VARIATION IN ABUNDANCE AND PHYSIOLOGICAL STATUS OF JUVENILE CHUM SALMON *(ONCORHYNCHUS KETA)* IN RELATION TO MARINE FACTORS IN SOUTHEAST ALASKA

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A

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Abstract

Little is known about the mechanisms influencing the critical early life stages of juvenile chum salmon (*Oncorhynchus keta*) from coastal to offshore marine waters. There is mounting evidence to suggest that fluctuations in early marine conditions affect juvenile salmon physiological status and year class strength. We investigated relationships of a suite of marine factors at local, regional, and basin scales to the physiological status and abundance of juvenile chum salmon in northern Southeast Alaska (SEAK) from 1997-2013. Correlation analyses were used to identify potential mechanisms influencing year class strength. Marine factors at the local scale were correlated to the observed physiological status of juvenile chum salmon: average June/July wind speed was negatively correlated to weight-at-length residuals, sea surface temperatures in July were positively correlated with length, and the June mixed-layer depth was positively correlated to the energy density of juvenile chum salmon in July. Marine factors at the regional scale influenced juvenile chum salmon abundance: freshwater discharge was positively correlated whereas upwelling was negatively correlated with abundance, linking high abundance to characteristics of strong Aleutian Low (AL) climatic conditions.

Comparisons of juvenile chum salmon physiological status were also made between: 1) SEAK habitats (Icy Strait and the Eastern Gulf of Alaska, EGOA), 2) stock groups (hatchery and wild), and 3) years 2010 and 2011 possible mechanisms influencing productivity of chum salmon. Between habitats, length of juvenile chum salmon did not differ. However, both weight-at-length residuals and energy density values were significantly higher in the EGOA, irrespective of year, indicating juvenile salmon allocate energy to somatic growth in Icy Strait, while the EGOA may serve as a habitat for juvenile chum salmon to store energy as lipids. Between chum salmon stocks, wild stocks were shorter and had higher weight-at-length residuals than hatchery stocks. Between years, the 2010 ocean year was associated with a strong AL that coincided with higher physiological status of juvenile chum salmon and relatively higher returning adult commercial harvests and ocean survival of hatchery fish compared to the 2011 ocean year. Our results suggest differences in juvenile chum salmon physiological status in 2010 and 2011 coincided with positive and negative anomalies of the coupled ocean-atmosphere system, which were linked to previous winter environmental conditions, and have the potential to be used as a predictive salmon management tool to forecast year class strength in SEAK.

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Chapter 1: Introduction

1.1 Background

Chum salmon (*Oncorhynchus keta*) are an important resource in Southeast Alaska (SEAK). Between the years 2001 and 2010, the total ex-vessel value of commercially harvested chum salmon in SEAK exceeded that of other salmon species, averaging $32 million a year (Piston and Heinl, 2011). In addition to their commercial value, chum salmon have a significant place in the recreational and cultural aspects of SEAK communities. The total abundance of wild chum salmon returning to more than 1,200 streams in SEAK is unknown and only recently have escapement goal ranges been established to conserve and manage wild stocks (Heinl, 2005). Annual commercial harvest of chum salmon in SEAK has increased since the early 1990s due to increased hatchery production, which accounted for approximately 70% of the region's commercial catch from 2001 to 2010 (Piston and Heinl, 2011). Brood year survival from hatcheries is highly variable and the mechanisms affecting marine survival of chum salmon are poorly understood (Heard and Wertheimer, 2012). Examining the mechanisms affecting the early life stages of juvenile chum salmon can increase our understanding of the effects of environmental change on chum salmon population dynamics and improve forecasts of chum salmon returns in the future.

Better understanding of the relationship between ocean-driven processes and early marine survival is needed to be able to identify how environmental conditions influence Pacific salmon (*Oncorhynchus* spp.) production (Beamish et al., 2004; Briscoe et al., 2005). The early marine stage is thought to be a 'critical period' (Hjort, 1914) where Pacific salmon experience fast growth (Healey, 1982b; Mortensen et al., 2000) and high mortality (Parker, 1962; Wertheimer and Thrower, 2007) compared to overall marine residency, but little is known about the mechanisms affecting the critical early life stages in nearshore and coastal marine environments and how these mechanisms influence survival. The quality of rearing conditions during this stage in estuarine and nearshore habitats determines the growth and mortality experienced by juvenile salmon. Fluctuation in marine conditions, such as physical ocean properties, prey availability, prey quality, and density-dependent factors in the early marine environment may affect the juvenile salmon physical condition and year class strength (Beauchamp et al., 2004; Moss et al., 2009).

1.2 Juvenile chum salmon early life history in SEAK

Due to the limited time chum salmon spend in freshwater, the early marine environment plays an especially important role in their recruitment (Healey, 1982b). Chum salmon embryos incubate for up to 4 months in freshwater streams and after hatching the fry migrate directly downstream to estuarine habitats (Salo, 1991). Although chum salmon eggs and alevins are large compared to those of other salmon, fry arriving in brackish waters in early spring to undergo smoltification are small and vulnerable to predation. After smoltification, a rapid summer growth period allows chum salmon to follow prey resources in marine environments away from estuaries (Simenstad and Salo, 1982). Juvenile chum salmon in northern SEAK migrate predominantly westward along a seaward corridor from the inshore waters in Icy Strait out to Cross Sound and further offshore into the Gulf of Alaska (GOA), transitioning from strait to coastal habitats extending off the outer coast continental shelf of the GOA (Orsi et al., 2000). Shifts in environmental influences and changing prey fields between habitats can lead to food limitation constraining juvenile salmon growth and energy allocation (Cross et al., 2009).

