ZOOPLANKTON COMMUNITY COMPOSITION IN RELATION TO ENVIRONMENT

AND JUVENILE SALMON DIETS IN ICY STRAIT, SOUTHEAST ALASKA

By

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Abstract

Zooplankton in the nearshore marine habitat function as an important prey resource for many pelagic fishes, are a major component of the lower tropic level, and serve as a vital ecosystem indicator. Understanding how the zooplankton community changes in response to fluctuations in biophysical factors is critical in a changing climate and is important to understanding the dynamics of commercially important upper-trophic level species that depend nutritionally on zooplankton. The Alaska Fisheries Science Center's Southeast Coastal Monitoring project has surveyed the pelagic ecosystem in eastern Icy Strait monthly from May to August since 1997 to understand how environmental variation affects the pelagic food web and the sustainability of salmon resources. I used this long-term dataset (1997–2017) to address the goals of this study: 1) to investigate the influence of temperature on the Icy Strait zooplankton community; and 2) to understand how juvenile salmon utilize zooplankton prey in relation to temperature driven fluctuations in the zooplankton community. In Chapter 1, I noted that the composition of the zooplankton community varied in years with anomalously high or low temperatures. I observed shifts in the timing of development in many key taxa during these anomalous years. For example, in anomalously cool years, several taxa were found in higher densities later in the summer than in anomalously warm years. In Chapter 2, I examined how oceanographic factors influenced the diet composition and quality of four species of juvenile Pacific salmon (*Oncorhynchus* spp.) in Icy Strait (Southeast Alaska) from 2013 to 2017. In 2015 I observed a change in diets, including zooplanktivorous (pink salmon *O. gorbuscha*, chum salmon *O. keta*, and sockeye salmon *O. nerka*) and piscivorous (coho salmon *O. kisutch*) species, from typically diverse diets to diets dominated by euphausiids. This year was notable for warm

waters, deep pycnoclines, and below average zooplankton nutritional quality. Juvenile salmon appeared to supplement their lipid intake and meet nutritional requirements by switching to larger euphausiid prey. The results from these studies increase our understanding of zooplankton community dynamics, salmon trophic relationships, and the resilience and flexibility of the food web during climate-driven reorganizations of the pelagic marine ecosystem.

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General Introduction

Overview

Advection, water temperature, salinity, wind, timing of the phytoplankton bloom, and predation influence zooplankton in marine waters across the globe, showing variation in species composition and abundance on both seasonal and interannual time scales (Brodeur and Ware, 1992; Coyle et al., 2013; Mackas et al., 2007, 2001). Regime shifts in the North Sea, Bering Sea, and Gulf of Alaska (GOA) have been characterized by a complex set of environmental variables including mean water temperature with resultant shifts in zooplankton community composition (Alvarez-Fernandez et al., 2012). During the 1977 regime shift in the North Sea, as waters cooled, cold-water copepods became more prevalent in the zooplankton community (Alvarez-Fernandez et al., 2012). In contrast, warm-water copepods were more abundant in the zooplankton community during the 1988 regime shift, which was characterized by warming waters. The Bering Sea ecosystem experienced warm and cool phases during the early 2000s, with resultant shifts in the zooplankton communities. During the warm phase, *Calanus marshallae* and euphausiids declined, which decreased the lipid-rich prey field utilized by walleye pollock (*Gadus chalcogrammus*) larvae and larger predators (Coyle et al., 2011). In the absence of the large zooplankton prey, predators increased consumption of walleye pollock larvae, which lead to a decline in the walleye pollock population. When the ecosystem entered the subsequent cool phase, large-bodied zooplankton rebounded, yet the larval walleye pollock population was slow to recover.

Copepod abundance is differentially influenced by localized and basin-scale El Niño–Southern Oscillation (ENSO) events through temperature-driven changes in species composition, metabolic rates, and developmental timing. During the first two years of the marine heat wave in

the GOA (2014–2015), there was an increase in abundance of small copepods and the timing of their residence in the upper water column was earlier in these two warm years compared to previous cooler years (Batten et al., 2018). Additionally, small-sized copepods have multiple generations per year, while larger copepods typically have only one generation per year. This differential reproductive strategy grants small copepods the ability to respond more quickly to environmental changes. For example, during periods of warm and cold temperatures in inside waters of Southeast Alaska (SEAK), the biomass and abundance of small copepods varied little between periods, while large copepods showed decreased abundance and biomass during years of extreme warm or cold temperatures (Park et al., 2004).

Zooplankton community structure is susceptible to top-down pressure from predation by carnivorous zooplankton (e.g., chaetognaths, amphipods), fishes, and marine mammals. Small copepods (*Pseudocalanus* spp., *Paracalanus* spp., and *Microcalanus* spp.) abundance was inversely related to abundance of the chaetognath *Sagitta elegans* in the North Sea, with predation pressure influencing the spring growth rates of the copepods (Clark et al., 2003). During warm periods in the Bering Sea, the abundance of large calanoid copepods and euphausiids decreased; one hypothesized mechanism was predation by walleye pollock and other planktivorous fishes (Stabeno et al., 2012). The influence of predation from fish predators on zooplankton is sometimes evident when fish abundance drastically decreases. For example, zooplankton abundance in the Barents Sea showed a marked increase when the capelin (*Mallotus villosus*) stock collapsed (Dalpadado et al., 2003; Skjoldal et al., 1992). The right whale (*Eubalaena glacialis*) population in the Bay of Fundy targeted the C5 stage of *Calanus finmarchicus* to the extent of depressing the population so much that the whales moved to other feeding grounds (Michaud and Taggart, 2007).

The zooplankton community in Icy Strait, AK contains some of the same species found in the GOA, but the overall zooplankton community structure is different. Small calanoid copepods numerically dominate the zooplankton community in Icy Strait while large calanoid copepods numerically dominate the GOA zooplankton community (Coyle and Paul, 1992; Orsi et al., 2012; Park et al., 2004). The dominant large copepod is *Metridia okhotensis* in Icy Strait and *Neocalanus* spp. in the GOA. While copepods numerically dominate the zooplankton community in Icy Strait, other less-numerous zooplankton taxa are equally important to the many fish stocks that inhabit Icy Strait. These zooplankton taxa include euphausiids, hyperiid amphipods, oikopleurans, barnacle larvae, and crab larvae, which are commonly found in the diets of planktivores captured in Icy Strait (Orsi et al., 2004; Sturdevant et al., 2012, 2004).

Many fish species use Icy Strait for a portion of their life history while concurrently feeding on the zooplankton community. These fish species include commercially important salmon (*Oncorhynchus* spp.), sablefish (*Anoplopoma fimbria*), and walleye pollock, in addition to capelin, sandlance (*Ammodytes hexapterus*), starry flounder (*Platichthys stellatus*), and herring (*Clupea pallasii*) (Sturdevant et al., 2012). Juvenile salmon migrate through Icy Strait in summer to transit from freshwater to the GOA (Farley and Munk, 1997; Jaenicke and Celewycz, 1994; Orsi et al., 2004). While in the strait, juvenile salmon feed on dense zooplankton prey to varying degrees (Orsi et al., 2004). Juvenile pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon consume a mixture of copepods, hyperiid amphipods, fish larvae (e.g., walleye pollock, herring, capelin, sandlance), euphausiids, decapod larvae, and larvaceans (Brodeur et al., 2007; Landingham et al., 1998; Sturdevant et al., 2004). Juvenile coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon are mainly piscivorous; however, decapod larvae

and euphausiids are important prey in certain years (Brodeur et al., 2007; Landingham et al., 1998).

The importance of a prey resource to fishes can be identified through long-term monitoring of fish diets, which incorporate prey availability and predator preference. The availability of a prey resource may be altered through environmental changes, trophic interactions, predator-prey mismatch, phenology, and fluctuations in the zooplankton community structure (Coyle et al., 2011; Hunt et al., 2011; Sturdevant et al., 2012). A reorganization of the community structure of a marine environment may alter the importance of a prey resource to a predator (Anderson and Piatt, 1999; Litzow and Ciannelli, 2007). For example, following the 1977 Pacific Decadal Oscillation (PDO) regime shift, the Pacific cod (*Gadus macrocephalus*) population in Pavlof Bay, Alaska drastically increased, coincident with a 3-fold decrease in the shrimp population; shrimp being the main prey of the cod (Albers and Anderson, 1985).

The zooplankton community in the nearshore marine habitat is an important prey resource for many pelagic fishes and, as a major component of the lower tropic level, can serve as a vital sign to monitor the health of the ecosystem. Warming events in the northeast Pacific are predicted to occur more frequently in coming years (Walsh et al., 2018), therefore understanding how the zooplankton community structure and nutritional status fluctuate is important is evaluating the trophic effects on juvenile salmon in Icy Strait. During the 2014–2016 marine heat wave, water temperatures in Icy Strait did not show a marked increase until spring of 2015, suggesting that Icy Strait was buffered from the strong forcing mechanisms driving change in the GOA (Orsi and Fergusson, 2017). If, as suspected, the Icy Strait nearshore habitat responds differently to environmental fluctuations than the GOA, it is important to

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understand how major physical and biological factors influence the zooplankton community dynamics and how that, in turn, impacts the trophic ecology of juvenile salmon in Icy Strait.

Thesis Goals

The goals of this thesis were to 1) investigate the role of temperature as a driver of the Icy Strait zooplankton community using a long-term dataset, and 2) understand how fish predators utilize zooplankton prey in relation to temperature driven fluctuations in the zooplankton community. I used data from the Alaska Fisheries Science Center's Southeast Coastal Monitoring project, which monitored the biophysical environment in eastern Icy Strait monthly from May to August from 1997 to 2017. Biophysical data collected include temperature, salinity, chlorophyll, zooplankton density and biomass, and juvenile salmon abundance, size, condition, diet, feeding intensity, and predator abundance. Multivariate statistical analyses were used to identify differences in, and characterize responses of, the zooplankton communities and juvenile salmon diets during warm and cool years, and to additionally identify key species contributing to these differences.

Literature Cited

Albers, W.D., Anderson, P.J., 1985. Diet of Pacific cod, *Gadus macrocephalus*, and predation on the northern pink shrimp, *Pandalus borealis*, in Pavlof Bay, Alaska. Fish. Bull. 83(4), 601–610.

Alvarez-Fernandez, S., Lindeboom, H., Meesters, E., 2012. Temporal changes in plankton of the North Sea: community shifts and environmental drivers. Mar. Ecol. Prog. Ser. 462, 21–38. doi:10.3354/meps09817

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. 189, 117–123. doi:10.3354/meps189117

Batten, S.D., Raitsos, D.E., Danielson, S., Hopcroft, R., Coyle, K., McQuatters-Gollop, A., 2018. Interannual variability in lower trophic levels on the Alaskan Shelf. Deep Sea Res. Part II Top. Stud. Oceanogr. 147, 58–68. doi: 10.1016/j.dsr2.2017.04.023

Brodeur, R.D., Daly, E.A., Sturdevant, M. V., Miller, T.W., Moss, J.H., Thiess, M.E., Trudel, M., Weitkamp, L.A., Armstrong, J.L., Norton, E.C., 2007. Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. Am. Fish. Soc. Symp. 57, 183.

Brodeur, R.D., Ware, D.M., 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fish. Oceanogr. 1, 32–38. doi:10.1111/j.1365-2419.1992.tb00023.x

Clark, R.A., Frid, C.L.J., Nicholas, K.R., 2003. Long-term, predation-based control of a central-west North Sea zooplankton community. ICES J. Mar. Sci. J. du Cons. 60, 187–197. doi:10.1016/S1054-3139(02)00253-9

Coyle, K.O., Eisner, L.B., Mueter, F.J., Pinchuk, A.I., Janout, M.A., Cieciel, K.D., Farley, E.V.,

Andrews, A.G., 2011. Climate change in the southeastern Bering Sea: impacts on pollock

stocks and implications for the oscillating control hypothesis. Fish. Oceanogr. 20, 139–

156. doi:10.1111/j.1365-2419.2011.00574.x

Coyle, K.O., Gibson, G.A., Hedstrom, K., Hermann, A.J., Hopcroft, R.R., 2013. Zooplankton

biomass, advection and production on the northern Gulf of Alaska shelf from simulations

and field observations. J. Mar. Syst. 128, 185–207. doi:10.1016/j.jmarsys.2013.04.018

Coyle, K.O., Paul, A.J., 1992. Interannual differences in prey taken by capelin, herring, and red

salmon relative to zooplankton abundance during the spring bloom in a southeast Alaskan

embayment. Fish. Oceanogr. 1, 294–305. doi:10.1111/j.1365-2419.1992.tb00002.x

Dalpadado, P., Ingvaldsen, R., Hassel, A., 2003. Zooplankton biomass variation in relation to

climatic conditions in the Barents Sea. Polar Biol. 26, 233–241. doi:10.1007/s00300-002-

0470-z

Farley Jr, E.V, Munk, K., 1997. Incidence of thermally marked pink and chum salmon in the

coastal waters of the Gulf of Alaska. Alaska Fish. Res. Bull 4, 181–187.

Hunt, G.L., Coyle, K.O., Eisner, L.B., Farley, E.V, Heintz, R.A., Mueter, F., Napp, J.M.,

Overland, J.E., Ressler, P.H., Salo, S., 2011. Climate impacts on eastern Bering Sea

foodwebs: a synthesis of new data and an assessment of the Oscillating Control

Hypothesis. ICES J. Mar. Sci. 68, 1230–1243. doi:10.1093/icesjms/fsr036

Jaenicke, H.W., Celewycz, A.G., 1994. Marine distribution and size of juvenile Pacific salmon in

Southeast Alaska and northern British Columbia. Fish. Bull. 92, 79–90.

Landingham, J.H., Sturdevant, M. V, Brodeur, R.D., 1998. Feeding habits of juvenile Pacific

    salmon in marine waters of southeastern Alaska and northern British Columbia. Fish.

    Bull. 96, 285–302.

