southeast Alaska, and northern and southern British Columbia, Canada. Thus, the anomalously high euphausiids in the diets across species in Icy Strait may be indicative of euphausiid abundance or juvenile salmon feeding opportunistically on less-preferred prey at a spatial scale beyond our study. Future regional and temporal comparisons of juvenile salmon diets as performed by Brodeur et al. (2007) would help in understanding the spatiotemporal extent of dominant prey and environmental drivers.

4.2. Diets and environmental drivers

In this study, we observed a weak correlation between juvenile salmon diets and the combination of water temperature, salinity above the pycnocline, and wind. During 2015, when euphausiids dominated the diets of the four juvenile salmon species, water temperatures were warm, winds were anomalously high, and pycnocline depth was anomalously deep. As juvenile salmon are visual predators, the increase of euphausiids in the diets in 2015 could have been because they were more abundant that year. Our zooplankton sampling methods were not designed to capture euphausiid abundance. However, recruitment timing of the common euphausiid species in inside waters of SEAK (*Thysanoessa rachii, T. longipes,* and *T. spinifera*) is associated with the timing of the spring phytoplankton bloom (Szabo and Batchelder, 2014), and this has also been shown in the shelf and nearshore waters

Table 2
Statistical comparison among juvenile pink, chum, sockeye, and coho salmon diets, with year and species as factors contributing to the diet differences using PRIMER analysis of similarity (ANOSIM) and similarity percentages (SIMPER) tests. The R statistic from the ANOSIM test ranges from near 0 (no difference between groups) to 1 (differences between groups) with a significance level p < 0.001 (indicated by asterisks). For the juvenile salmon diets that are statistically different, the average dissimilarity (Avg. diss.), prey contributing to the dissimilarity, and percent contribution to that dissimilarity (% cont.) from the SIMPER test are presented. The prey category Other (in 2014 & 2015) included barnacle larvae, insects, and unidentified digested tissue.

Group	R statistic	Avg. diss.	Prey	% cont.
Year				
2013, 2015	0.598*	65.6	Euphausiids	31.1
			Gastropods	14.3
2014, 2015	0.481*	60.3	Euphausiids	31.1
			Other	15.0
2015, 2016	0.648*	67.1	Euphausiids	32.5
			Gastropods	14.1
2015, 2017	0.756*	76.82	Euphausiids	33.2
			Amphipods	18.9
2013, 2014	0.037			
2013, 2016	−0.048			
2013, 2017	0.061			
2014, 2016	0.046			
2014, 2017	0.067			
2016, 2017	0.200			
Species				
Chum, Coho	0.639*	66.5	Gelatinous prey	26.9
			Fish larvae	21.1
Coho, Pink	0.413*	62.7	Decapods	21.8
			Fish larvae	20.7
Coho, Sockeye	0.327*	55.3	Fish larvae	24.0
			Decapods	19.0
Chum, Pink	0.042			
Chum, Sockeye	0.293			
Pink, Sockeye	−0.071			

of the northern Gulf of Alaska for *T. spinifera* and *T. inermis* (Pinchuk et al., 2008). The spring phytoplankton bloom as well as secondary blooms throughout the summer are strongly driven by wind-mixing of the water column and subsequent upwelling of nutrients into the upper water column (Iverson et al., 1974; Ladd and Cheng, 2016). Due to logistic constraints, no surface chlorophyll-*a* (chl-*a*) sampling was performed in May of 2016 and 2017. However, in May of 2015, the chl-*a* concentration in Icy Strait was approximately 3 times higher than observed in May of 2013 and 2014 (Orsi and Fergusson, 2015; Orsi and Fergusson, 2016, 2017). We suggest that the increased winds brought nutrients to the surface which triggered phytoplankton blooms that provided the required nutrients to support euphausiid population growth, resulting in increased feeding on euphausiids by juvenile salmon in 2015.