1.2.1 Growth and survival of juvenile chum salmon

During the initial emigration to estuarine and marine environments, juvenile salmon experience high levels of mortality (Parker, 1962; Pearcy, 1992; Wertheimer and Thrower, 2007). Food limitation and predation, factors that contribute to mortality, have been hypothesized to affect salmon abundance in two stages. The first stage may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker, 1968). The size of smolts at ocean entry influences the degree of mortality in certain salmon stocks (Parker, 1971; Henderson and Cass, 1991). In their first summer at sea, it is critical for juvenile salmon to find habitats that provide enough food to support the allocation of energy to somatic growth and lipid storage in order to prepare for the first winter at sea. Nearshore marine environments have productive prey communities that provide favorable foraging conditions and valuable nursery habitats providing juvenile salmon with the opportunity to build energy stores (Healey, 1982a; Simenstad and Salo, 1982). The nearshore habitat for juvenile salmon is also an area of high potential predation, thus emphasizing the need for faster growth to be capable of seaward migration (Willette et al., 2001).

Faster growing individuals avoid being prey to gape-limited predators (Sogard, 1997). Consequently, juvenile salmon that grow faster are associated with higher marine survival (Ruggerone et al., 2003; Ruggerone and Goetz, 2004)

When juvenile salmon enter their first fall and winter at sea, a second stage of early marine mortality is thought to occur. Mortality at this stage is likely due to starvation or the increased risk of predation when foraging for prey. Therefore, survival is hypothesized to be dependent upon sufficient energy reserves stored during the first summer at sea (Beamish and Mahnken, 2001). As a result of these two critical stages of mortality, survival trends for juvenile salmon are dependent upon growth and energy stores (Beamish and Mahnken, 2001; Farley et al., 2007). In summary, larger individuals with better condition likely have a higher probability of survival, emphasizing the importance of growth during the first summer at sea.

1.2.2 Predation

Predation is thought to be a main cause of mortality for juvenile chum salmon during their initial residency in estuarine and marine environments. Because predation events are coupled with prey size, if juvenile salmon undergo rapid early marine growth they may be less vulnerable to predators. However, the relationship between early ocean growth or smolt size and marine survival is not always positive; years with good growth but poor survival could be due to particularly high rates of predation (Mortensen et al., 2000). Although many studies have found that high growth rates enable juvenile salmon to avoid predation, other factors that make juvenile salmon more susceptible to predation might also be important. Foraging behavior and location of nearshore rearing habitat could affect the exposure level to predators (Clark and Levy, 1988). Additionally, ocean conditions influence the suite of predators and alternate prey availability influencing the predation rate on juvenile salmon (Emmett and Brodeur, 2000). Many predators including larger salmon (Orsi et al., 2000; Parker, 1971), spiny dogfish (*Squalus acanthias,* Orsi et al., 2013), sablefish (*Anoplopoma fimbria*, Sturdevant et al. 2009*),* sculpin, birds and marine mammals (Emmett, 1997), feed on juvenile salmon when residing in estuaries and nearshore environments (Parker, 1968) as well as during their seaward summer migration out into the GOA (Sturdevant et al., 2012).

1.2.3 Density-dependent factors

Chum salmon production by hatcheries is significant in SEAK, as well as in other Pacific Rim regions. This hatchery production has been implicated in causing adverse competitive interactions with wild stocks (Ruggerone et al., 2012). The large numbers of hatchery-reared juvenile chum salmon in northern SEAK are presumably also constrained by environmental factors and prey availability. The carrying capacity of localized areas, such as northern SEAK, may be approached when high numbers of hatchery chum salmon are produced. This could lead to competition with wild juvenile chum and pink salmon (*O. gorbuscha*) for limited food supplies. For example, in the Sea of Japan marine survival of chum salmon is negatively correlated with the number of hatchery juvenile chum salmon released and their abundance is negatively related to abundance of prey organisms (Fukuwaka and Suzuki, 2000), indicating food limitation. Spatial and temporal overlap has been reported between hatchery releases of chum salmon and the outmigration of wild populations in the estuarine habitat around release sites (Reese et al., 2009). In a study of hatchery-wild interactions, Sturdevant et al. (2010) found that wild populations were smaller and had lower energy content (a measurement of physiological condition) in the estuarine habitat. As stocks moved offshore, the energy content of hatchery and wild salmon converged indicating no density dependent effects even though hatchery chum salmon were 20 times more abundant than wild chum salmon in the estuary.

Another potential factor contributing to density dependent dynamics is interspecific competition between juvenile pink and chum salmon. Unlike chum salmon, pink salmon harvest in SEAK is almost entirely (>97%) from wild stocks (McNair, 2002). Pink salmon are also the most abundant species caught in SEAK with chum salmon having the second highest harvest (Eggers et al., 2005). Chum and pink salmon have similar life histories during early marine life. Both species enter the estuarine habitat of the marine environment as fry after minimal feeding and rear in nearshore waters for weeks to months before migrating offshore (Healey, 1980; Heard, 1991). Studies in Japan investigating interspecific density-dependent factors have concluded that there is competition for habitat and prey between juvenile chum and pink salmon during early ocean life (Salo, 1991; Nagata et al., 2007).

Prey species composition of juvenile pink and chum salmon has been found to be similar, both in inside waters and in the outer coast waters of SEAK (Landingham et al., 1998). Diet overlap between pink and chum salmon decreases with increasing density of pink salmon because juvenile chum salmon shift to forage on less nutritious prey items in years of high pink salmon abundance (Birman, 1969; Salo, 1991). Therefore, overlapping distribution patterns of pink and chum salmon in a food-limited environment could result in density-dependent limitations on growth (Azumaya and Ishida, 2000).

1.3 Marine environment of SEAK

Spatio-temporal patterns of freshwater runoff, ocean temperature, and other oceanographic features may influence the distribution and trophic interactions of juvenile chum salmon in SEAK. The availability and energetic quality of prey and the metabolic response to environmental conditions are factors that affect the condition of juvenile salmon (Farley et al., 2007). Indirectly, climate variability alters the distribution and abundance of prey communities and therefore habitat selection and migration pathways of juvenile salmon from estuaries to offshore environments (Armstrong et al., 2005). Directly, thermal conditions can constrain growth by influencing metabolic responses and subsequent allocation of energy in juvenile salmon (Heintz, 2009). The mechanisms that determine the availability and quality of prey and the thermal environment that juvenile chum salmon reside in during their early marine life appear spatially and temporally variable in the Eastern Gulf of Alaska (EGOA).