Litzow, M.A., Ciannelli, L., 2007. Oscillating trophic control induces community reorganization

    in a marine ecosystem. Ecol. Lett. 10, 1124–1134. doi:10.1111/j.1461-

    0248.2007.01111.x

Mackas, D.L., Batten, S., Trudel, M., 2007. Effects on zooplankton of a warmer ocean: recent

    evidence from the Northeast Pacific. Prog. Oceanogr. 75, 223–252.

    doi:10.1016/j.pocean.2007.08.010

Mackas, D.L., Thomson, R.E., Galbraith, M., 2001. Changes in the zooplankton community of

    the British Columbia continental margin, 1985–1999, and their covariation with

    oceanographic conditions. Can. J. Fish. Aquat. Sci. 58, 685–702. doi:10.1139/f01-009

Michaud, J., Taggart, C.T., 2007. Lipid and gross energy content of North Atlantic right whale

    food, *Calanus finmarchicus*, in the Bay of Fundy. Endanger. Species Res. 3, 77–94.

    doi:10.3354/esr003077

Orsi, J.A., Fergusson, E.A., 2017. Annual Survey of Juvenile Salmon, Ecologically-Related

    Species, and Biophysical Factors in the Marine Waters of Southeastern Alaska, May–

    August 2015. North Pacific Anadromous Fish Commission Doc. 1739. 71pp.

Orsi, J.A., Fergusson, E.A., Sturdevant, M. V., Farley Jr., E.V, Heintz, R.A., 2012. Annual

    survey of juvenile salmon, ecologically-related species, and biophysical factors in the

    marine waters of southeastern Alaska, May–August 2012 1, 92.

Orsi, J.A., Wertheimer, A.C., Sturdevant, M. V, Fergusson, E.A., Mortensen, D.G., Wing, B.L., 2004. Juvenile chum salmon consumption of zooplankton in marine waters of southeastern Alaska: a bioenergetics approach to implications of hatchery stock interactions. Rev. Fish Biol. Fish. 14, 335–359. doi:10.1007/s11160-004-3813-8

Park, W., Sturdevant, M., Orsi, J., Wertheimer, A., Fergusson, E., Heard, W., Shirley, T., 2004. Interannual abundance patterns of copepods during an ENSO event in Icy Strait, southeastern Alaska. ICES J. Mar. Sci. 61, 464–477. doi:10.1016/s1054-3139(04)00047-5

Skjoldal, H.R., Gjøsæter, H., Loeng, H., 1992. The Barents Sea ecosystem in the 1980s: ocean climate, plankton, and capelin growth, in: ICES Marine Science Symposia. pp. 278–290.

Stabeno, P.J., Kachel, N.B., Moore, S.E., Napp, J.M., Sigler, M., Yamaguchi, A., Zerbini, A.N., 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep. Res. Part II Top. Stud. Oceanogr. 65–70, 31–45. doi:10.1016/j.dsr2.2012.02.020

Sturdevant, M.V., Orsi, J.A., Fergusson, E.A., 2012. Diets and Trophic Linkages of Epipelagic Fish Predators in Coastal Southeast Alaska during a Period of Warm and Cold Climate Years, 1997–2011. Mar. Coast. Fish. 4. doi:10.1080/19425120.2012.694838

Sturdevant, M. V, Fergusson, E.A., Orsi, J.A., Wertheimer, A.C., 2004. Diel feeding and gastric evacuation of juvenile pink and chum salmon in Icy Strait, southeastern Alaska, May–September 2001. North Pacific Anadromous Fish Comm. Tech. Rep. 5, 107–109.

Walsh, J.E., Thoman, R.L., Bhatt, U.S., Bieniek, P.A., Brettschneider, B., Brubaker, M., Danielson, S., Lader, R., Fetterer, F., Holderied, K., 2018. The high latitude marine heat wave of 2016 and its impacts on Alaska. Bull. Am. Meteorol. Soc. 99, S39–S43. doi:10.1175/bams-d-17-0105.1

Chapter 1: Zooplankton Community Response to Environmental Changes[1]

Abstract

Zooplankton are an essential link between primary producers and higher trophic level species. Therefore, changes in zooplankton communities in response to shifts in physical and biological mechanisms are important for understanding how food webs are affected by climate change. Here, we examined how variation in water temperature influenced the zooplankton community in Icy Strait (Southeast Alaska) from 1997 to 2017. Over the 21 years, water temperatures shifted from cool to warm phases in conjunction with fluctuations in basin-scale metrics. We identified four years with anomalous water temperatures throughout the summer sampling periods: two years were anomalously cool (2002 and 2008), and two years were anomalously warm (2005 and 2016). The abundance of key zooplankton species and community composition differed between anomalously warm and cool years, with increases in *Calanus marshallae* and *Limacina helicina* in warm years and increases in euphausiid larvae and *Metridia* spp. in cool years. Additionally, we observed shifts in the timing of peak densities of key taxa; *C. marshallae* and euphausiid larvae peak densities shifted from May in cool years to July/August of warm years. The timing of zooplankton development can affect the degree to which climate-driven ecosystem reorganizations will impact species that rely on zooplankton as a prey resource. This conclusion has implications for community studies and monitoring programs, especially those that rely on single, fixed sampling periods.

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[1] Fergusson, E.A., Eckert, G.L., Strasburger, W. Zooplankton community response to environmental changes. Manuscript in preparation for ICES Journal of Marine Science.

1.1 Introduction

Understanding how zooplankton communities change in response to fluctuations in physical and biological mechanisms is critical when using zooplankton data to characterize an ecosystem, model a commercially important upper-trophic level species, or study the trophic transfer of energy throughout the food web. Furthermore, zooplankton are key to understanding how larger ecosystems respond to climate changes (Alvarez-Fernandez et al., 2012; Dalpadado et al., 2003; Kane, 2009; Kirby et al., 2007; Mackas et al., 2001; Pershing et al., 2004; Skjoldal et al., 1992). For example, a regime shift in the North Sea during the 1990s was characterized by a complete structural change in the calanoid copepod population (Beaugrand, 2004). This change propagated up the food web and resulted in declining survival of forage fishes (especially herring, *Clupea pallasii*, and sandeel, *Ammodytes* spp.), which contributed to a seabird breeding failure (Alvarez-Fernandez et al., 2012). Zooplankton link primary producers and higher trophic level species (Cooney et al., 2001; Kane, 2009); they are fairly easy to sample (Kane, 2009); and they respond quickly to environmental conditions due to their short life cycles (Alvarez-Fernandez et al., 2012; Mackas et al., 2007, 2001).

Fluctuations in zooplankton communities can have cascading impacts throughout the food web (Alvarez-Fernandez et al., 2012; Brodeur and Ware, 1992; Clark et al., 2003; Kirby et al., 2007) and can mediate environmental forcing on higher trophic level species. For example in the North Sea, changing environmental forces, including increases in air temperature, Atlantic water flow, and wind speed, altered the zooplankton community by decreasing the density of neritic copepods that are a major prey resource for fishes such as herring. This decrease in neritic

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copepods coincided with the failure of herring recruitment in subsequent years (Alvarez-Fernandez et al., 2012). Climate-induced fluctuations can also alter zooplankton quality, which may influence fish survival (Cooney et al., 2001; Coyle et al., 1990; DeLorenzo Costa et al., 2006; Pershing et al., 2005; Sameoto, 1984). For example, lipid-rich copepods in the Bering Sea are more abundant during a cold phase than during a warm phase, when lipid-poor copepods dominate the prey field (Coyle et al., 2011). Greater density of lipid-rich copepods in cold years corresponds to better overwinter survival of larval walleye pollock (*Gadus chalcogrammus*), because walleye pollock must reach an energy minimum if they are to survive through the food-limited winter (Heintz et al., 2013). During cold years in the Bering Sea, age-0 walleye pollock enter winter with a higher energy content, reached by consuming a lipid-rich diet, which results in an increased recruitment of age-1 walleye pollock compared to the recruitment during warm years.

This study examined the zooplankton community composition in inside waters of northern Southeast Alaska over interannually cool and warm stanzas using an oceanographic and zooplankton time series collected by the NOAA Alaska Fisheries Science Center's Southeast Coastal Monitoring (SECM) project from 1997 to 2017 (Fergusson et al., 2018). The monthly summer surveys occur in the strait habitat of northern Southeast Alaska, a major migration corridor used by juvenile salmon (*Oncorhynchus* spp.) as they migrate from inshore waters to the Gulf of Alaska (GOA; Fergusson et al., 2018; Orsi et al., 2004). Here, we use biophysical data from the survey to 1) examine the relationship between zooplankton community composition and temperature; and 2) assess changes in seasonal timing of key species in the zooplankton community during warm and cool events. Ultimately, our results can provide a better

understanding of the mechanisms linking physical drivers, such as temperature, to lower trophic level species responses.

1.2 Methods

1.2.1 Field and lab collections

We conducted field sampling in summer months in the northern region of Southeast Alaska from May to August 1997 to 2017. Oceanographic, zooplankton, and surface (upper 20 m) trawl sampling were conducted during daylight hours at four stations in Icy Strait each month (Figure 1.1). Stations were 3 km apart and the shoreside stations were 3 km from shore. A detailed description of the methods are provided in Orsi et al. (2013) and described briefly here. Hydrographic data were collected using a conductivity-temperature-depth (CTD) profiler (SBE 19plus V2 SeaCAT Profiler; Seabird Scientific) deployed from the surface to 200 m depth or within 10 m of the bottom. For each station, the average upper 20-m water column temperature was calculated and then used to calculate monthly and annual temperature means.

Zooplankton samples were collected at each station with a bongo net towed obliquely from the surface to 200 m or within 20 m of the bottom and back to the surface in a V-shaped path. The bongo net had a double ring (60-cm diameter) frame with mesh sizes of 333- and 505-µm. 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 each of the bongo nets for calculation of water volume filtered. Immediately after the tow, zooplankton samples were preserved in a 5% formalin-seawater solution for later analysis.

A total of 336 zooplankton samples from the 333-µm mesh nets were examined from May to August 1997–2017 (except August 2006). Each 333-µm mesh sample was sequentially

split using a Folsom splitter until ~200 of the dominant taxa remained in the subsample. Zooplankton were then identified to the lowest possible taxonomic level (hereafter referred to as 'taxa group'), including sex and stage when applicable, and enumerated. Following this step, each of the previous splits were scanned for rare species not previously included, these zooplankton were identified to the lowest possible taxonomic level and enumerated. Densities (number/m^3) were then estimated using subsample counts, split fractions, and volume of water filtered.

1.2.2 Data analyses

We used hierarchical cluster analysis to objectively group years with similar water column temperatures. Annual water temperature anomalies were calculated as the average monthly anomalies for each year. We used Euclidean distance measures of the mean annual water temperature anomalies to create a resemblance matrix for the hierarchical cluster analysis routine. Therefore, each year was assigned to a temperature group that was used as a factor in the zooplankton analysis described below.

Zooplankton densities were averaged by taxa groups and station for each month and year, and each year was assigned to the temperature group identified in the cluster analysis. Prior to performing statistical analyses, we used a 4th root transformation to prevent large values from skewing data distributions. Then, to address the high occurrence of zeros in the dataset, we used Bray-Curtis dissimilarity measures to create resemblance matrices for use in further multivariate analyses. All multivariate data analyses were conducted in PRIMER v. 7 (Clarke and Gorley, 2015), with density heatmaps created in R v.4.0.1 (R Core Team, 2015).

We examined the response of the zooplankton community to temperature using the monthly densities of each taxa group at each station with the previously identified annual mean temperature groups as a grouping factor. First, we used the bootstrap average routine to visualize the average and nominal 95% of the zooplankton community by temperature groups. The bootstrap routine calculates the average through resampling the dataset 100 times and the nominal 95% coverage is similar to a 95% confidence interval (Clarke and Gorley, 2015). We then performed a one-way analysis of similarity (ANOSIM) test with the null hypothesis of no differences in the zooplankton community among the temperature groups. The resulting R statistic ranges from close to zero (null hypothesis) to 1, which indicates clear separation between the temperature groups with a significance level $p < 0.01$ (when 9999 permutations are selected). We used pairwise comparisons to identify temperature groups with significantly different zooplankton communities. We used the Similarity Percentages (SIMPER; Clarke and Ainsworth, 1993) procedure to identify the species that contributed most to dissimilarity between zooplankton communities in the significantly different temperature groups. Lastly, we visually identified patterns of change in density for key zooplankton taxa between temperature groups with density heatmaps. Data for heatmaps were the normalized monthly density anomalies calculated individually for each species.

We assessed changes in developmental timing of zooplankton taxa in response to temperature by first using non-metric multidimensional scaling (nMDS) to visualize the average monthly zooplankton community based on taxa density. We then selected the overlay trajectory option to show the progression of seasonality within and among temperature groups and anomalously warm and cool years (Clarke and Gorley, 2015). We again created heatmaps of the

monthly density anomalies to identify patterns of change in density for key species between

temperature groups.

1.3 Results

Water temperatures varied over the 21-year time series (Figure 1.2). Years sorted into

seven temperature groups through cluster analysis (Figure 1.3). Although the cluster analysis did

not identify any significant breaks, it did separate out warm and cold years in the first split then

further split out the anomalous and average temperature years. Four anomalous years were

identified, two warm (2005 and 2016) and two cool (2002 and 2008), all with temperatures

greater than one standard deviation from the long-term time series mean (Figure 1.2). It was

curious that two years (2003 and 2015) with mean water temperatures that were one standard

deviation warmer than the long-term time series average temperature did not cluster with 2005

and 2016; instead they clustered with 2004 and 2010, years with temperatures that were just

below the standard deviation break. Water temperatures in 2003, 2004, 2010 and 2015 tended to

be warm, but not consistently in all months sampled (Figure 1.4). The monthly temperatures in

2005 and 2016 were consistently anomalously warm through all sampling months. The cool year

groups separated similarly to the warm groups (Figure 1.3) with years that were consistently cool

over the summer months (2002 and 2008) separating from other years with fluctuating patterns

of warm and cool among the summer months.