4.3. Prey quality

Climate-induced fluctuations can alter both zooplankton abundance and zooplankton quality, which has the potential to influence fish survival (Cooney et al., 2001; Coyle et al., 1990; DeLorenzo Costa et al., 2006; Pershing et al., 2005; Sameoto, 1984). For juvenile salmon in the coastal waters off Washington and Oregon, survival has been positively correlated with cold years and the dominance of high-lipid copepods at the time of ocean entry (Bi et al., 2011; Peterson et al., 2014; Peterson and Schwing, 2003). In contrast, survival of juvenile salmon in Southeast Alaska has been positively correlated with warm sea surface temperatures and early timing of the spring phytoplankton bloom (Malick et al., 2015; Mueter et al., 2002). Warm water temperatures and early

phytoplankton blooms may set up favorable growing conditions for juvenile salmon, but higher temperatures increase metabolic rate, requiring high quality and/or high quantities of food. Although zooplankton lipid content was below average in 2015, the lipid intake was not dramatically lower than other years, in part due to the switch to euphausiid prey. Euphausiids were the largest-bodied prey taxa in this study and therefore had the highest total lipid per individual compared to the other zooplankton, meaning that salmon had to eat fewer numbers of individuals to meet growth and energetic demands. In 2017, lipid intake was low for pink, chum, and sockeye salmon. In theory, cooler water temperatures could have lessened the metabolic impact of reduced lipid availability, although as noted previously, pink salmon migrating through Icy Strait in 2017 had poor adult returns in 2018.

Diet studies have limitations in their ability to capture feeding behavior of an organism, with potential biases occurring with limited sample sizes in space and time providing only snapshots of feeding behavior, and there are potential biases related to differential digestion rates of purported prey (Cortés 1997). The results of our study were consistent with other studies within Alaska and from the Northern California Current, indicating that we captured much of the spatio-temporal feeding behavior of juvenile salmonids during the time period of our study. Moreover, the taxonomic level of our analyses has been shown in other juvenile salmon diet studies to express trophic and consumption shifts related to warm/cool shifts in ocean conditions in the North Pacific (Brodeur et al. 1992; Gladics et al. 2014; Daly and Brodeur 2015). Differential digestion of prey can bias results toward those prey that are more resistant to digestion, and by extension, our estimates of lipid consumption based on the diets. This potential bias was likely minimal as we examined general prey groups, and these varied interannually to the extent that the main driver of lipid consumption was based on notable shifts in prey consumed. Our estimates of lipid consumption, while not highly precise, likely provided sufficient resolution to connect underlying energetic and trophic processes.