Previous studies of juvenile chum salmon recruitment suggest environmental processes in nearshore and coastal habitats affect juvenile chum physiological status of early life stages and subsequent marine survival (Mueter et al., 2002; Mueter et al., 2005; Orsi et al., 2005; Moss et al., 2009; Saito et al., 2010). Pyper et al. (2002) found that the relationship between environmental variables and chum salmon recruitment processes are strongest on a regional scale, thus indicating that overall survival of chum salmon hinges on how environmental conditions affect the early marine residency of juvenile chum salmon in areas such as northern SEAK.

1.3.1 Eastern Gulf of Alaska

Juvenile salmon migrate through the inside waters of SEAK, ultimately entering the EGOA. The Alaska Coastal Current (ACC) is a dominant feature characterizing circulation in the EGOA. The ACC flows counterclockwise along the GOA shelf. Its position varies seasonally, but it generally flows within 40 km of the coast and northward along SEAK. The bathymetry in the EGOA critically influences the oceanography of the region (Weingartner et al., 2009). Deep channels direct inside waters through the island archipelago of Southeast and out to the relatively narrow (5-10 km) continental shelf of the EGOA. Alongshore winds and freshwater discharge drive circulation in this 'coastal downwelling domain' (Ware and McFarlane, 1989) with stronger downwelling in the winter and reduced downwelling and a freshwater lens that extends further offshore in the summer (Stabeno et al., 2004). Freshwater runoff from the coastal margin is transported through Icy Strait and contributes to the cyclonic, swift flow of the ACC or is entrained in eddies that transport the nutrients further offshore (Fellman et al., 2010). During more intense downwelling periods (Nov-March), onshore surface transport of nutrients over the inner shelf converges at coastal margins (Mundy, 2005). Advection is a key feature of the ACC, implying that ocean circulation and climate influence both ocean conditions and biological production in the EGOA.

1.3.2 Icy Strait

Icy Strait is a neritic habitat with a shallow epipelagic zone averaging 12-13 km wide and extending from inshore waters to the continental shelf of the GOA. This study area was selected because it is the primary transit corridor to the GOA for juvenile wild and hatchery chum salmon (Orsi et al., 2005). This strait habitat is very dynamic due to large influxes of freshwater runoff and tidal energy transiting through passages with complex bathymetry. Channels such as Icy Strait in northern Southeast Alaska facilitate continuity of water properties between strait and coastal habitats (Weingartner et al., 2009). Deep channels direct inside waters through the island archipelago of SEAK and out to the relatively narrow (5-10 km) continental shelf of the EGOA.

1.4 Possible mechanisms influencing early marine condition of salmon

Ocean thermal conditions influence salmon growth (Farley and Trudel, 2009) and are important in determining the critical-size and critical-period thresholds for juvenile salmon survival (Beamish and Mahnken, 2001). Ocean conditions observed in the previous winter and spring before marine emigration can influence the early marine environment that juvenile salmon experience during the first summer at sea when survival, maturation, and migration schedules are being defined (Friedland et al., 1998). Basin-scale indices have been found to influence salmon production (Beamish and Bouillon, 1993), although variation at the regional level affects how salmon abundances respond (Fukuwaka et al., 2011). In the GOA, salmon distribution, growth, and survival are influenced by inter-annual variability in ocean physical processes (Mantua et al., 1997). Variability in the ocean processes in the GOA can be attributed in part to variability in the Aleutian Low (AL) pressure system, a dominant atmospheric feature during the winter in the Northern Pacific. The AL reflects longer-term fluctuations in the atmosphere-ocean coupled system.

Marine environments strongly influence the physiological status of juvenile chum salmon and subsequent marine survival. The possible mechanisms connecting the marine environment to chum salmon growth and survival vary spatially and temporally, but specific hypotheses can be formulated from previous studies on how marine environments in SEAK influence chum salmon during their early marine life.

1.4.1 Aleutian Low (AL)

The AL is the principal driver affecting the physical forcing and biological production in the GOA. The AL can be characterized as having strong and weak phases. An intensified or strong phase of the AL is associated with warmer sea surface temperatures (SSTs) in the EGOA, enhanced circulation, stronger cross-shelf transport, enhanced precipitation, increased discharge and increased flow into the ACC (Mundy, 2005). More freshwater runoff and stronger cross-shelf transport aids in supplying nutrients to nearshore rearing habitats of juvenile salmon. Warmer spring SST is thought to increase growth and survival of salmon. The metabolic response to direct thermal effects determines the allocation of energy in a juvenile salmon: colder than average SSTs result in a decrease in growth that is needed to avoid size-selective predation and accumulate adequate energy storage for winter survival (Beauchamp et al., 2007). In the long term, strong AL ocean conditions seem to favor the production of salmon in the GOA (Mundy, 2005).

1.4.2 Freshwater runoff

Freshwater runoff from the coastal margin is transported through Icy Strait and contributes to the ACC or is entrained in eddies that transport the nutrients further offshore (Fellman et al., 2010). Freshwater discharge is greatest in the fall when precipitation levels are high and decreases rapidly over the winter when snow accumulates. During a strong AL, higher precipitation levels in the winter produce more snow pack and subsequent summer freshwater runoff. Freshwater runoff may affect circulation patterns in the GOA as well as seasonality of nutrient inputs into nearshore and coastal waters affecting prey fields during a critical growth period for juvenile chum salmon.