1.3.1 Zooplankton community response by warm/cold temperature groupings

Overall, the zooplankton communities were significantly different by temperature groups

(ANOSIM, global R = 0.036, p = 0.002; Figure 1.5) but the low R statistic indicated that average

temperature was not the only factor driving variation in the zooplankton community. Pairwise tests indicated only six of the 21 comparisons were statistically different (Table 1.1). The zooplankton communities in the two warm year groups (Groups E and F) were significantly different from each other, as were the two cool year groups (Groups B and C). However, the zooplankton communities did not differ when warm and cool groups were compared. The zooplankton communities in the average temperature group (Group D) differed from both warm groups and one cool group. The zooplankton communities in the anomalous temperature groups were significantly different from each other but were not different from the zooplankton communities in any of the other years.

Species that primarily contributed to the differences between the zooplankton communities among temperature groups included *M. pacifica*, *C. marshallae*, and *M. okhotensis* copepodites, euphausiid larvae (egg, nauplii, calyptopis, and furcilia), barnacle cyprids, and *L. helicina*. The density trends of each of these species were different, but periods of highest densities seem to occur during the years with anomalous temperatures (Figure 1.6).

1.3.2 Zooplankton community response to anomalous warm and cold events

Overall, the zooplankton community differed significantly among the four years with anomalously warm or cold temperatures (ANOSIM, global R = 0.33, p < 0.001; Figure 1.7). Furthermore, pairwise tests indicated that the zooplankton communities in all four years were significantly different (ANOSIM, p < 0.001; Table 1.2). Species that primarily contributed to the differences between these groups included *M. pacifica*, *C. marshallae*, *Pseudocalanus* spp., *Acartia longiremis*, and *Neocalanus* spp. (including *N. plumchrus* and *N. flemingeri*) copepodites, euphausiid larvae (egg, nauplii, calyptopis, and furcilia), barnacle nauplii, and *L.*

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helicina (Table 1.2). Heatmaps of these taxa showed variable responses in density between warm and cold years (Figure 1.8). In cool years, the densities of barnacles, euphausiid larvae, *M. pacifica* and *C. marshallae* (2002 only) were highest in May, while highest densities were delayed until August in warm years. Differences between warm and cool years for the remaining species were more equivocal. The densities of *A. longiremis* (C5), *Neocalanus* spp. (C5) and *Pseudocalanus* spp. (C4-5) copepodites were above average in all months of 2008, a cold year. *L. helicina* density was above average in June and August of warm years 2005 and 2016, respectively, and was also above average in May of cold year 2002.

1.3.3 Zooplankton timing in anomalous warm and cold years

Overall, the mean monthly trajectory of the zooplankton community species composition revealed a significant temporal component to community structure (Figure 1.9). Communities sampled in May were consistently located to the left of those sampled in June and so on. Despite the predictable seasonal component, community composition also varied among temperature groups including the four anomalous temperature years (Figure 1.9 right panel). In the anomalously cool years, the May community structure was considerably different from that of the anomalously warm years and the overall distance between the monthly communities in the cool years suggest greater variation in the monthly community compositions due to temperature. The two anomalously warm years showed an accelerated May community structure, in closer proximity to the June community structures of the cool years. Additionally, the differences among the monthly communities were relatively small in the warm years, suggesting that little change in the community structure took place. This is especially evident in 2005, when the monthly communities showed very little change from June through August highlighting the

difference in communities in the two anomalously warm years. Furthermore, the monthly communities were associated along the nMDS 2 axis, indicating a different mechanism was influencing the zooplankton community structure in these anomalously warm months.

Heat maps showed distinct monthly shifts in the density of taxa between cool and warm years, but the shifts were not consistent among the species (Figure 1.8). Euphausiid and barnacle larvae density were highest in May in cool years and highest in August in warm years. The gastropod *L. helicina* density was highest in the warm years, June in 2005 an August in 2016. *C. marshallae* density was highest in May of the cold year 2002 but peak density shifted later in warm years, July in 2005 and June 2016.

1.4 Discussion

Temperature can influence the zooplankton community composition and abundance; however, in Icy Strait the zooplankton community was remarkably consistent until local temperatures were anomalously warm or cool. Temperature drove the rate at which the zooplankton community structure progressed from spring through summer, with slower rates of change occurring over longer periods in cool years. This phenological response to temperature could result in different zooplankton species dominating the prey field that are available to juvenile salmon while they are migrating through Icy Strait.

Water temperatures in the Icy Strait region varied with larger, basin scale events and included two strong warming periods in 2005 (coincident with El Niño) and 2015–16 (marine heatwave and El Niño) and two strong cooling periods in 2002 (PDO negative phase) and 2008 (La Niña). Studies of zooplankton in the nearby GOA corroborate these findings from 21 years of zooplankton sampling in Icy Strait. Batten et al. (2018) found annual variation in the GOA

zooplankton community composition with temperature as a strong driver. While the statistical effect of temperature on the zooplankton community composition within each temperature group cluster was weak, our results show a strong temperature effect on the timing and evolution of the monthly zooplankton communities over time as well as the importance of key taxa to the zooplankton community. We find a compelling difference in zooplankton community composition and abundance of key taxa when comparing between anomalously cool (2002 and 2008) and anomalously warm (2005 and 2016) years.

1.4.1 Zooplankton community response to anomalous warm and cold years

We observed shifts in density of key taxa among the four anomalously cool and warm years. For example, in anomalously warm years we saw more *L. helicina* and *C. marshallae* compared to when water temperatures were anomalously cool. As expected, not all the taxa responded similarly to the anomalous temperatures, as we saw higher densities of *Metridia* spp. and euphausiid larvae in anomalously cool years. In general, high densities of large and small copepodites were observed in cool years compared to warm years, but *M. pacifica* was the only species to show this pattern in both cold years. In 2008, the densities of small copepod species and young stages of *Neocalanus* spp. were particularly high yet, no notable increase in these species was observed in 2002 or the warm years. The increase in density in the cool year may have been driven by the notably cool winters that were occurring during this time (Coyle et al., 2011; Eisner et al., 2017), and underscores the need to include antecedent conditions in future studies (Beamish and Bouillon, 1993; Kohan et al., 2019).

The early copepodites of *C. marshallae* in our study showed an increase in density in warm years. It was interesting to see this increase in the warm years as these large-bodied and

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lipid-rich copepods have been observed in highest density during cold years in the Bering Sea and off the Oregon coast (Coyle et al., 2011; Hunt Jr et al., 2008; Liu and Hopcroft, 2006). For example, the Bering Sea ecosystem experienced warm and cool phases during the early 2000s, with resultant shifts in the zooplankton communities (Coyle et al., 2011, 2008). During the warm phase, *C. marshallae* declined, which decreased the lipid rich prey field utilized by walleye pollock larvae and larger predators. We propose that this opposite response reflects a change in the timing of *C. marshallae* in the water column and discuss further in section 1.4.2.

1.4.2 Zooplankton timing in warm and cold years

Temperature is a key factor in the development of zooplankton both directly through delaying or accelerating metabolism and growth or indirectly through food availability. Our results demonstrated variation in the timing of when key species appear in the zooplankton community, especially in anomalously warm and cool years. This variation was reflected, for example, in the timing of euphausiid larvae in the zooplankton communities of the anomalously warm and cool years. We saw a warm year shift in peak density of euphausiid larvae from May to July/August. *Thysanoess raschii* is the most numerous euphausiid species in Southeast Alaska and the spawning timing of this species coincides with the onset of the spring plankton bloom (Szabo and Batchelder, 2014). However, *T. raschii* can have prolonged spawning throughout the summer if conditions warrant (Pinchuk and Coyle, 2008), and in 2016 we did capture a late summer phytoplankton bloom which provides evidence of conditions supporting late summer spawning and the increase in density of euphausiid larvae in the August 2016 samples (unpublished data, ABL).

A similar shift in timing occurred for the large calanoid copepod *C. marshallae* in warm versus cold years, suggesting a possible delay in or prolonged development in cooler years. In the two anomalously warm years, *C. marshallae* copepodites were in highest density in June and July in contrast to the high density observed in May in the cold year of 2002. Conditions of the upper water column including temperature play a role in the timing of *C. marshallae* growth development (Baier and Napp, 2003, Batten et al., 2018). During early spring, the young stages of *C. marshallae* must feed in the pelagic waters until they satisfactorily meet minimum lipid levels of diapause (Conover, 1988). When the copepodites enter diapause, they drop down in the water column to depths greater than 400 m where they remain until the following spring. The timing of this development is dependent on the water temperatures in early spring; with progression to diapause accelerated when waters are cool and phytoplankton blooms are strong and delayed when waters are warm and food is limited. It has also been suggested that in anomalously warm years, the high temperatures may trigger misleading cues for zooplankton timing which has consequences not only for the zooplankton but on the predators of the zooplankton (Mackas et al., 2007).

The marine environment in the Gulf of Alaska has undergone shifts over the last 20 plus years, and continued changes are expected to continue (Walsh et al., 2018). A better understanding of the response of key taxa in the zooplankton community will aid in evaluating the degree to which climate-driven ecosystem reorganizations will impact the upper-trophic level species that rely on zooplankton as a prey resource. Timing of the zooplankton can affect interpretation of results and is particularly important to studies (including long-term monitoring) that rely on single, fixed sampling periods. For example, had we only sampled in May we would have concluded that euphausiids were not abundant in warm years. Further investigation at the

monthly level will better assess the community response to temperature, and subsequently the

seasonal importance of key taxa to the zooplankton community. Additionally, the biological

consequences of shifts in density peaks is a mismatch in energy transfer from primary producers

to secondary consumers. The next important step is identifying how these data can be better

incorporated into statistical models to improve our ability to anticipate ecosystem change and

inform management and policy (Schindler and Hilborn, 2015).

1.5 Literature Cited

Alvarez-Fernandez, S., Lindeboom, H., Meesters, E., 2012. Temporal changes in plankton of the

    North Sea: community shifts and environmental drivers. Mar. Ecol. Prog. Ser. 462, 21–

    38. doi:10.3354/meps09817

Baier, C.T., Napp, J.M., 2003. Climate-induced variability in *Calanus marshallae* populations. J.

    Plankton Res. 25, 771–782. doi:10.1093/plankt/25.7.771

Beamish, R.J., Bouillon, D.R., 1993. Pacific salmon production trends in relation to climate.

    Can. J. Fish. Aquat. Sci. 50, 1002-1016. doi:10.1139/f93-116

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and

    consequences. Prog. Oceanogr. 60, 245–262. doi:10.1016/j.pocean.2004.02.018

Brodeur, R.D., Ware, D.M., 1992. Long-term variability in zooplankton biomass in the subarctic

    Pacific Ocean. Fish. Oceanogr. 1, 32–38. doi:10.1111/j.1365-2419.1992.tb00023.x

Clark, R.A., Frid, C.L.J., Nicholas, K.R., 2003. Long-term, predation-based control of a central-

    west North Sea zooplankton community. ICES J. Mar. Sci. J. du Cons. 60, 187–197.

    doi:10.1016/S1054-3139(02)00253-9

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to

    environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219. doi:10.3354/meps092205

Clarke, K.R., Gorley, R.N., 2015. PRIMER v7: User Manual. Tutorial. Prim. Plymouth Sci. Res.

    Publ.

Conover, R.J., 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high

    latitudes of the northern hemisphere. Hydrobiologia 167–168, 127–142.

    doi:10.1007/BF00026299

Cooney, R.T., Coyle, K.O., Stockmar, E., Stark, C., 2001. Seasonality in surface-layer net

    zooplankton communities in Prince William Sound, Alaska. Fish. Oceanogr. 10, 97–109.

    doi:10.1046/j.1054-6006.2001.00037.x

Coyle, K.O., Eisner, L.B., Mueter, F.J., Pinchuk, A.I., Janout, M.A., Cieciel, K.D., Farley, E.V.,

    Andrews, A.G., 2011. Climate change in the southeastern Bering Sea: impacts on pollock

    stocks and implications for the oscillating control hypothesis. Fish. Oceanogr. 20, 139–

    156. doi:10.1111/j.1365-2419.2011.00574.x

Coyle, K.O., Paul, A.J., Ziemann, D.A., 1990. Copepod populations during the spring bloom in

    an Alaskan subarctic embayment. J. Plankton Res. 12, 759–797.

    doi:10.1093/plankt/12.4.759

Coyle, K.O., Pinchuk, A.I., Eisner, L.B., Napp, J.M., 2008. Zooplankton species composition,

    abundance and biomass on the eastern Bering Sea shelf during summer: the potential role

    of water-column stability and nutrients in structuring the zooplankton community. Deep

    Sea Res. Part II Top. Stud. Oceanogr. 55, 1775–1791. doi:10.1016/j.dsr2.2008.04.029

Dalpadado, P., Ingvaldsen, R., Hassel, A., 2003. Zooplankton biomass variation in relation to

    climatic conditions in the Barents Sea. Polar Biol. 26, 233–241. doi:10.1007/s00300-002-

    0470-z

DeLorenzo Costa, A., Durbin, E.G., Mayo, C.A., 2006. Variability in the nutritional value of the

    major copepods in Cape Cod Bay (Massachusetts, USA) with implications for right

    whales. Mar. Ecol. 27, 109–123. doi:10.1111/j.1439-0485.2006.00087.x

Eisner, L.B., Pinchuk, A.I., Kimmel, D.G., Mier, K.L., Harpold, C.E., Siddon, E.C., 2017.
Seasonal, interannual, and spatial patterns of community composition over the eastern
Bering Sea shelf in cold years. Part I: zooplankton. ICES J. Mar. Sci. 75, 72–86.
doi:10.1093/icesjms/fsx156

Fergusson, E.A., J. Watson, A. Gray, and J. Murphy. 2018. Annual survey of juvenile salmon,
ecologically-related species, and biophysical factors in the marine waters of southeastern
Alaska, May–August 2016. NPAFC Doc. 1771. 65 pp. National Oceanic and
Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS),
Alaska Fisheries Science Center, Auke Bay Laboratories, Ted Stevens Marine Research
Institute (Available at http://www.npafc.org).