Although the marine heat wave altered the Gulf of Alaska ecosystem, juvenile salmon were able to meet their energetic demands by switching to an alternative and presumably abundant prey. A more complete understanding of the role of flexibility in the trophic ecology of juvenile Pacific salmon will aid in evaluating the degree to which climate-driven ecosystem reorganizations will impact the resilience of these species under future climate scenarios. Statistical models and historical time series are limited in their ability to anticipate ecosystem change (Litzow et al. 2018), highlighting the need for high-quality monitoring and assessment of ecosystems to inform policy (Schindler & Hilborn, 2015). Given predicted increases in the frequency of extreme warming events for the northeast Pacific (Walsh et al., 2018), continued monitoring that incorporates trophic and nutritional information of juvenile Pacific salmon will help in understanding mechanisms that impact survival and contribute to more informed management.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
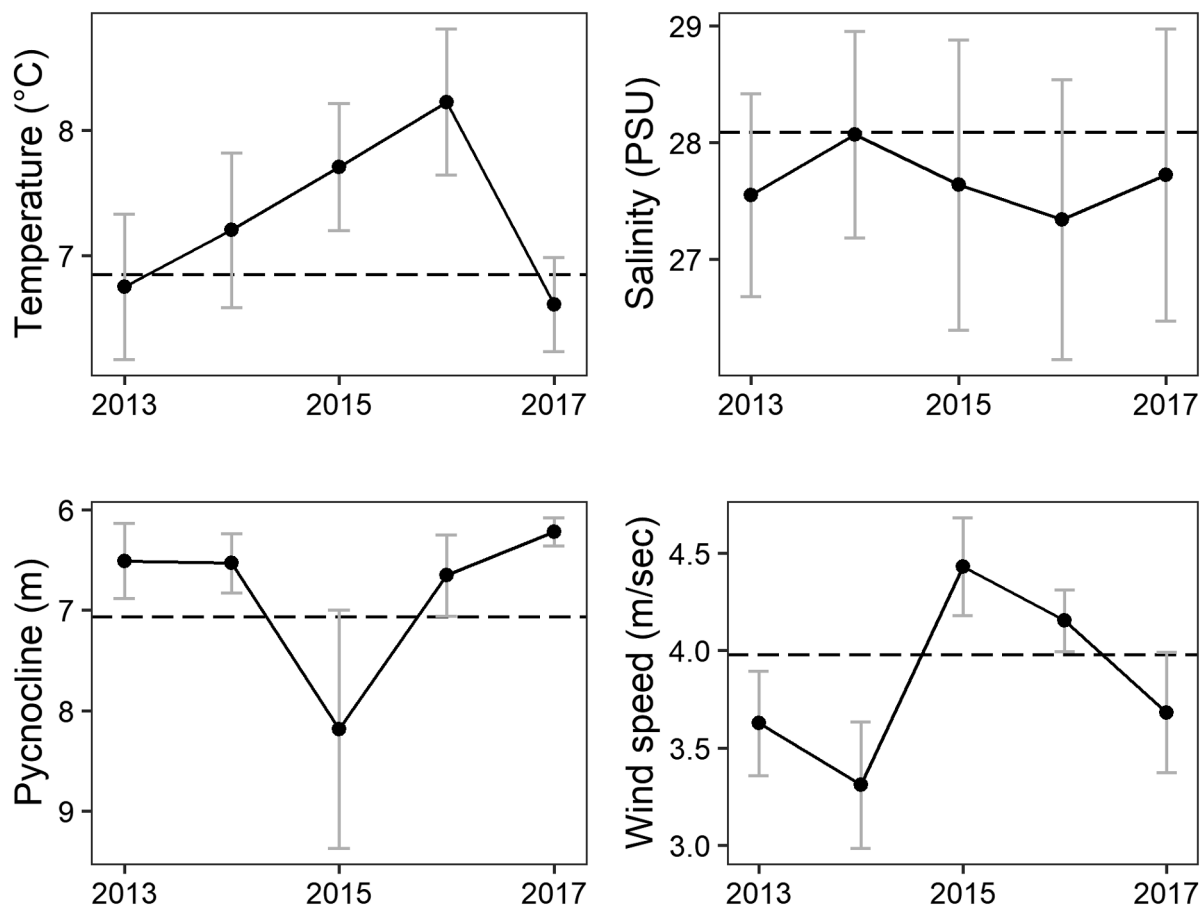
Fig. 3. Annual mean (+/- SE) water temperature (°C, average water column), salinity (PSU, average above pycnocline), pycnocline depth (m), and wind speed (m/s) in Icy Strait, Alaska, from May to August 2013–2017. Long-term average from 1997 to 2017 (see Appendix C) noted by dashed line.

Fig. 4. Average (±SE) annual lipid content (%) of select zooplankton taxa collected in Icy Strait, AK, from May to August 2013–2017. Average from 2013 to 2017 is indicated by the dashed line. The 2013 values for *C. marshallae*, euphausiid (young), and *T. pacifica* are point estimates as there was only one sample of each species collected in that year.