1.4.3 Stratification

In her ‘optimal stability window’ hypothesis, Gargett (1997) suggested that increased water column stability increases salmon production at high latitudes by enhancing primary productivity. Since water density in the GOA is largely determined by salinity, freshwater runoff and precipitation are environmental factors affecting stability with above-average discharge producing above-average stability. A strong winter/spring AL brings greater stability to EGOA waters due to high precipitation and freshwater run off (Simpson, 1992). In the spring, a decrease in AL intensity and seasonal sea surface warming initiates thermal stratification of the water column. The shoaling of the mixed layer in the spring causes more phytoplankton cells to inhabit the euphotic zone (Mann and Lazier, 1996). Growth rates of out-migrating juvenile salmon are closely coupled with spring stratification (Bilton et al., 1982), which may determine food availability. There is more stratification in the summer when a strong AL in the previous winter facilitates the formation of a shallow mixed layer in the spring.

1.4.4 Prey production and availability

The mixed-layer dynamics of the water column trigger the timing, duration and intensity of primary production in the GOA. Warming and freshening of the water surface promotes photosynthesis; however, a continued supply of inorganic nutrients is needed to continue the bloom of phytoplankton. Changes in nutrient supply and primary production can be influenced by physical forces causing water column mixing such as strong wind events and tides (Stabeno et al. 2004). Although previous winter strong AL characteristics are thought to positively influence spring production, Waite and Mueter (2013) found that in SEAK, spring primary production, reflected by chlorophyll-a concentrations, was enhanced during times of reduced downwelling and low SST (lagged 16 and 8 days, respectively), which are characteristics of a weak AL indicating that primary production mechanisms vary temporally in SEAK.

1.5 Study focus

The goal of this project was to explore the relationships between juvenile chum salmon physiological status and environmental processes in strait and coastal marine environments of northern SEAK in order to identify potential local, regional, and basin-scale mechanisms that influence marine survival. Specifically, we addressed the following questions:

1. What marine factors influence juvenile chum salmon physiological status and abundance in the strait habitat (Icy Strait) of SEAK?
2. Does juvenile chum salmon physiological status differ across habitats and stock in SEAK in two different ocean-atmosphere years (strait and coastal, hatchery and wild, 2010 and 2011)?

Findings from this study provided: 1) insight into potential mechanisms related to chum salmon early marine physiological status and abundance; 2) a better understanding of the ecosystem dynamics specific to Icy Strait; and 3) an ecosystem metric that could be used as a forecasting tool to improve hatchery and wild chum salmon management in SEAK.

1.6 Approach

To address the above questions, this study used complementary sampling efforts connecting strait and coastal habitats used by juvenile chum salmon during early marine residency. We used data from two projects, the Gulf of Alaska Integrated Research Project (GOAIERP; http://www.nprb.org/gulf-of-alaska-project) and the Southeast Alaska Coastal Monitoring Project (SECM; www.afsc.noaa.gov/ABL/EMA), which sampled coastal (EGOA) and strait (Icy Strait) stations to collect juvenile chum salmon and biophysical data. These sampling efforts provide spatially explicit data on juvenile chum salmon during their early marine residency in northern SEAK.

Chapter 2 addresses the first research question, which retrospectively explored what marine environmental factors influence juvenile chum salmon physiological condition and abundance in the inshore habitat (Icy Strait) over 17 years (1997-2013). Specifically, we identified correlations between physiological status and abundance of juvenile chum salmon and local, regional and large-scale environmental conditions. In chapter 3, we address the second research question by quantifying the differences in physiological status of wild and hatchery juvenile chum salmon between 2010 and 2011 and between Icy Strait and the EGOA.

Chapter 2: Variation in physiological status and abundance of juvenile chum salmon (*Oncorhynchus keta*) in relation to marine factors in Southeast Alaska[1]

Abstract

A better understanding of the relationship between ocean-driven processes and early marine survival is needed to be able to identify how environmental conditions influence Pacific salmon (*Oncorhynchus* spp.) production. This study identifies links between large-scale and local-scale biophysical variables and their relationship to the abundance and physiological status of juvenile chum salmon (*O. keta*) in Icy Strait of the Alexander Archipelago, Southeastern Alaska. Correlation analyses were used to investigate the effects of a suite of marine factors at local, regional and basin scales on physiological status variables and the abundance of juvenile chum salmon in Icy Strait. Marine factors at the local scale influenced the observed physiological status of juvenile chum salmon: average June/July wind speed was negatively correlated with weight-at-length residuals, sea surface temperatures in July were positively correlated with length, and the June mixed-layer depth was positively correlated with the energy density of juvenile chum salmon in July. The abundance of juvenile chum salmon was positively related to freshwater discharge and negatively correlated with upwelling, indicating that in years with higher spring discharge and stronger previous winter downwelling, both characteristics of a strong Aleutian Low, there are more juvenile chum salmon in Icy Strait in July.

[1] Kohan, M.L., J.A. Orsi, F.J. Mueter, and M.V. McPhee. Variation in physiological status and abundance of juvenile chum salmon *(Oncorhynchus keta)* in relation to marine factors in Southeast Alaska. Prepared for submission in Deep Sea Research II: Topical Studies in Oceanography.

2.1 Introduction

Juvenile salmon experience high levels of mortality during the initial emigration to estuarine and marine environments (Parker, 1962; Pearcy, 1992; Hare et al., 1999). A critical period for survival may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker, 1968; Beamish and Mahnken, 2001). Nearshore marine environments have productive prey communities that provide favorable foraging conditions, enhancing growth opportunities for juvenile salmon (Healey, 1982; Simenstad and Salo, 1982). However, nearshore habitats are also areas of high predation, emphasizing the need for faster growth to be capable of seaward migration (Willette et al., 2001). Consequently, larger smolts at ocean entry (Parker, 1971; Henderson and Cass, 1991) and faster juvenile growth rates (Beckman et al., 1999; Ruggerone et al., 2003; Ruggerone and Goetz, 2004) are associated with increased marine survival in a number of salmon stocks.