Heintz, R.A., Siddon, E.C., Farley, E.V., Napp, J.M., 2013. Correlation between recruitment and
fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea
under varying climate conditions. Deep. Res. Part II Top. Stud. Oceanogr. 94, 150–156.
doi:10.1016/j.dsr2.2013.04.006

Hunt Jr, G.L., Stabeno, P.J., Strom, S., Napp, J.M., 2008. Patterns of spatial and temporal
variation in the marine ecosystem of the southeastern Bering Sea, with special reference
to the Pribilof Domain. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 1919–1944.
doi:10.1016/j.dsr2.2008.04.032

Kane, J., 2009. A comparison of two zooplankton time series data collected in the Gulf of Maine.
J. Plankton Res. 31, 249–259. doi:10.1093/plankt/fbn119

Kirby, R.R., Beaugrand, G., Lindley, J.A., Richardson, A.J., Edwards, M., Reid, P.C., 2007.
Climate effects and benthic-pelagic coupling in the North Sea. Mar. Ecol. Prog. Ser. 330,
31–38. doi:10.3354/meps330031

Kohan, M.L., Mueter, F.J., Orsi, J.A., McPhee, M. V., 2017. Variation in size, condition, and

    abundance of juvenile chum salmon (*Oncorhynchus keta*) in relation to marine factors in

    Southeast Alaska. Deep-sea Res. Pt. II Top. Stud. Oceanogr. 165, 340-347.

    https://doi.org/10.1016/j.dsr2.2017.09.005

Liu, H., Hopcroft, R.R., 2006. Growth and development of *Metridia pacifica* (Copepoda:

    Calanoida) in the northern Gulf of Alaska. J. Plankton Res. 28, 769–781.

    doi:10.1093/plankt/fbl009

Mackas, D.L., Batten, S., Trudel, M., 2007. Effects on zooplankton of a warmer ocean: recent

    evidence from the Northeast Pacific. Prog. Oceanogr. 75, 223–252.

    doi:10.1016/j.pocean.2007.08.010

Mackas, D.L., Thomson, R.E., Galbraith, M., 2001. Changes in the zooplankton community of

    the British Columbia continental margin, 1985–1999, and their covariation with

    oceanographic conditions. Can. J. Fish. Aquat. Sci. 58, 685–702. doi:10.1139/f01-009

Orsi, J.A., Fergusson, E.A., Sturdevant M.V., Farley, E.V., and Heintz, R.A. 2013. Annual

    survey of juvenile salmon, ecologically-related species, and biophysical factors in the

    marine waters of southeastern Alaska, May–August 2012. (NPAFC Doc. 1485). Auke

    Bay Lab., Alaska Fish. Sci. Cent., Natl. Mar. Fish., NOAA, NMFS, 17109 Point Lena

    Loop Road, Juneau, 99801, USA. 92 pp. (Available at http://www.npafc.org).

Orsi, J.A., Wertheimer, A.C., Sturdevant, M.V, Fergusson, E.A., Mortensen, D.G., Wing, B.L.,

    2004. Juvenile chum salmon consumption of zooplankton in marine waters of

    southeastern Alaska: a bioenergetics approach to implications of hatchery stock

    interactions. Rev. Fish Biol. Fish. 14, 335–359. doi:10.1007/s11160-004-3813-8

Pershing, A.J., Greene, C.H., Jossi, J.W., O'Brien, L., Brodziak, J.K.T., Bailey, B.A., 2005. Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. ICES J. Mar. Sci. J. du Cons. 62, 1511–1523. doi:10.1016/j.icesjms.2005.04.025

Pershing, A.J., Greene, C.H., Planque, B., Fromentin, J.M. (2004). The influence of climate variability on North Atlantic zooplankton populations. Marine Ecosystems and Climate Variation: the North Atlantic—a Comparative Perspective, 59–94. doi:10.1093/acprof:oso/9780198507499.003.0005

Pinchuk, A.I., Coyle, K.O., 2008. Distribution, egg production and growth of euphausiids in the vicinity of the Pribilof Islands, southeastern Bering Sea, August 2004. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 1792–1800. doi:10.1016/j.dsr2.2008.04.030

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013.

Sameoto, D.D., 1984. Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. J. Plankton Res. doi:10.1093/plankt/6.5.767

Schindler, D.E., Hilborn, R., 2015. Prediction, precaution, and policy under global change. Science. 347, 953–954. doi:10.1126/science.1261824

Skjoldal, H.R., Gjøsæter, H., Loeng, H., 1992. The Barents Sea ecosystem in the 1980s: ocean climate, plankton, and capelin growth, in: ICES Marine Science Symposia, pp. 278–290.

Szabo, A.R., Batchelder, H.P., 2014. Late spring and summer patterns of euphausiid reproduction in Southeast Alaska fjord waters. Mar. Ecol. Prog. Ser. 516, 153–161. doi:10.3354/meps11003

Walsh, J.E., Thoman, R.L., Bhatt, U.S., Bieniek, P.A., Brettschneider, B., Brubaker, M., Danielson, S., Lader, R., Fetterer, F., Holderied, K., 2018. The high latitude marine heat wave of 2016 and its impacts on Alaska. Bull. Am. Meteorol. Soc. 99, S39–S43. doi:10.1175/bams-d-17-0105.1

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., 2019. Welcome to the Tidyverse. J. Open Source Softw. 4, 1686.

Wilke, C.O., Wilke, M.C.O., 2019. Package cowplot. Streamlined Plot Theme Plot Annot. 'ggplot2.