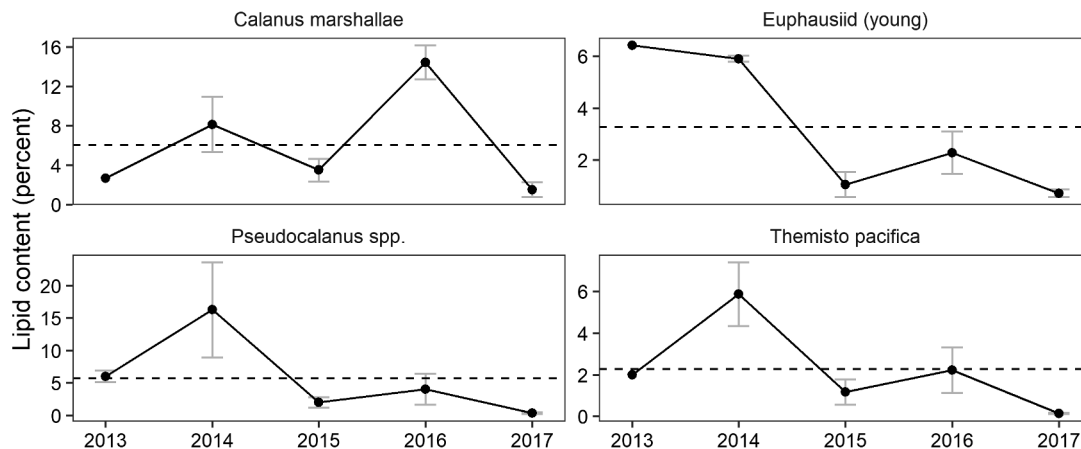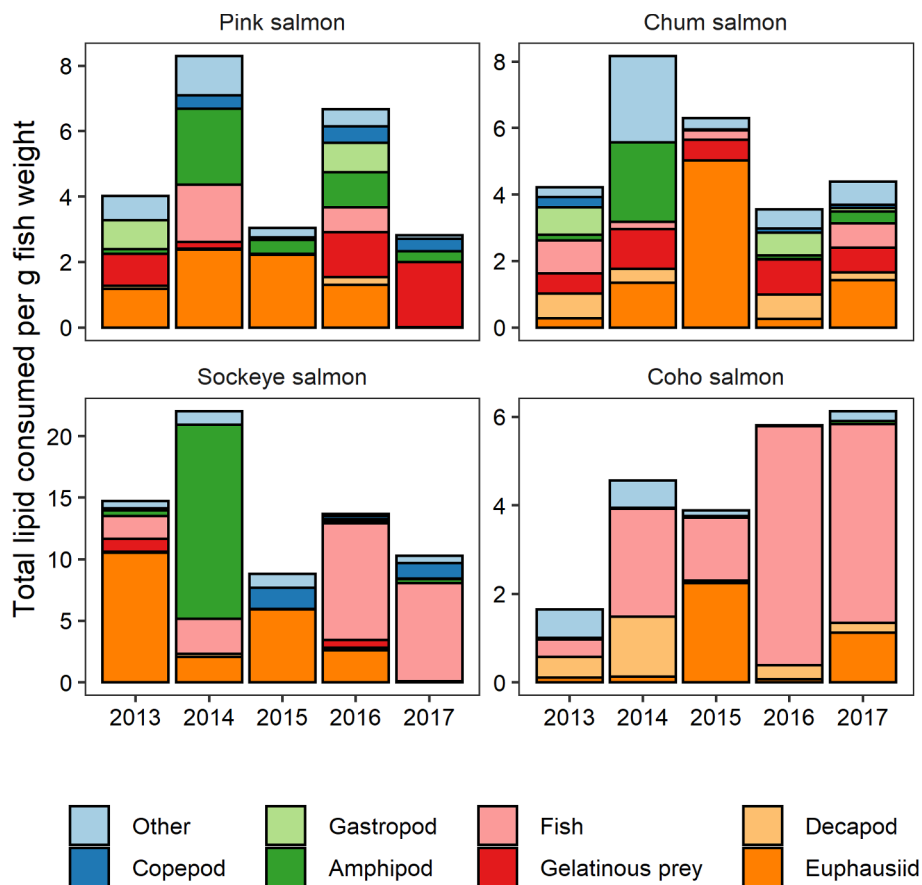**Fig. 5.** Total lipid (g) consumed by juvenile pink, chum, sockeye, and coho salmon standardized by fish wet weight (g). Fish were captured by rope trawl at the surface in the marine waters of northern Southeast Alaska from 2013 to 2017. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix A