The first fall and winter at sea is thought to be when juvenile salmon experience the second critical stage of early marine mortality. Mortality at this stage is likely due to starvation or the increased risk of predation when foraging for prey, so survival is dependent upon sufficient energy reserves stored during the first summer at sea (Beamish and Mahnken, 2001; Farley et al., 2007). Therefore, it is imperative that during their first spring and summer at sea, juvenile salmon find habitats that provide enough food to support somatic growth and lipid storage.

Atmospheric, oceanographic, and terrestrial drivers all interact to influence the quality of marine habitats for juvenile salmon. Habitat quality, in turn, affects the physiological status of juvenile salmon by constraining their metabolic response to environmental conditions and the availability and energetic quality of prey (Farley et al., 2007). Thermal conditions directly constrain metabolic rates, growth and the subsequent allocation of energy in juvenile salmon (Brett, 1952). Indirectly, climate variability alters the distribution and abundance of prey communities and therefore the habitat selection and migration pathways of juvenile salmon from estuaries to offshore environments (Armstrong et al., 2005). The effects of marine conditions might be particularly acute for salmon species, such as chum and pink (*O. gorbuscha*) salmon, that spend limited time rearing in freshwaters and therefore enter the marine environment at a relatively small size (Salo, 1991; Quinn, 2005).

Previous studies of juvenile chum salmon recruitment have concluded that environmental processes in nearshore and coastal habitats influence the physiological status of early life stages and subsequent marine survival (Mueter et al., 2002, 2005; Orsi et al., 2005; Moss et al., 2009; Saito et al., 2010). Pyper et al. (2002) found that the relationship between environmental variables and chum salmon recruitment processes are strongest on a regional scale, indicating that overall survival of chum salmon hinges on how environmental conditions specific to northern Southeast Alaska (SEAK) affect early marine residency of juvenile chum salmon. Northern SEAK has varying spatio-temporal patterns of ocean temperature, freshwater runoff and other oceanographic features that control shifting assemblages of organisms and may consequently alter distribution patterns of juvenile chum salmon.

Variability in ocean processes influencing the marine environment in northern SEAK is predominantly affected by the Aleutian Low (AL) pressure system, a dominant atmospheric feature during the winter in the North Pacific Ocean. Multi-decadal variability in the AL affects the abundance of Pacific salmon in the Gulf of Alaska (GOA; Beamish and Bouillon, 1993). A strong AL is associated with warmer sea surface temperatures (SSTs) in the GOA, enhanced circulation, stronger cross-shelf transport, enhanced precipitation, increased discharge and increased flow in the Alaska Coastal Current (Mueter, 2004). Strong AL ocean conditions seem to favor the production of salmon in the GOA (Mundy, 2005). Additionally, warmer spring SSTs are thought to increase growth and survival of salmon (Beauchamp et al., 2007). Inter-annual variability in ocean processes in the GOA is also affected by basin-scale processes such as the El Niño Southern Oscillation (ENSO; Mann and Lazier, 1996), reflected in variations in sea surface temperature.

We examined marine factors that potentially influence juvenile chum salmon physiological status and abundance in the strait habitat (Icy Strait) of northern SEAK using a 17-year time series (1997-2013). Specifically, our objective was to identify correlations of physiological status and abundance of juvenile chum salmon with regional and large-scale oceanographic conditions.

2.2 Material and methods

2.2.1 Study area

Icy Strait is located between the Alaska mainland and Chichagof Island in the Alexander Archipelago of SEAK. Icy Strait is a neritic habitat with a shallow epipelagic zone averaging 12-

13 km wide and extending 250 km from inshore waters to the continental shelf of the GOA (Fig. 2.1).

2.2.2 Data collection

The Southeast Alaska Coastal Monitoring Project (SECM) dataset consists of 17 years (1997-2013) of annual measurements of juvenile salmon catch, physiological status and biophysical variables associated with juvenile salmon habitat from up to 13 stations encompassing Auke Bay, Upper Chatham Strait, Icy Strait, and Icy Point (Orsi et al., 2000; Wertheimer et al., 2012). For the purposes of this study, we analyzed data from the four most consistently sampled stations in strait habitat (ISA, ISB, ISC and ISD; Fig. 2.1). Juvenile salmon samples were collected by surface trawl using a Nordic 264 rope trawl, fished at ~1.5 m/s for 20 minutes (Orsi et al., 2009). Fork length measurements (FL, to the nearest mm) of juvenile chum salmon were collected at station and fish were frozen for lab analysis. Otoliths were extracted in the lab and individuals were identified to specific stocks based on otolith patterns following Volk et al. (1984). Juvenile chum salmon without otolith thermal markings were assumed to originate from mixed wild stocks. At each station, associated oceanographic measurements were collected including vertical profile data on salinity and temperature (Orsi et al., 2000). Zooplankton samples were collected with BONGO nets equipped with 333 and 505 μm mesh sizes. Nets were towed obliquely at 1m/sec from a depth of 200 m or 10 m from the bottom if depth was less than 200m at each station. Average monthly zooplankton settled volumes (ml) were calculated by averaging across both mesh sizes and all hauls for a given month and year.

2.2.3 Biophysical data

2.2.3.1 Water characteristic data

All biophysical data were collected in the months May, June and July in Icy Strait. SST and sea surface salinity (SSS) were collected with a SeaBird SBE 19plus profiler and averaged for each month. Mixed layer depths (MLD) were calculated for each month using a constant temperature difference criterion, T (5 m) -T(MLD) = 0.2° C, where T (5 m) and T (MLD) are values of water temperature at 5 m below the ocean surface and at the bottom of the mixed layer, respectively. Chlorophyll-a (chl-a) values were collected once every month for most years (1999-2013). No chl-a samples were taken in 1997 and 1998 and therefore these years could not be used in analyses involving chl-a.