Figures
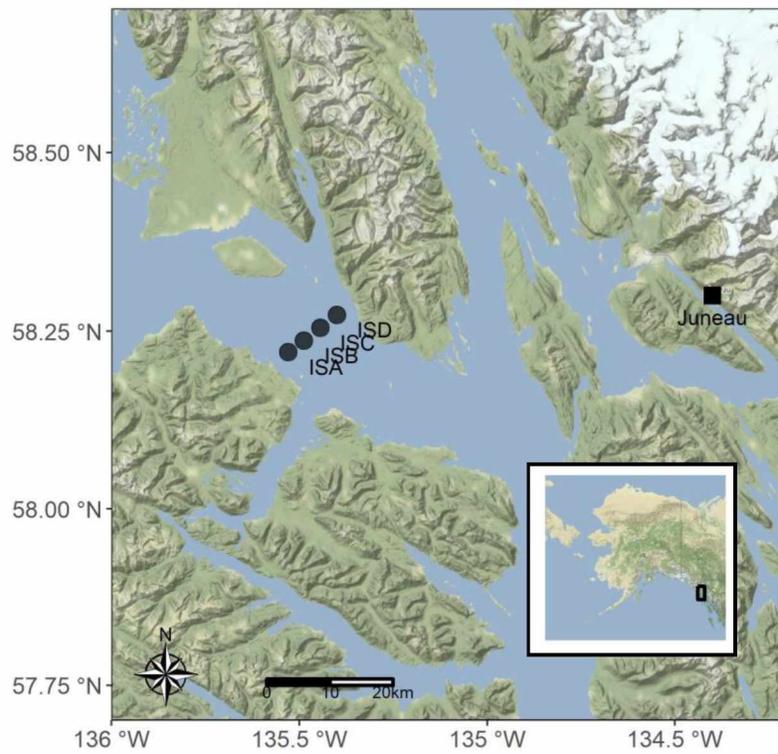
Figure 1.1 Sampling locations in Icy Strait in the northern region of Southeast Alaska from May to August, 1997–2017.
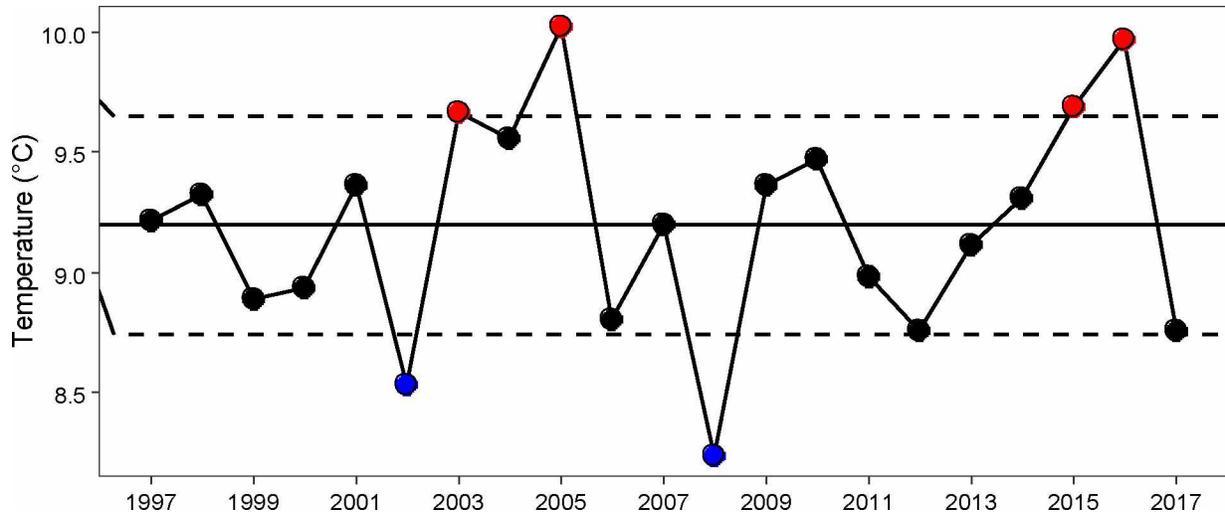
Figure 1.2. Mean annual temperatures (20-m upper water column) in Icy Strait, AK, May to August 1997–2017. Solid line indicates overall mean and dashed line indicates one standard deviation from the mean. Colored data points indicate years with temperatures greater/less than one standard deviation from the mean and include the four years in the anomalous temperature groups.
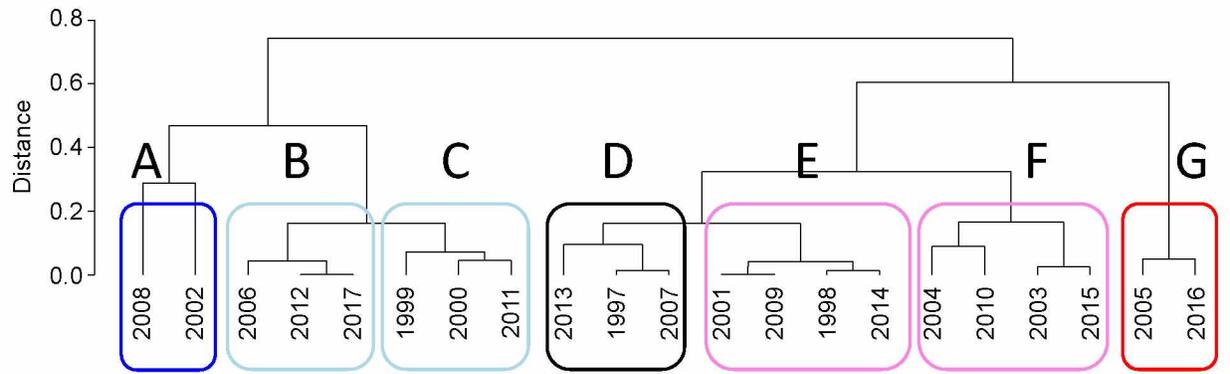
Figure 1.3. Temperature groups identified through hierarchical cluster analysis of mean annual temperature (20-m upper water column) anomalies in Icy Strait, AK, May to August 1997–2017. Colored boxes indicate temperature groups: blue is anomalously cool, light blue is cool, black is average, pink is warm, and red is anomalously warm. Letter assignments correspond with multivariate cluster in Figure 1.5.
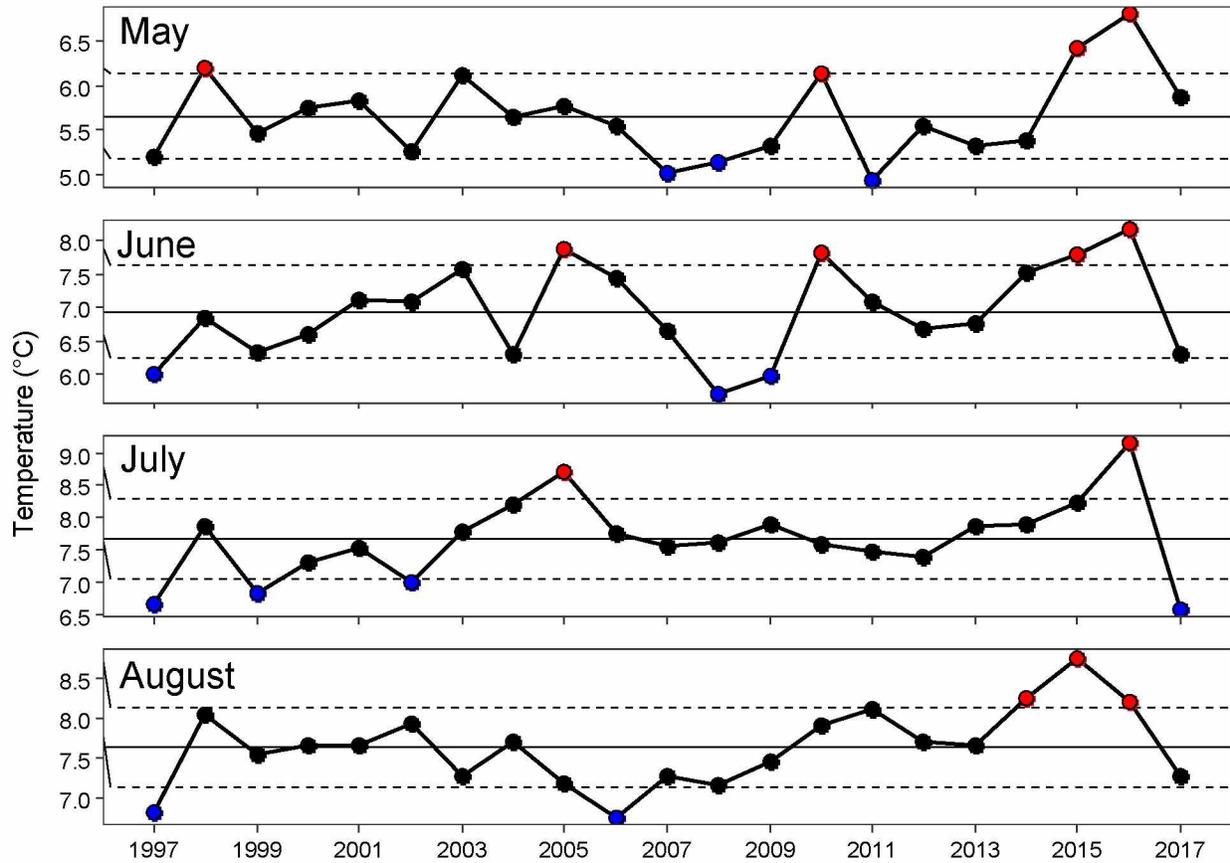
Figure 1.4. Mean monthly temperatures (20-m upper water column) in Icy Strait, AK, May to August 1997–2017. Overall mean (solid line) and one standard deviation from the mean (dashed line) are indicated for each month. Colored data points indicate months with temperatures greater/lesser than one standard deviation from the mean.
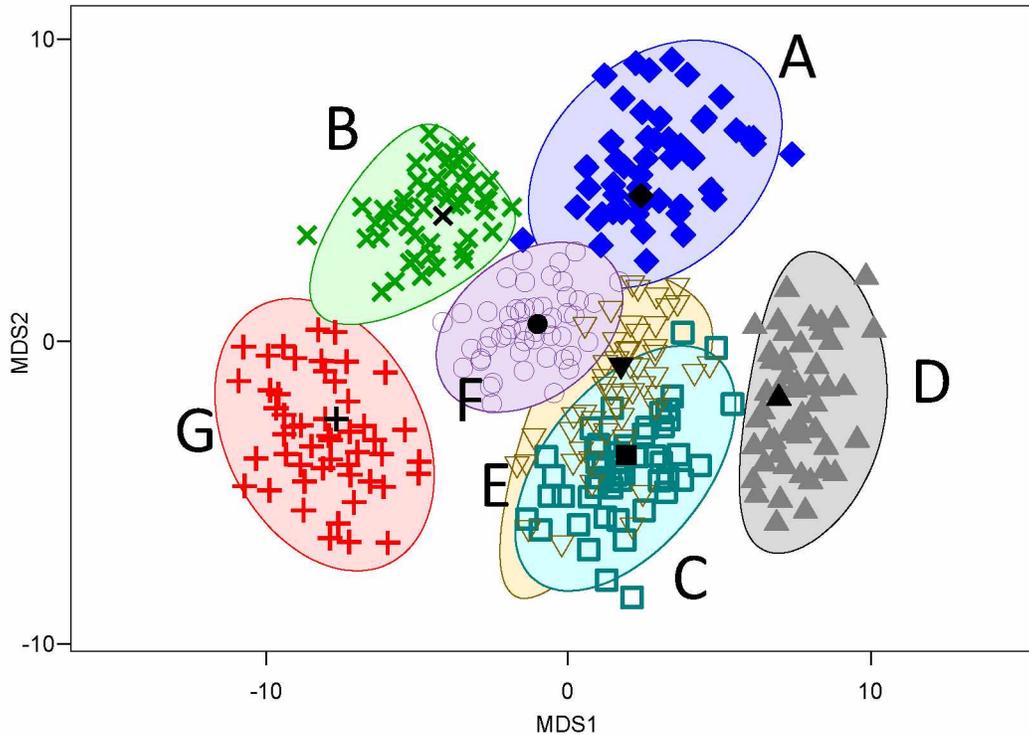
Figure 1.5. Zooplankton community composition multidimensional scaling (MDS) plots (bootstrap averages and nominal 95% regions) by temperature groups (2-D Stress: 0.2). See Figure 1.3 and Table 1.1 for year assignments to temperature groups. The colored points are the individual bootstrap averages of the zooplankton communities within each temperature group, calculated during the bootstrap routine's resampling of the dataset. The black points are the overall bootstrap average of the zooplankton community within each temperature group.
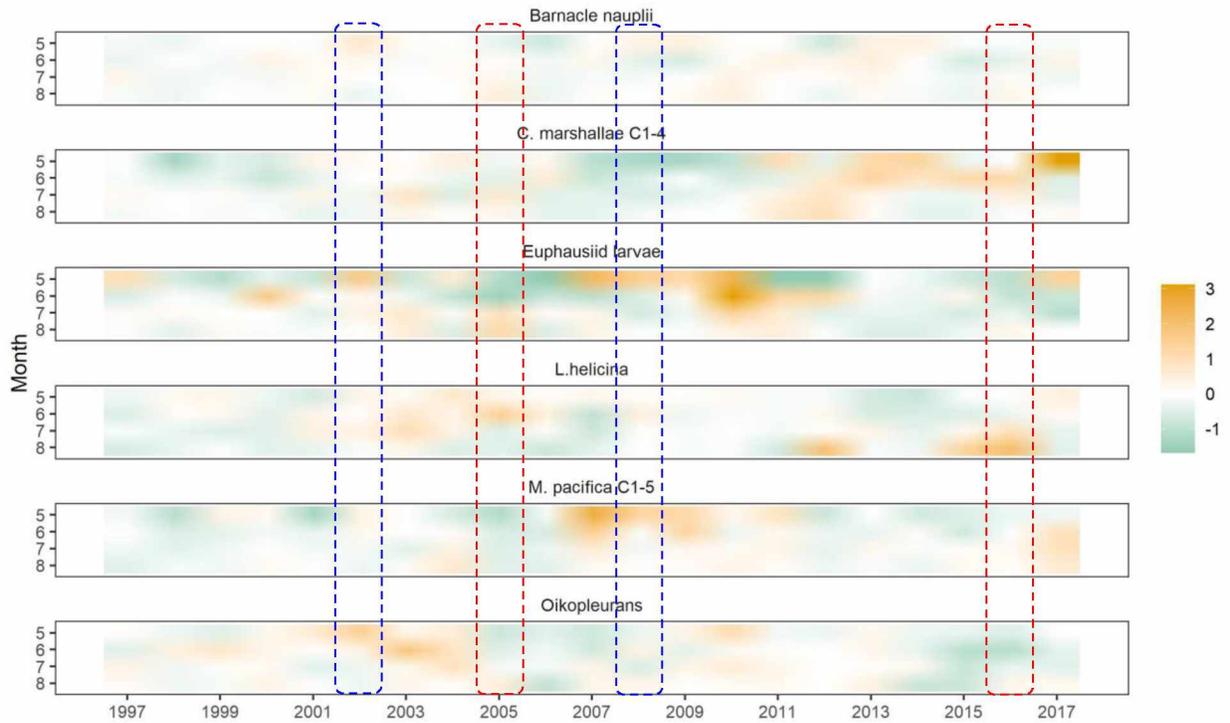
Figure 1.6 Heat maps showing density anomalies of individual zooplankton taxa from Icy Strait, AK, May to August 1997–2017. These taxa were identified in Similarity Percentages (SIMPER) analyses as contributing to the difference in density of the zooplankton communities among the temperature groups. Dashed boxes indicate anomalously warm and cool years. Note that the data are spring and summer samples so are not contiguous between years. Also note that no data were collected in August 2006.
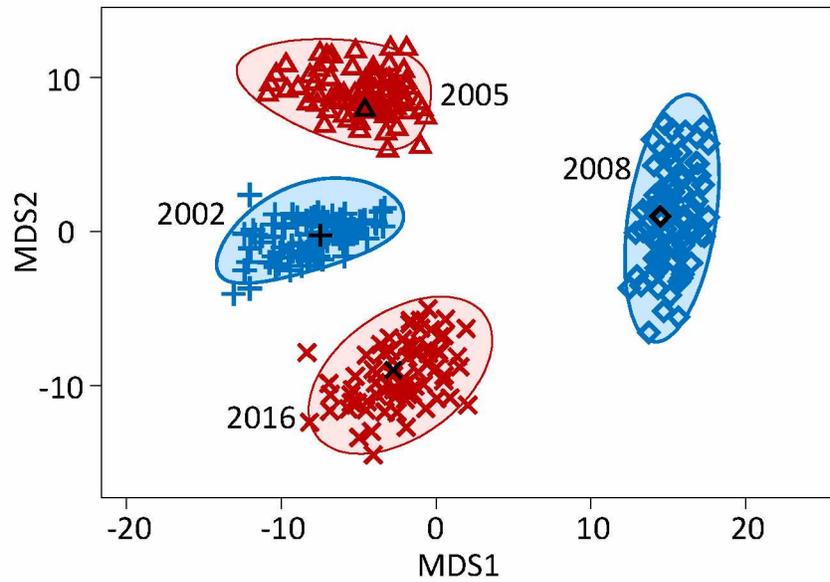
Figure 1.7. Zooplankton community composition MDS plots (bootstrap averages and nominal 95% regions) for anomalous temperature years (2-D Stress: 0.16). The colored points are the individual bootstrap averages of the zooplankton communities within each temperature group, calculated during the bootstrap routine's resampling of the dataset. The black points are the overall bootstrap average of the zooplankton community within each temperature group.
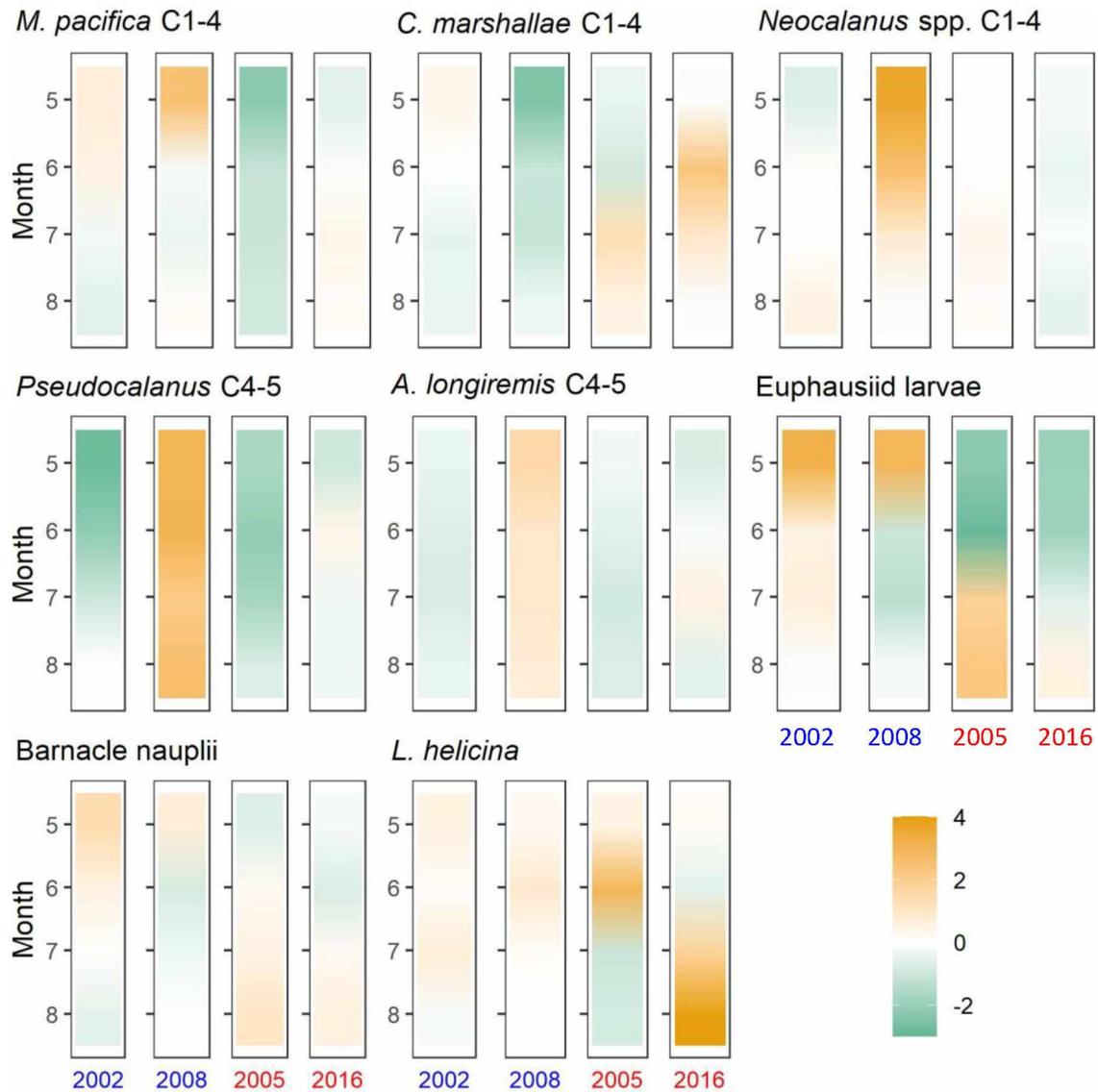
Figure 1.8. Heat maps showing density anomalies (#/m^3) of individual zooplankton taxa from Icy Strait, AK, May to August in 2002, 2005, 2008 and 2016. These taxa were identified in SIMPER analyses as contributing to the difference in density of the zooplankton communities among the four anomalous temperature years.
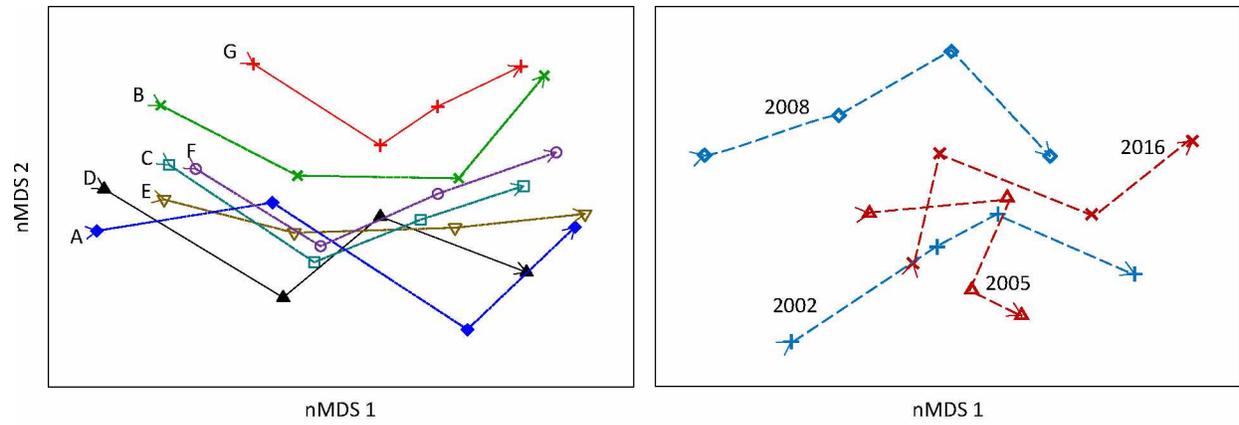
Figure 1.9. Zooplankton mean monthly community composition nMDS plots by temperature group (left panel, 2-D stress: 0.09) and anomalous temperature years (right panel, 2-D stress: 0.12). The lines show the seasonal progression of the zooplankton community structure from May to August for each temperature group or year.