Percent composition of prey taxa pooled in the "other" category from diets of juvenile pink, chum, sockeye, and coho salmon. See Table 1 for complete diet composition. Dashes indicate no samples were available for analysis. Prey taxa that were not present in stomach contents are blank

Year	Month	Barnacle cyprid	Barnacle molt	Bivalve larvae	Cephalopod	Chaetognath	Crustacean	Eucarida	Insect	Invertebrate egg	Malacostraca	Digested tissue
Pink salmon												
2013	Jun								7.7			92.3
2013	Jul		0.2						74.3		25.5	
2013	Aug								100			
2014	Jun											100
2014	Jul											100
2014	Aug											100
2015	Jun			6.1								93.9
2015	Jul								1.3			98.7
2015	Aug											
2016	Jun											100
2016	Jul											100
2016	Aug											100
2017	Jun	–	–	–	–	–	–	–	–	–	–	–
2017	Jul								100			
2017	Aug	–	–	–	–	–	–	–	–	–	–	–
Chum salmon												
2013	Jun						2.0		69.4			28.6
2013	Jul								50.0			50.0
2013	Aug		60.0						40.0			
2014	Jun						100					
2014	Jul											
2014	Aug							100				
2015	Jun											
2015	Jul											100
2015	Aug											
2016	Jun											100
2016	Jul											100
2016	Aug											

Year	Month								
2017	Jun	20.4	39.5				38.6	1.5	
2017	Jul								
2017	Aug	–	–	–	–	–	–	–	–

Sockeye salmon

Year	Month								
2013	Jun								100
2013	Jul								100
2013	Aug								100
2014	Jun								100
2014	Jul								100
2014	Aug								100
2015	Jun								
2015	Jul								100
2015	Aug								
2016	Jun								100
2016	Jul								100
2016	Aug						100		
2017	Jun		83.3				16.7		
2017	Jul				100				
2017	Aug	–	–	–	–	–	–	–	–

Coho salmon

Year	Month								
2013	Jun	–	–	–	–	–	–	–	–
2013	Jul								100
2013	Aug	–	–	–	–	–	–	–	–
2014	Jun						100		
2014	Jul			6.2					93.8
2014	Aug								
2015	Jun					90.9			9.1
2015	Jul								
2015	Aug								
2016	Jun								
2016	Jul								
2016	Aug								100
2017	Jun						100		
2017	Jul						100		
2017	Aug	–	–	–	–	–	–	–	–

Appendix B

Lipid content (count, percent value, and standard deviation) for potential prey items of juvenile salmon. If more than one sample was available in a month, the lipid value is the average. Prey items were captured in the surface marine waters of Icy Strait, AK, June to August 2013–2017 with a bongo net equipped with a 333- and 505-μm mesh nets

		Lipid content		
Year	Month	*n*	value	sd
Copepods				
Acartia longiremis C5-C6F				
2013	August	2	2.9	0.6
2014	May	1	3.5	
	August	1	11.4	
Acartia longiremis C5				
2015	June	1	0.003	
2016	July	1	13.1	
Acartia longiremis C6F				
2015	July	3	0.1	0.1
2016	May	1	0.3	
Calanus marshallae C4				
2013	June	1	2.7	
2014	May	1	5.3	
2015	May	1	0.4	
	June	1	0.6	
2017	August	1	0.1	
Calanus marshallae C5				
2014	July	1	10.9	
2015	May	2	4.1	2.1
	July	1	10.5	
	August	1	9.7	
2016	May	3	11.5	2.8
	June	3	17.4	3.1
	July	3	14.3	6.4
2017	June	3	2.3	3.4
	August	2	1.1	1.5
Calanus marshallae C6F				

2015	July	1	0.9	
	August	1	0.2	
2016	June	1	17.5	

Calanus pacificus C5
2016	May	1	4.9	

Centropages abdominalis C5-C6F
2013	July	1	0.2	

Centropages abdominalis C6F
2015	June	4	0.2	0.1

Metridia okhotensis C5
2016	July	1	26.9	1.9
	August	1	36.2	

Neocalanus sp. C5
2015	May	2	4.3	1.9
2017	August	1	1.6	

Paraeuchaeta elongata C6F
2015	May	1	3.3	
2016	August	1	22.9	

Pseudocalanus sp. C4-C6F
2013	June	1	7.6	
	July	2	5.9	2.6
	August	2	4.5	0.1
2014	May	1	9.0	
	July	4	23.6	10.0