2.2.3.2 Physiological status data

Annual indices of physiological status were constructed from the SECM database for fish collected in July each sampling year. Based on preliminary examination of the data, the month of July was chosen to best represent juvenile chum transiting through Icy Strait since it is usually the peak month of abundance. Each station in Icy Strait was sampled up to 3 times in July, and annual physiological status indices were computed by averaging length, weight-at-length residuals, and energy density (hereafter referred to as energy) across these samples.

All indices were obtained from frozen samples returned to the laboratory for analysis. Juvenile chum salmon were thawed and fork lengths (FL, to the nearest mm) and wet weights (to the nearest gram) were recorded for individual fish. A total of 4,456 juvenile chum salmon were measured for length and weight in July over the 17-year time series. We computed the mean length of juvenile chum salmon in July of each year, as well as their coefficients of variation to examine variability in lengths within each year. To obtain weight-at-length residuals we fit a linear regression of weight against length (both ln-transformed) to remove the effects of size variation and analyzed the residuals. Weight-at-length residuals were separated into three groups for the calculation of regressions over all years: Hatchery, Wild, and Overall weight-at-length residuals. Finally, a random subset of 10 juvenile chum salmon caught in Icy Strait in July each year (n = 170) were analyzed for energy content analysis using oxygen bomb calorimetry as described in Orsi et al. (2005).

2.2.3.3 Abundance data

Abundance at each station was estimated as catch per unit effort (CPUE), calculated as the number of individuals caught in 20 minutes of fishing effort. CPUE values from each haul for all years were ln(x+1) transformed to normalize the data. The constant (1) was added to account for hauls in which no juvenile salmon were caught. Annual mean CPUEs were then calculated by averaging the CPUEs for all hauls sampled in July of a given year.

2.2.4 Environmental data

Indices of both basin-scale and regional environmental conditions thought to influence juvenile chum salmon physiological status in SEAK were identified (Table 2.1) and compiled from long-term data sets for the 1997-2013 period. Basin-scale variables included the Multivariate ENSO index (MEI), and the North Pacific Index (NPI), while regional variables included freshwater discharge, upwelling, and local wind speeds. The intensification of winter atmospheric circulation in the North Pacific identifies the time of most variability and therefore conditions during the previous winter, at both basin-wide and regional scales, are believed to have a strong effect on ocean conditions during the following spring and summer (Yeh et al., 2011).

The MEI integrates El Niño and La Niña events with 6 coupled ocean-atmosphere variables: sea level pressure, zonal and meridional components of surface wind, SST, surface air temperature and cloud cover (Wolter and Timlin, 2011). Bimonthly MEI values were obtained from the NOAA Earth System Research Laboratory (www.esrl.noaa.gov/psd/enso/mei/) and averaged over the previous winter, November through March, for each sampling year. A positive winter MEI indicates warmer conditions and a strong AL. Previous winter ocean conditions at the basin scale are assumed to affect the early marine environment that juvenile chum salmon were exposed to in Icy Strait. Higher MEI values were expected to result in better physiological status and larger abundances of juvenile chum salmon.

The NPI is defined as the area-weighted sea level pressure over the region from 30° N to 65° N and from 160° E to 140° W (Trenberth and Hurrell, 1994). The NPI is one measure of the strength of the AL, covering a low-pressure zone controlling winter storm activity in the GOA. The NPI reflects changes in the intensity of the AL in the GOA, with lower NPI values associated with a stronger AL exhibiting characteristics of relaxed coastal downwelling, higher precipitation and freshwater runoff into the GOA (Trenberth and Hurrell, 1994). Monthly NPI values (https://climatedataguide.ucar.edu) were averaged over the previous winter months, November through March, corresponding to the peak of the AL. Similar to the MEI, the winter phase of the NPI was selected to capture the effect the NPI could have on out-migration of juvenile salmon the following year. A negative relationship was expected between NPI and juvenile chum salmon abundance and physiological status.

Mean monthly freshwater discharge in SEAK was indexed using a monthly time series based on Royer (1982), which estimates total discharge from coastal precipitation, air temperature, glacial runoff and river discharge (Royer, pers. comm., August 9, 2012; www.ims.uaf.edu/gak1/.) We averaged monthly discharge values for the spring period (March-

May) to capture variability in the strength of water column stratification. The magnitude and timing of freshwater discharge, through its effects on stratification, is likely to affect primary production (Yin et al., 1997). In SEAK, glacial runoff accounts for 50% of the annual freshwater runoff (Neal et al., 2010). Specifically, high spring freshwater discharge in the spring could aid in stratification and thus increase productivity in the nearshore rearing habitats and be positively correlated with the abundance and physiological status of juvenile chum salmon (sensu Gargett, 1997). Freshwater runoff can also provide nutrients to the nearshore marine environment. In SEAK, glacial runoff accounts for 50% of the annual freshwater runoff (Neal et al., 2010). A recent study found that glacial runoff from GOA watersheds contained high percentages of biodegradable dissolved organic carbon that facilitates the metabolic stability of coastal food webs (Fellman et al., 2010). Additionally, high levels of freshwater discharge in the spring could provide a safe and timely migration for juvenile chum salmon from freshwater streams to marine migration corridors and be positively correlated to the abundance of juvenile chum salmon in Icy Strait.

Wind speeds (mph) recorded daily at the Juneau International Airport were downloaded from the National Oceanic and Atmospheric Administration Alaska Climate Database (http://pajk.arh.noaa.gov/cliMap/akClimate.php) and averaged over two time periods: April-May and June-July for the years 1997-2013. Wind mixing can weaken water column stability and introduce more nutrients into the euphotic zone. This mechanism could be influential at two stages: 1) April-May, wind mixing could provide nutrients to the euphotic zone to enable spring bloom-events and 2) June-July, wind mixing could provide nutrients to stratified layers of the water column resulting in secondary phytoplankton blooms during the summer (Iverson et al., 1974). Short-term mixing of the water column can influence the timing of the phytoplankton productivity pulses (Iverson et al., 1974). Increased wind speed in the spring and summer could indicate more prey resources for juvenile chum salmon, leading to greater abundance and better physiological status.