Tables

Table 1.1. Statistical comparison among annual zooplankton communities in Icy Strait, AK grouped by temperature groups using the PRIMER analysis of similarity (ANOSIM) tests. Data presented is the R statistic with a significance level $p < 0.001$ (indicated by asterisks).

Groups	Years included in group	B	C	D	E	F	G
A	2002, 2008	0.05	0.04	0.04	-0.002	0.04	0.13*
B	2006, 2012, 2017		0.05*	0.06*	0.03	0.04	0.06
C	1999, 2000, 2011			0.03	-0.01	0.01	0.03
D	1997, 2007, 2013				0.06*	0.08*	0.07
E	1998, 2001, 2009, 2014					0.03*	0.01
F	2003, 2004, 2010, 2015						0.03
G	2005, 2016						

Table 1.2. Statistical comparison among zooplankton communities in Icy Strait, AK grouped by anomalous temperature groups using the PRIMER analysis of similarity (ANOSIM) tests. Data presented is the R statistic with a significance level p < 0.001 (indicated by asterisks). The average dissimilarity (Avg. diss.), taxa contributing to the dissimilarity, and percent contribution to that dissimilarity (% cont.) from the SIMPER test are presented for the statistically different zooplankton groups.

Group	R statistic	Avg. diss.	Prey	% cont.
Cold vs Warm (by year)				
2002, 2005	0.213*	26.0	*M. pacifica* C1-5	6.1
			C. marshallae C1-4	5.3
			Euphausiid larvae	4.7
			Barnacle nauplii	4.6
2002, 2016	0.189*	28.0	*L. helicina*	6.8
			C. marshallae C1-4	4.7
			M. pacifica C1-5	4.4
			Euphausiid larvae	4.2
2005, 2008	0.504*	32.3	*A. longiremis* C4-5	5.4
			Pseudocalanus spp. C4-5	5.1
			C. marshallae C1-4	5.0
			M. pacifica C1-5	4.8
2008, 2016	0.421*	33.2	*L. helicina*	5.3
			Neocalanus spp. C5	4.7
			Pseudocalanus spp. C4-5	4.6
			C. marshallae C1-4	4.3

Chapter 2: Trophic Responses of Juvenile Pacific Salmon to Warm and Cool Periods Within Inside Marine Waters of Southeast Alaska[2]

Abstract

Marine growth and survival of juvenile Pacific salmon (*Oncorhynchus* spp.) has 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

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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.

2.1 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 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.

2.2 Methods

2.2.1 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 (Figure 2.1).

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 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.

2.2.2 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.

2.2.3 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 minutes. 100 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 minutes. 20 μL of concentrated sulfuric acid was added

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to each well and incubated at 100°C for an additional 10 minutes, 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 minutes. 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, malacostraca, and unidentified digested tissue (Appendix 2.1). 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 2.2). Annual lipid intake values were graphically summarized for each juvenile salmon species.

2.2.4 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 three 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

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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 ($\alpha = 0.05$).

2.3 Results

A total of 441 juvenile pink, chum, sockeye, and coho salmon were examined that were

captured from June to August of 2013–2017 (Table 2.1). Due to budget limitations, only

oceanographic surveys were conducted in August 2017; no fish sampling occurred.

2.3.1 Diets by year and species

Overall, diets of juvenile salmon were significantly different by year (ANOSIM, global R =

0.332, p < 0.001; Figure 2.2) 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 to 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 2.2).

Decapods and fish larvae contributed 19 to 22% and 21 to 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 2.1). The highest frequency of occurrence of empty stomachs was observed for juvenile coho salmon in June of 2017 (4 of 10 fish analyzed).

2.3.2 Diet trends in relation to environmental factors

Environmental parameters varied over the five years examined (Figure 2.3). 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.

2.3.3 Prey quality and diet trends

The overall annual trends in zooplankton lipid content fluctuated concomitantly among taxa (Figure 2.4, Appendix 2.2). 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 euphausiids (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 (Figure 2.5). 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 2.2).

2.4 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 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

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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.

2.4.1 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 (Figure 2.2), 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. Healy et al. 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.

2.4.2 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 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 et al., 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.

2.4.3 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 and Pyper, 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.

2.5 Acknowledgments

2.6 Literature Cited

Beamish, R.J., Mahnken, C., 2001. A critical size and period hypothesis to explain natural

    regulation of salmon abundance and the linkage to climate and climate change. Prog.

    Oceanogr. 49, 423–437. https://doi.org/10.1016/S0079-6611(01)00034-9

Beamish, R.J., Sweeting, R.M. and Neville, C.M., 2004. Improvement of juvenile Pacific salmon

    production in a regional ecosystem after the 1998 climatic regime shift. Trans. Am. Fish.

    Soc. 133(5):1163–1175.

Beauchamp, D.A., Cross, A.D., Armstrong, J.L., Myers, K.W., Moss, J.H., Boldt, J.L.,

    Haldorson, L.J., 2007. Bioenergetic responses by Pacific salmon to climate and

    ecosystem variation. N. Pac. Anadr. Fish Comm. Bull. 4, 257–269.

Bi, H., Peterson, W.T., Lamb, J., Casillas, E., 2011. Copepods and salmon: characterizing the

    spatial distribution of juvenile salmon along the Washington and Oregon coast, USA.

    Fish. Oceanogr. 20, 125–138.

Boldt, J.L., Haldorson, L.J., 2003. Seasonal and geographic variation in juvenile pink salmon

    diets in the northern Gulf of Alaska and Prince William Sound. Trans. Am. Fish. Soc.

    132, 1035–1052.

Bond, N.A., Cronin, M.F., Freeland, H., Mantua, N., 2015. Causes and impacts of the 2014

    warm anomaly in the NE Pacific. Geophys. Res. Lett. 42, 3414–3420.

    https://doi.org/10.1002/2015GL063306

Brodeur, R.D., Daly, E.A., Sturdevant, M.V., Miller, T.W., Moss, J.H., Thiess, M.E., Trudel, M.,

    Weitkamp, L.A., Armstrong, J.L., Norton, E.C., 2007. Regional comparisons of juvenile

    salmon feeding in coastal marine waters off the west coast of North America. Am. Fish.

    Soc. Symp. 57:183–203.

Brodeur, R.D., Francis, R.C. and Pearcy, W.G., 1992. Food consumption of juvenile coho
(*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) on the continental shelf
off Washington and Oregon. Can. J. Fish. Aquat. Sci. 49(8):1670–1685.

Cavole, L., Demko, A., Diner, R., Giddings, A., Koester, I., Pagniello, C., Paulsen, M.L.,
Ramirez-Valdez, A., Schwenck, S., Yen, N., Zill, M., Franks, P., 2016. Biological
impacts of the 2013–2015 warm-water anomaly in the northeast Pacific: winners, losers,
and the future. Oceanography 29. https://doi.org/10.5670/oceanog.2016.32

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure.
Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to
environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219.
https://doi.org/10.3354/meps092205

Clarke, K.R., Gorley, R.N., 2015. PRIMER v7: User Manual. Tutorial. Prim. Plymouth Sci. Res.
Publ. https://updates.primer-e.com/primer7/manuals/user_manual_v7a.pdf

Clarke, K.R., Warwick, R.M., 1998. Quantifying structural redundancy in ecological
communities. Oecologia 113, 278–289. https://doi.org/10.1007/s004420050379

Cooney, R.T., Coyle, K.O., Stockmar, E., Stark, C., 2001. Seasonality in surface-layer net
zooplankton communities in Prince William Sound, Alaska. Fish. Oceanogr. 10, 97–109.
https://doi.org/10.1046/j.1054-6006.2001.00037.x

Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of
stomach contents: application to elasmobranch fishes. Can. J. Fish. Aquat. Sci. 54(3):
726–738. https://doi.org/10.1139/f96-316

Coyle, K.O., Paul, A.J., Ziemann, D.A., 1990. Copepod populations during the spring bloom in

> an Alaskan subarctic embayment. J. Plankton Res. 12, 759–797.

Daly, E.A., Brodeur, R.D., 2015. Warming ocean conditions relate to increased trophic

> requirements of threatened and endangered salmon. PloS One 10(12): p.e0144066.

Danielson, S., Eisner, L., Weingartner, T., Aagaard, K., 2011. Thermal and haline variability

> over the central Bering Sea shelf: Seasonal and interannual perspectives. Cont. Shelf Res.
>
> 31, 539–554. https://doi.org/10.1016/j.csr.2010.12.010

DeLorenzo Costa, A., Durbin, E.G., Mayo, C.A., 2006. Variability in the nutritional value of the

> major copepods in Cape Cod Bay (Massachusetts, USA) with implications for right
>
> whales. Mar. Ecol. 27, 109–123. https://doi.org/10.1111/j.1439-0485.2006.00087.x

Duffy, E.J., Beauchamp, D.A., Sweeting, R.M., Beamish, R.J., Brennan, J.S., 2010. Ontogenetic

> diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound.
>
> Trans. Am. Fish. Soc. 139, 803–823. https://doi.org/10.1577/T08-244.1

Farley, E.V., Murphy, J.M., Adkison, M.D., Eisner, L.B., Helle, J.H., Moss, J.H., Nielsen, J.,

> 2007. Early marine growth in relation to marine-stage survival rates for Alaska sockeye
>
> salmon (*Oncorhynchus nerka*). Fish. Bull., U.S. 105, 121–130.

Fergusson, E.A., Sturdevant, M.V, Orsi, J.A., 2013. Trophic relationships among juvenile

> salmon during a 16-year time series of climate variability in Southeast Alaska. N. Pac.
>
> Anadr. Fish. Comm. Tech. Rep. 9, 112–117.

Fergusson, E.A., Watson, J., Gray, A., Murphy, J.M., 2018. Annual survey of juvenile salmon,

> ecologically-related species, and biophysical factors in the marine waters of Southeastern
>
> Alaska, May–August 2016. N. Pac. Anadr. Fish Comm. Doc. 1771. 65pp.

Gladics, A.J., Suryan, R.M., Brodeur, R.D., Segui, L.M. and Filliger, L.Z., 2014. Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. Mar. Biol. 161(4): 837–851.

Heinl, S.C., Piston, A.W., Jones, E.L., Richards, P., Elliott, B.W., Nichols, J.V, Shaul, L.D., Miller, S.E., Brenner, R., 2017. Review of salmon escapement goals in Southeast Alaska, 2017. Alaska Department of Fish and Game, Division of Sport Fish, and Commercial Fisheries. http://www.adfg.alaska.gov/static/regulations/regprocess/fisheriesboard/pdfs/2017-2018/se/WR7_FMS17-11.pdf

Kohan, M.L., Mueter, F.J., Orsi, J.A., McPhee, M.V., 2017. Variation in size, condition, and abundance of juvenile chum salmon (*Oncorhynchus keta*) in relation to marine factors in Southeast Alaska. Deep-sea Res. Pt. II Top. Stud. Oceanogr. 165, 340-347. https://doi.org/10.1016/j.dsr2.2017.09.005

Ladd, C., Cheng, W., 2016. Gap winds and their effects on regional oceanography Part I: Cross Sound, Alaska. Deep-sea Res. Pt. II Top. Stud. Oceanogr. 132, 41–53. http://dx.doi.org/10.1016/j.dsr2.2015.08.006

Leising, A.W., Schroeder, I.D., Bograd, S.J., Abell, J., Durazo, R., Gaxiola-Castro, G., Bjorkstedt, E.P., Field, J., Sakuma, K., Robertson, R.R., 2015. State of the California Current 2014–15: impacts of the warm-water "BLOB." Calif. Coop. Ocean. Fish. Invest. Rep. 56, 31–68.

Link, J.S., 2002. Ecological considerations in fisheries management: when does it matter? Fisheries 27, 10–17.

Litzow, M.A., Ciannelli, L., Puerta, P., Wettstein, J.J., Rykaczewski, R.R. and Opiekun, M.,
     2018. Non-stationary climate–salmon relationships in the Gulf of Alaska. Proc. Royal
     Soc. B 285(1890): 20181855.

Malick, M.J., Cox, S.P., Mueter, F.J., Peterman, R.M., 2015. Linking phytoplankton phenology
     to salmon productivity along a north–south gradient in the Northeast Pacific Ocean. Can.
     J. Fish. Aquat. Sci. 72, 697–708.