Pseudocalanus sp. C5
2015	May	2	3.7	0.3
	June	6	0.3	0.3
	July	2	2.5	1.2
2016	May	2	2.6	0.08
	June	2	6.5	2.4
	August	1	32.1	
2017	June	3	0.6	0.1
	August	2	0.3	0.3

Pseudocalanus sp. C6F
2015	May	2	4.1	5.6
	June	5	0.02	0.01
	July	2	0.1	0.1
	August	2	2.6	0.4
2016	May	2	0.7	0.2
2017	June	2	0.3	0.4
	August	2	0.1	0.01

Euphausiids
Euphausiid furcilia
2013	June	1	6.4	
2014	May	1	5.8	
2015	June	1	0.3	
2016	June	2	2.2	0.1

Euphausia pacifica (10–15 mm)
2014	July	1	1.9	

Thysanoessa raschii (10–15 mm)
2014	July	4	7.7	3.2
2015	May	1	1.2	
2015	July	2	0.6	0.2
	August	3	2.4	0.6
2016	June	2	0.7	0.3
	July	3	7.2	3.5
	August	5	2.9	0.8

Thysanoessa raschii (15–20 mm)
2016	June	3	3.9	4.9

Thysanoessa spinifera (10–15 mm)
2015	May	1	0.7	
2016	July	3	0.8	0.8
	August	2	3.9	1.1

Thysanoessa sp. (<10 mm)
2014	July	1	3.5	
2016	May	2	0.4	0.4
2017	June	1	0.9	
	July	2	0.6	0.2

Hyperiids
Themisto pacifica
2013	August	1	2.0	

2014	July	2	12.4	7.0
	August	1	4.3	
2015	July	1	0.6	
	August	1	1.8	
2016	May	1	0.7	
	July	3	1.7	1.5
	August	2	4.3	0.02
2017	June	2	0.1	0.01
	July	1	0.2	
	August	2	0.1	0.1
Themisto libellula				
2015	May	2	3.7	0.2
2016	August	1	0.4	
Decapods				
Brachyuran zoea				
2016	May	1	0.7	
	July	1	1.3	
2017	June	3	0.04	0.005
	July	1	0.9	
Brachyuran megalopae				
2014	July	1	20.1	
2015	June	1	0.2	
2016	July	3	1.2	0.5
	August	1	2.0	
Pagurid zoea				
2015	June	1	0.4	
Pinnotheridae zoea				
2014	August	1	2.9	
Pandalidae mysis larvae				
2014	May	1	3.3	
Hippolytidae larvae				
2014	August	1	4.5	
2015	May	1	0.6	
Other				
Barnacle nauplii				
2016	May	1	0.04	
Barnacle cyprid				
2014	May	1	9.8	
2015	May	1	0.6	
Oikopleura sp.				
2014	July	1	16.7	
Sagitta elegans (5–20 mm)				
2014	July	1	3.2	
	August	1	1.2	
2015	May	2	1.3	0.5
	July	1	0.5	
2016	June	3	1.2	0.2
	July	1	1.5	
	August	2	1.8	1.4
2017	June	2	0.6	0.1
	July	2	0.6	0.2
Clione limacina				
2015	May	2	3.8	0.7
2016	June	1	0.4	
Limacina helicina				
2015	July	1	0.06	
	August	2	0.2	0.1
2016	May	3	0.4	0.2
	June	3	0.5	0.3
	August	2	1.3	0.8
Cyphocaris challengeri				
2015	May	1	1.3	
Octopus larvae				
2016	May	2	0.1	0.04