Daily upwelling intensity, as measured at 57° N, 137° W by the Bakun index (http://www.pfeg.noaa.gov/index.html), was averaged over the previous winter (November-March) for each sampling year. More negative upwelling index values indicate stronger downwelling ocean conditions. Downwelling facilitates cross-shelf nutrient movement and creates a well-mixed surface layer of the water column in the shelf habitat in the GOA (Childers et al., 2005). High winter downwelling could increase surface ocean nutrients and set up the ocean environment in the spring for enhanced primary and secondary production that would improve chum salmon physiological status and potentially promote production and overall abundance.

2.2.5 Statistical analyses

We used Pearson's product-moment (r) correlation coefficients to represent pairwise comparisons between the biophysical indices and juvenile chum salmon response variables (length, energy density, length-weight residuals, and CPUE). Outliers were identified and visually examined to reduce the potential for spurious results. Significance levels in the correlation analyses were not corrected for multiple comparisons due to the small size of the dataset. However, for correlations between explanatory variables and chum salmon responses, we predicted the direction of correlation *a priori* (Table 2.1), so in those cases we employed one-tailed tests of significance at $\alpha < 0.10$.

2.3 Results

2.3.1 Correlations among biophysical explanatory variables

All pairwise correlation coefficients among explanatory variables are listed in Table A-1 and significant correlations are depicted in a path diagram (Fig. 2.2). The NPI and MEI were inversely related (r = -0.65, p = 0.005). The NPI was positively correlated with upwelling (weak downwelling; r = 0.66, p < 0.005) while the MEI was negatively correlated with upwelling (stronger downwelling; r = -0.60, p = 0.011). Freshwater discharge was not significantly correlated with the MEI, NPI, or upwelling. May SST was positively correlated with the MEI (r = 0.63, p = 0.006); however the MEI was not significantly related to SST in other months. Juneau wind in April and May was negatively correlated with May SST (r = -0.60, p = 0.011) and positively correlated with May MLD (r = 0.56, p = 0.018). Juneau wind speed in June and July was positively correlated with June MLD (r = 0.51, p = 0.037) and June chl-a (r = 0.53, p = 0.043). Among physical water properties, May was the only month with significant correlations: SSS was positively correlated with MLD (r = 0.47, p = 0.052) and SST was negatively correlated with MLD (r = -0.48, p = 0.054) and SSS (r = -0.61, p = 0.009). Of the significant zooplankton correlations, June (r = -0.54, p = 0.024) and July (r = -0.51, p = 0.035) zooplankton volumes were negatively correlated with June MLD, while, June zooplankton volume was negatively correlated with July chl-a ($r = -0.63$, $p = 0.012$).

2.3.2 Physiological status and abundance

All pairwise correlation coefficients and respective p-values among juvenile chum salmon physiological response variables are given in Table A-2. Energy density was positively correlated with length ($r = 0.42$, $p = 0.096$). Weight-at-length residuals were highly correlated between hatchery and wild individuals ($r = 0.84$, $p < 0.001$). Therefore, we limited our correlation analysis between biophysical variables and weight-at-length residuals to those calculated from the regression of all individuals (hatchery plus wild).

Relationships between physiological response variables and biophysical explanatory variables are summarized in Table 2.2. Weight-at-length residuals were negatively correlated with Juneau wind in June and July ($r = -0.41$, $p = 0.098$). Energy density of juvenile chum salmon in July was positively correlated with May SSS ($r = 0.49$, $p = 0.047$), June MLD ($r = 0.54$, $p = 0.026$), and June/July wind speed ($r = 0.45$, $p = 0.070$). The coefficient of variation in July length was negatively correlated with June MLD ($r = -0.53$, $p = 0.030$), June chl-a ($r = -0.56$, $p = 0.032$), and June/July wind speed ($r = -0.59$, $p = 0.013$). Length in July was positively correlated with July SST ($r = 0.49$, $p = 0.047$). Significant correlations of physiological status variables and biophysical explanatory variables are summarized in Figure 2.2.

The CPUE of juvenile chum salmon was positively correlated with freshwater discharge ($r = 0.55$, $p = 0.022$) and negatively correlated with the upwelling index ($r = -0.52$, $p = 0.033$) indicating that in years with higher spring discharge and weaker previous winter upwelling values (stronger downwelling) more juvenile chum salmon occurred in Icy Strait in July. Juvenile chum salmon CPUE was positively correlated with juvenile pink salmon CPUE in Icy Strait ($r = 0.79$, $p<0.001$). These correlations are summarized in Figure 2.3.

To further examine the variability in lengths, we pooled fish within low wind and high wind years (June/July wind) based on the upper and lower quartiles. A two-sample Kolmogorov-Smirnov (K-S) test determined if the lengths of fish from high and low wind years were from different distributions. There were 1,324 fish that represented the low wind years and 1,068 fish that represented the high wind years. In high wind years, fish were significantly shorter than low wind years (K-S test; $p<0.00$, Fig. 2.4).

2.4 Discussion

The overall goal of this study was to evaluate the relationships of juvenile chum salmon physiological status and abundance with biophysical variables at basin-wide to local scales to develop a better understanding of ecosystem dynamics in Icy Strait. The correlation analysis offered varying degrees of support for the relationships we hypothesized between biophysical explanatory variables and chum salmon physiological status and abundance responses (summarized in Table 2.1).

As expected, a number of biophysical variables were correlated with each other. The positive relationship between NPI and upwelling supports a known system mechanism whereby higher than normal NPI values indicate a weaker Aleutian Low, resulting in relaxed downwelling along the coastal margin (Mundy, 2005; Fig. 2.2). The known inverse relationship between NPI and MEI (Trenberth and Hurrell, 1994) explains the negative relationship between MEI and upwelling.