McKinstry, C.A.E., Campbell, R.W., 2018. Seasonal variation of zooplankton abundance and
     community structure in Prince William Sound, Alaska, 2009–2016. Deep-sea Res. Pt. II
     Top. Stud. Oceanogr. 147, 69–78. https://doi.org/10.1016/j.dsr2.2017.08.016

Mueter, F.J, Peterman, R.M., Pyper, B.J., 2002. Opposite effects of ocean temperature on
     survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and
     southern areas. Can. J. Fish. Aquat. Sci. 59, 456–463.

Orsi, J.A., Wertheimer, A.C., Sturdevant, M.V, Fergusson, E.A., Mortensen, D.G., Wing, B.L.,
     2004. Juvenile chum salmon consumption of zooplankton in marine waters of
     southeastern Alaska: a bioenergetics approach to implications of hatchery stock
     interactions. Rev. Fish Biol. Fish. 14, 335–359.

Orsi, J.A., Fergusson, E.A., 2015. Annual Survey of Juvenile Salmon, Ecologically-Related
     Species, and Biophysical Factors in the Marine Waters of Southeastern Alaska, May–
     August 2013. North Pacific Anadromous Fish Commission Doc. 1554. 86pp.

Orsi, J.A., Fergusson, E.A., 2016. Annual Survey of Juvenile Salmon, Ecologically-Related
     Species, and Biophysical Factors in the Marine Waters of Southeastern Alaska, May–
     August 2014. North Pacific Anadromous Fish Commission Doc. 1617. 64pp.

Orsi, J.A., Fergusson, E.A., 2017. Annual Survey of Juvenile Salmon, Ecologically-Related

Species, and Biophysical Factors in the Marine Waters of Southeastern Alaska, May–

August 2015. North Pacific Anadromous Fish Commission Doc. 1739. 71pp.

Pershing, A.J., Greene, C.H., Jossi, J.W., O'Brien, L., Brodziak, J.K.T., Bailey, B.A., 2005.

Interdecadal variability in the Gulf of Maine zooplankton community, with potential

impacts on fish recruitment. ICES J. Mar. Sci. J. du Cons. 62, 1511–1523.

https://doi.org/10.1016/j.icesjms.2005.04.025

Peterson, W.T., Bond, N., Robert, M., 2016. The Blob (part three): going, going, gone? PICES

Press 24(1), 46–48. https://meetings.pices.int/publications/pices-

press/volume24/issue1/PPJan2016.pdf

Peterson, W.T., Fisher, J.L., Peterson, J.O., Morgan, C.A., Burke, B.J., Fresh, K.L., 2014.

Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform

fisheries management in the California Current. Oceanography 27, 80–89.

Peterson, W.T., Schwing, F.B., 2003. A new climate regime in northeast Pacific ecosystems.

Geophys. Res. Lett. 30, 1–4. https://doi.org/10.1029/2003GL017528

Pinchuk, A.I., Coyle, K.O., Hopcroft, R.R., 2008. Climate-related variability in abundance and

reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003. Progr.

Oceanogr. 77 (2–3), 203–216.

Preikshot, D., Beamish, R.J., Sweeting, R.M., Preikshot, D., Beamish, R.J., Sweeting, R.M. and

Doc, N.P.A.F.C., 2010. Changes in the diet composition of juvenile sockeye salmon in

the Strait of Georgia from the 1960s to the present. N. Pac. Anadr. Fish Comm. Doc.,

1285, 438–449.

Saito, T., Shimizu, I., Seki, J., Nagasawa, K., 2009. Relationship between zooplankton abundance and the early marine life history of juvenile chum salmon *Oncorhynchus keta* in eastern Hokkaido, Japan. Fish. Sci. 75, 303–316.

Sameoto, D.D., 1984. Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. J. Plankton Res. 6(5), 767–792. https://doi.org/10.1093/plankt/6.5.767

Savage, K. 2017. Alaska and British Columbia large whale unusual mortality event summary report. NOAA Fish Report, Juneau, pp. 42 https://repository.library.noaa.gov/view/noaa/17715/noaa_17715_DS1.pdf.

Schindler, D.E. and Hilborn, R., 2015. Prediction, precaution, and policy under global change. Science 347(6225), 953–954.

Sturdevant, M.V., Orsi, J.A., Fergusson, E.A., 2012. Diets and trophic linkages of epipelagic fish predators in coastal Southeast Alaska during a period of warm and cold climate years, 1997–2011. Mar. Coast. Fish. 4. https://doi.org/10.1080/19425120.2012.694838

Van Handel, E., 1985. Rapid determination of total lipids in mosquitoes. J. Am. Mosq. Control Assoc. 1, 302–304.

Walsh, J.E., Thoman, R.L., Bhatt, U.S., Bieniek, P.A., Brettschneider, B., Brubaker, M., Danielson, S., Lader, R., Fetterer, F., Holderied, K. and Iken, K., 2018. The high latitude marine heat wave of 2016 and its impacts on Alaska. Bull. Am. Meteorol. Soc. 99(1), S39–S43.

Weitkamp, L.A., Sturdevant, M. V., 2008. Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish. Oceanogr. 17, 380–395. https://doi.org/10.1111/j.1365-2419.2008.00485.x

Whitney, F.A., 2015. Anomalous winter winds decrease 2014 transition zone productivity in the

    NE Pacific. Geophys. Res. Lett. 42, 428–431.

Zavolokin, A.V., Zavolokina, E.A., Khokhlov, Y.N., 2009. Changes in size and growth of

    Anadyr chum salmon (*Oncorhynchus keta*) from 1962–2007. N. Pac. Anadr. Fish Comm.

    Bull., 5, 157–163.

Figures
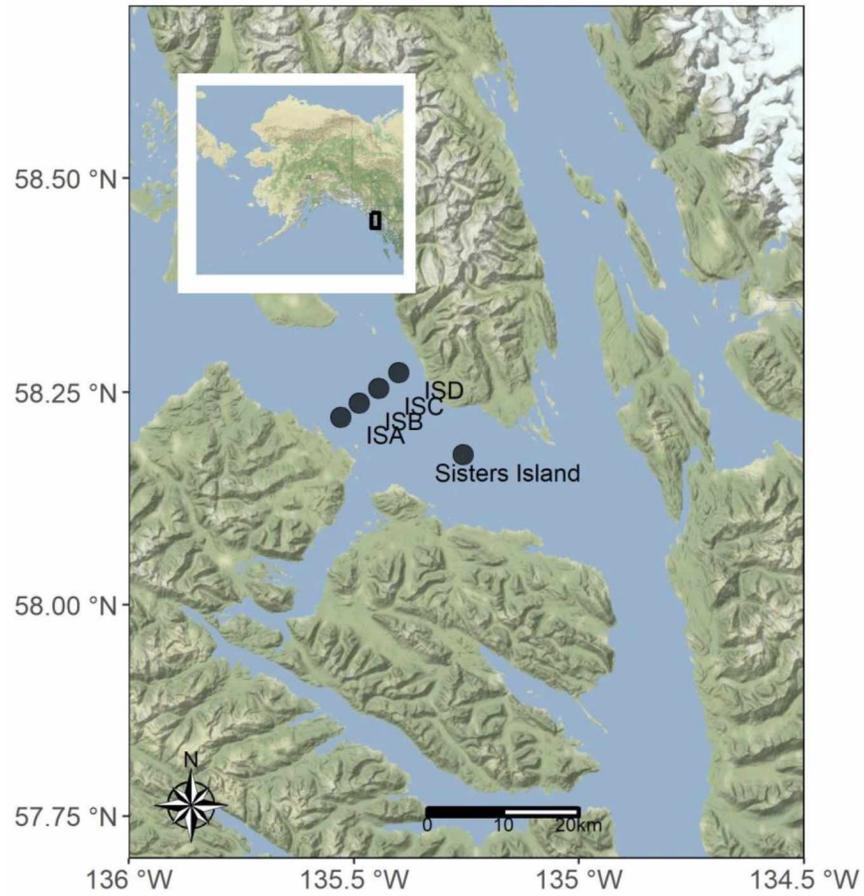
Figure 2.1. Sampling and weather station locations in the strait habitat of the northern region of Southeast Alaska from June to August 2013–2017. The Sisters Islands weather station is run by the National Data Buoy Center.
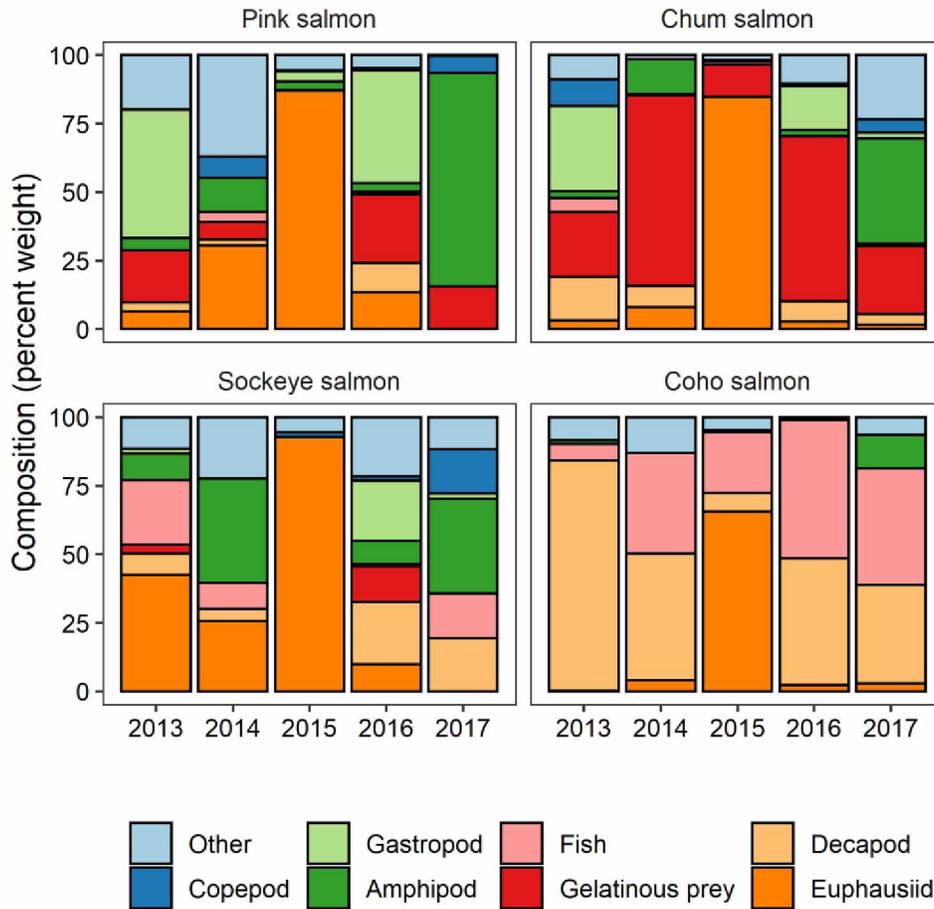
Figure 2.2. Diet composition by major prey taxa of juvenile pink, chum, sockeye, and coho salmon captured in surface marine waters of northern Southeast Alaska, 2013 to 2017. Annual values are averaged over June, July, and August.
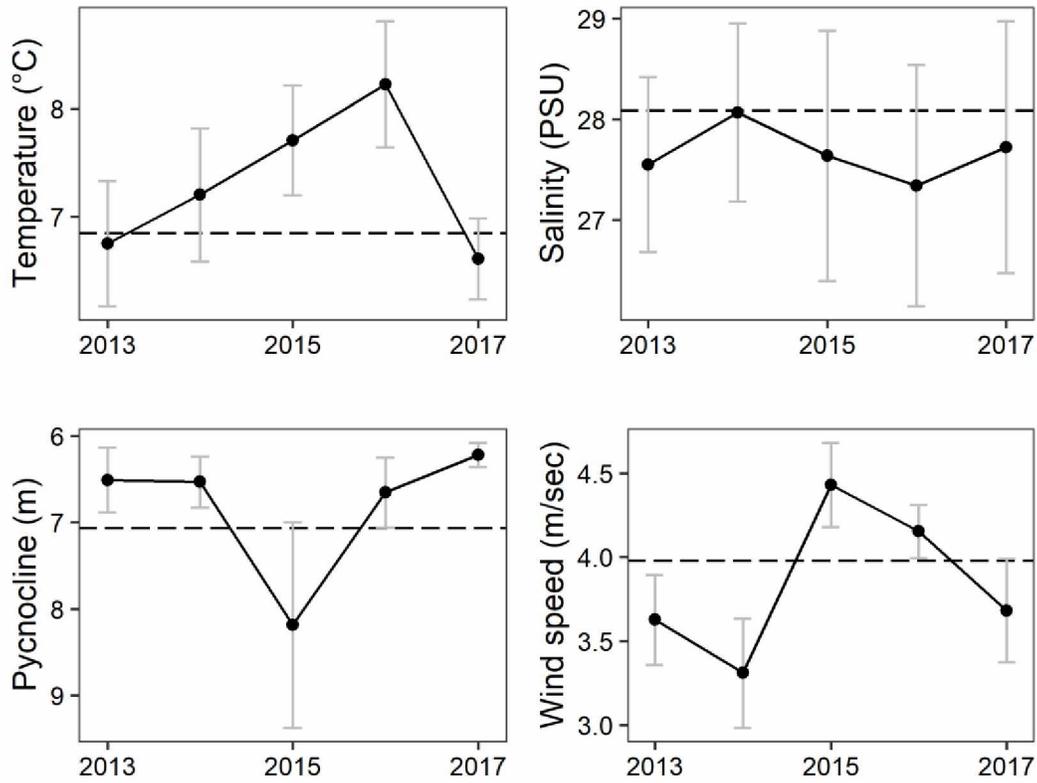
Figure 2.3. Annual mean (+/- SE) water temperature (°C, average water column), salinity (PSU, average above pycnocline), pycnocline depth (m), and wind speed (m/s) in Icy Strait, Alaska, from May to August 2013–2017. Long-term average from 1997–2017 (see Appendix 2.3) noted by dashed line.
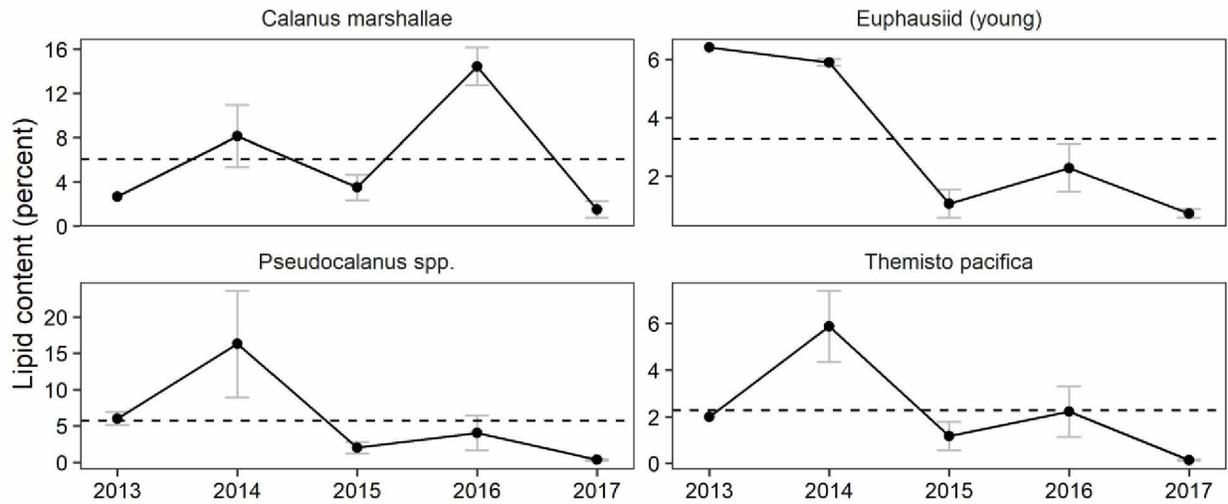
Figure 2.4. Average (± SE) annual lipid content (%) of select zooplankton taxa collected in Icy Strait, AK, from May to August 2013–2017. Average from 2013 to 2017 is indicated by the dashed line. The 2013 values for *Calanus marshallae*, euphausiid (young), and *Themisto pacifica* are point estimates as there was only one sample of each species collected in that year.
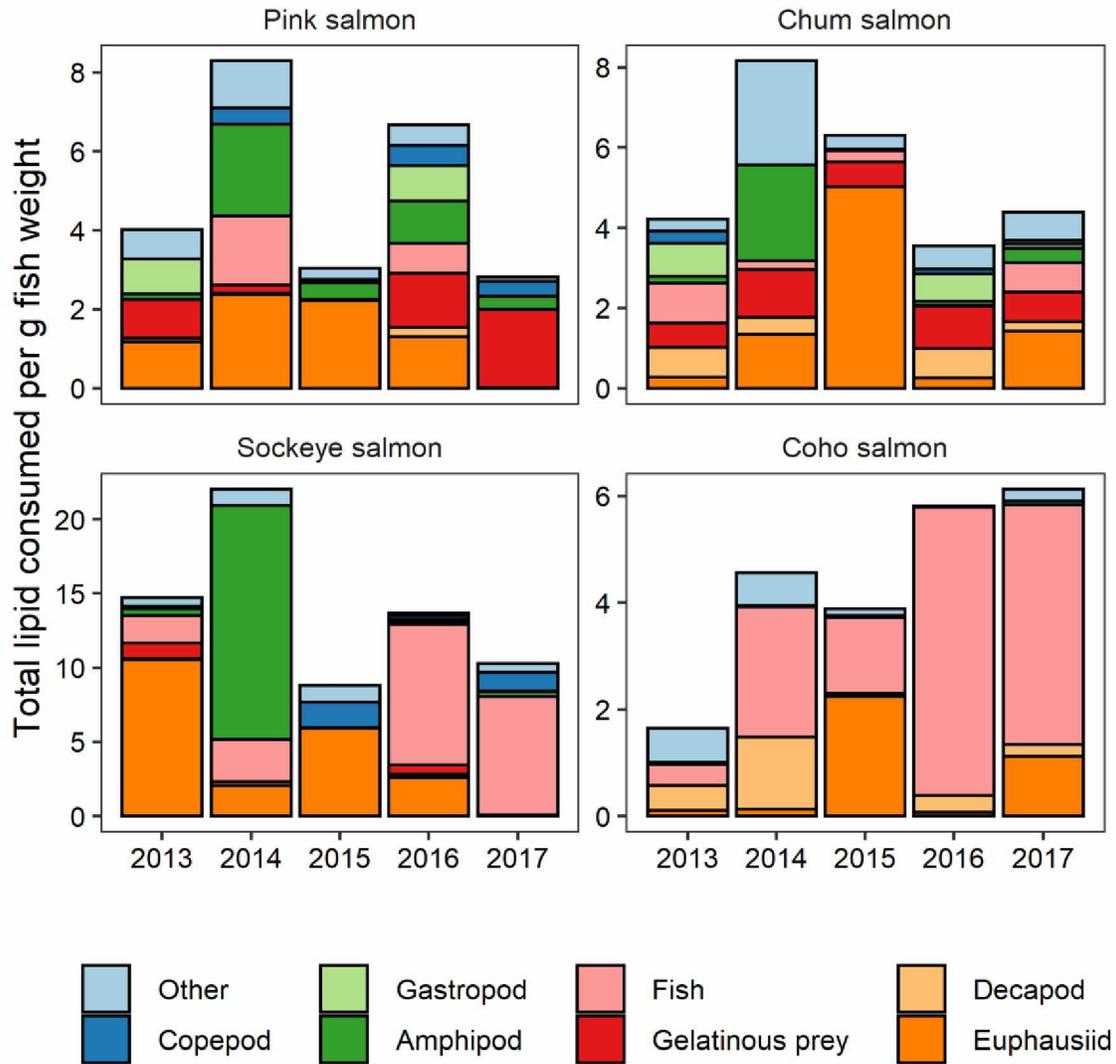
Figure 2.5. Total lipid (g) consumed by juvenile pink, chum, sockeye, and coho salmon standardized by fish wet weight (g). Fish were captured by rope trawl at the surface in the marine waters of northern Southeast Alaska from 2013 to 2017.