Appendix C

Annual mean (+ /- SE) water temperature (°C, average water column), salinity (PSU, average above pycnocline), pycnocline depth (m), and wind speed (m/sec) in Icy Strait, Alaska from May to August 1997–2017. Time series average indicated by dashed line. Note that wind speed data were not available prior to 2007
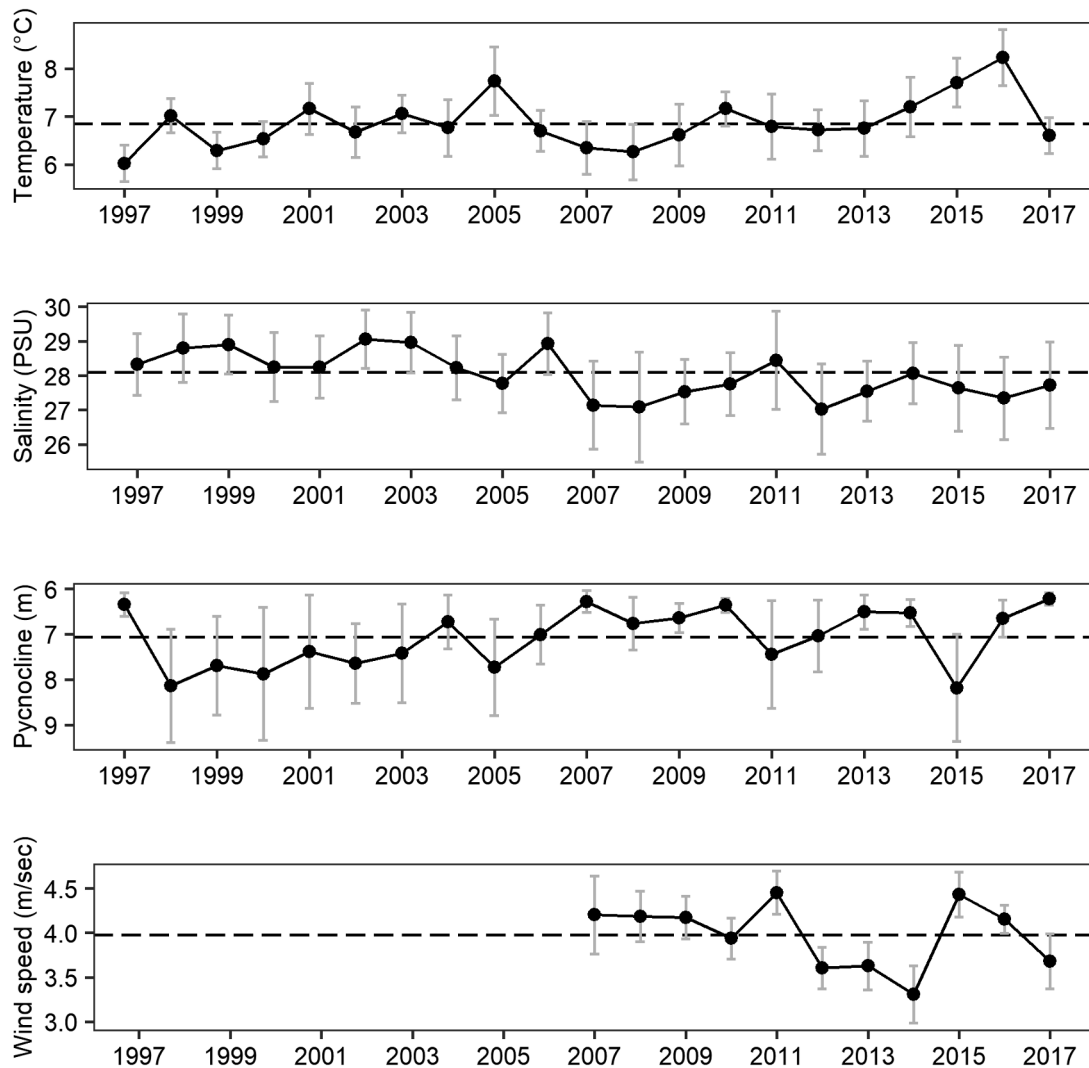
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