Tables

Table 2.1. 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 2.1 for details of the Other category.

				Prey categories							
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	-	-	-	-	-	-	-	-	-	-

Table 2.1 continued

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	-	-	-	-	-	-	-	-	-	-

Table 2.2. Statistical comparison among juvenile pink, chum, sockeye, and coho salmon diets in Icy Strait, AK, 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			

Appendices

Appendix 2.1. Percent composition of prey taxa pooled in the "other" category from diets of juvenile pink, chum, sockeye, and coho salmon in Icy Strait, AK from 2013 to 2017. See Table 2.1 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											
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 2.2. 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.

Year	Month	n	value	sd
			Lipid content	

Copepods

Acartia longiremis **C5-C6F**

Year	Month	n	value	sd
2013	August	2	2.9	0.6
2014	May	1	3.5	
	August	1	11.4	

Acartia longiremis **C5**

Year	Month	n	value	sd
2015	June	1	0.003	
2016	July	1	13.1	

Acartia longiremis **C6F**

Year	Month	n	value	sd
2015	July	3	0.1	0.1
2016	May	1	0.3	

Calanus marshallae **C4**

Year	Month	n	value	sd
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**

Year	Month	n	value	sd
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**

Year	Month	n	value	sd
2015	July	1	0.9	
	August	1	0.2	
2016	June	1	17.5	

Calanus pacificus **C5**

Year	Month	n	value	sd
2016	May	1	4.9	

Centropages abdominalis **C5-C6F**

Year	Month	n	value	sd
2013	July	1	0.2	

Centropages abdominalis **C6F**

Year	Month	n	value	sd
2015	June	4	0.2	0.1

Metridia okhotensis **C5**

Year	Month	n	value	sd
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 **(10–15mm)**

2014	July	1	1.9	

Thysanoessa raschii **(10–15mm)**

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 (15–20mm)

2016	June	3	3.9	4.9

Thysanoessa spinifera (10–15mm)

2015	May	1	0.7	
2016	July	3	0.8	0.8
	August	2	3.9	1.1

Thysanoessa sp. (<10mm)

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 megalope

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 **(5–20mm)**

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
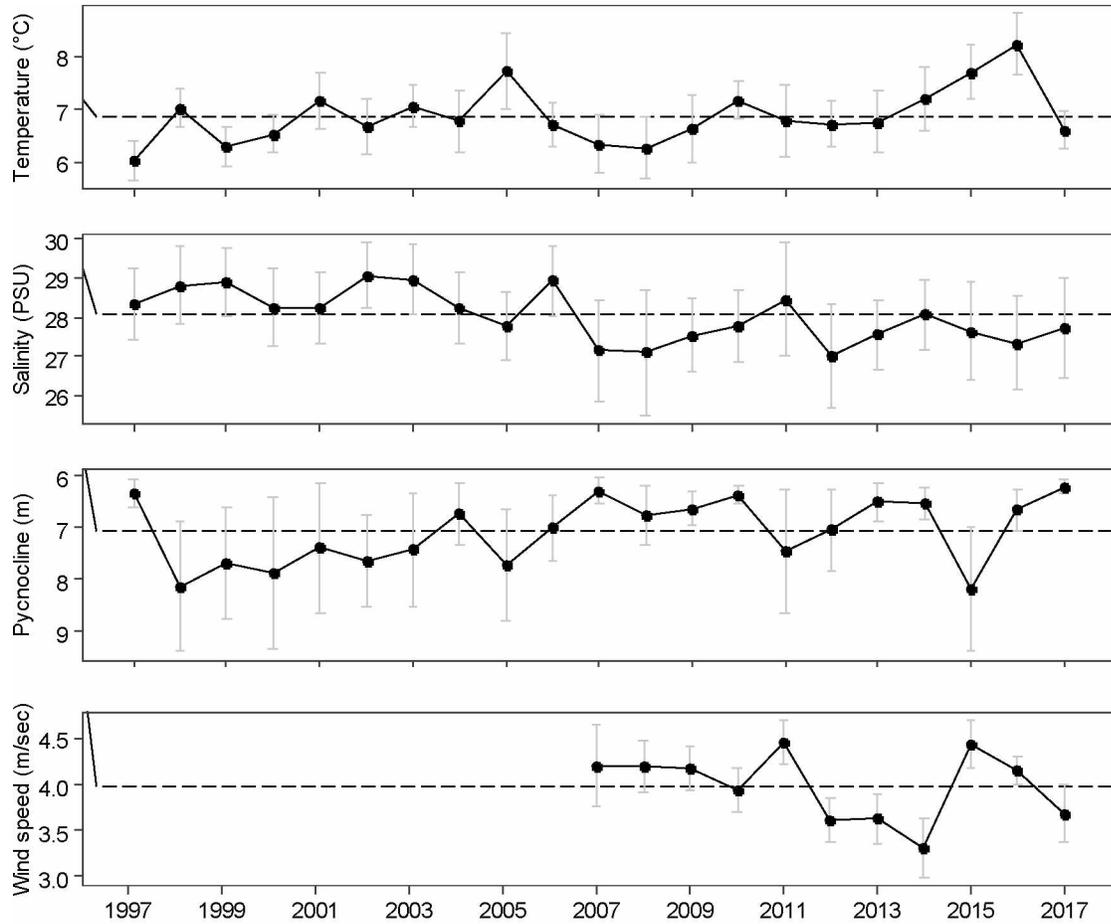
Appendix 2.3. Annual mean (+/- SE) water temperature (°C, average water column), salinity (PSU, average above pycnocline), pycnocline depth (m), and wind speed (m/sec) in Icy Strait, Alaska from May to August 1997–2017. Time series average indicated by dashed line. Note that wind speed data were not available prior to 2007.

General Conclusions

Juvenile salmon are visual and opportunistic predators, and this thesis describes how these salmon selectively feed of the smaller size fraction of macrozooplankton in the upper water column. Juvenile pink, chum, and sockeye salmon consume similar prey during their early marine residency in Icy Strait, AK, consisting of a range of zooplankton including copepods, amphipods, oikopleurans, and euphausiid larvae, while juvenile coho salmon feed mainly on crab and fish larvae. However, these diets varied across years. For example, gastropods comprised a fair proportion of the diets in 2013 and 2016, amphipods composed >65% of the diets in 2017, and the diets of all four species converged to feeding almost exclusively on euphausiids in 2015. The striking increase in euphausiids in the diets appeared to be influenced by local factors of temperature, salinity, and wind speed as opposed to larger climate-scale measures such as ENSO and the PDO.

The inside waters of Icy Strait are buffered from larger basin-scale forces that we see influencing the GOA or other large marine ecosystems, and this buffering was evident by the lack of a reorganization in the zooplankton community and upper trophic levels during the recent warming events. However, increased atmospheric warming may influence localized freshwater discharge and precipitation which could decrease salinity along the shoreline, altering the distribution and structure of the zooplankton community and juvenile salmon prey field.

Long-term monitoring is essential in understanding how factors are influencing the zooplankton community and trophic relationships. The Southeast Coastal Monitoring project provides scientists with an invaluable long-term dataset from more than two decades of annual summer ecosystem sampling and we have only begun to scratch the surface of this complex

dataset. Furthermore, the relationships between environmental factors, the zooplankton community, and juvenile salmon trophic response are likely to become even less predictable as the frequency of anomalously warm conditions in the Gulf of Alaska increase. Consequently, continued ecosystem monitoring is critical to better understanding the importance of local and regional factors that ultimately lead to the growth and survival of juvenile salmon in Southeast Alaska.