2.4.1 Icy Strait spring dynamics

Previous winter MEI values were positively correlated with May water temperatures in Icy Strait, suggesting that winter basin-scale processes could ‘set up’ the local water characteristics in the following spring. These results are supported by previous work showing a two-month lag from basin atmospheric drivers, such as the MEI, to local SSTs (Trenberth and Hurrell, 1994). Additionally, Sturdevant et al. (2012) found a relationship connecting the MEI (lagged 6 months) with an Icy Strait 1-20m water temperature index (ISTI) from May to August.

Previous work examining chum salmon in SEAK found that spring freshwater discharge was a promising correlate of survival and harvest (Orsi and Fergusson, 2009). The positive correlation between discharge and abundance of juvenile chum salmon in this study could be explained by higher discharge rates in the spring providing a safe, rapid migration for juvenile chum salmon from freshwater streams, through estuaries, and out into marine migration corridors (Solomon, 1982). Additionally, higher spring discharge increases water column stratification (Royer et al., 2001) possibly enhancing primary production; however, we did not find a positive relationship between spring discharge and summer chlorophyll-a values in Icy Strait. The positive relationship between discharge and abundance and the negative relationship between discharge and primary production in the summer could be due to the timing of the mechanistic processes at work. Freshwater discharge affecting salmon earlier during their freshwater phase could result in differences in abundance that would not be connected to the marine availability of food later in their marine migration.

The moderately negative correlation between abundance and upwelling supported our hypothesis that strong winter downwelling promotes juvenile chum salmon abundance. However, although not significant, weak winter downwelling (high upwelling) was positively correlated with July chl-a supporting results found by Waite and Mueter (2013); a reduction in downwelling-favorable winds indicates high chlorophyll-a levels. These results suggest that additional ocean-environment variables should be evaluated to further understand the mechanism connecting juvenile chum salmon abundance and previous winter downwelling intensity.

Strong downwelling during the previous winter and high spring freshwater discharge are both characteristics of strong AL conditions. Although the NPI (a measure of the AL) was not correlated with abundance, previous winter downwelling and spring discharge were significantly correlated and are AL related elements important in understanding the mechanism that affects abundance of juvenile chum salmon in Icy Strait. As mentioned above, discharge was positively correlated with abundance while upwelling was negatively correlated suggesting that chum salmon abundance in Icy Strait is higher in strong AL years.

2.4.2 Icy Strait summer dynamics

The fjord landscape of Icy Strait can be viewed as a large estuary, with sustained chl-a levels through summer caused by a renewal of nutrients from mixing (Etherington et al., 2007). After a period of stratification in the spring, a deepening of the MLD in June appears to promote zooplankton population growth or retention in both June and July, as seen in the positive correlation between June MLD and zooplankton volumes (Table A-1). The negative relationship between zooplankton volumes in June with chlorophyll-a values in July could be a result of grazing pressure by zooplankters effectively limiting the overall abundance of primary producers (Strom, 2001).

Juneau wind speeds averaged over April and May could also be a factor contributing to spring environmental conditions in Icy Strait. Higher wind speeds in April/May and June/July related to deeper mixed layers in May and June, respectively (Table A-1). An increase in wind mixing breaks down the stability of the water column and mixes colder, more saline, nutrient-rich water into the upper water column. Salinity is a driving factor influencing water column stratification in the coastal waters of the GOA just adjacent to Icy Strait (Weingartner et al., 2002). Short-term, intense storms, as evident in higher April-May or June-July wind speeds, can be a source of mechanical energy for vertical mixing, weakening water column stability and bringing new nutrients into the euphotic zone (Mann and Lazier, 1996). In years of high wind, fish were significantly smaller than years of low wind. Wind speeds in June/July were negatively correlated with the variability in length and weight-at-length residuals, but positively correlated to the energy density of juvenile chum salmon in July, suggesting that fish are allocating energy to storing lipids rather than growing in length in years of higher June/July wind speeds. These results should be viewed carefully, because wind speed measured at the Juneau International Airport may not have correlated well with wind speeds in Icy Strait. It was not possible to use buoy data from Icy Strait to investigate this relationship, because data were inconsistent or were not recorded prior to 2007.

As stated previously, strong summer wind events can de-stabilize the water column and introduce more nutrients and subsequent food to the surface layer (Iverson et al., 1974) and possibly more food for fish to allocate to energy stores. The energy density of juvenile chum salmon in July was positively related to June mixed layer depth. The delay between the deepening of the mixed layer depth and the energy density of fish caught a month later could be due to the time span of the production of primary and secondary producers to be available as food for juvenile chum salmon.

July SSTs were positively correlated with the length of juvenile chum salmon supporting previous research in Icy Strait showing that declines in temperature resulted in a decrease in juvenile chum salmon growth rates (Orsi et al., 2000). Higher surface temperatures in July may be indicative of increased solar radiation, which is associated with a shoaling of the nutrient-enriched mixed layer. This could result in renewed primary production (Alexander et al., 2000) and subsequently the growth of juvenile chum prey. To further explore the relationship between sea surface temperature and juvenile chum salmon length, we found that summer (May-July) warm years had significantly longer fish than cold years.

The lack of correlation between MLD and SSS in Icy Strait could be explained by re-stratification of the water column in the summer resulting from solar radiation and not freshwater input with the possibility of infrequent wind mixing obscuring the relationship. May SSS was positively correlated with June chl-a values, supporting a mechanistic connection between spring water column properties and subsequent local primary production.

The positive correlation between juvenile chum and pink salmon abundance in Icy Strait could indicate that both species respond in similar ways to previous spring environmental conditions. Chum and pink salmon have similar life histories during early marine life. Both species enter the marine environment after minimal feeding in the estuarine habitat and rear in nearshore waters for weeks to months before moving offshore (Healey, 1980; Heard, 1991). Pink salmon harvest in SEAK is almost all (>97%) from wild stock (McNair, 2002), whereas chum salmon harvest primarily (~70%) originates from hatchery stocks (Piston and Heinl, 2011). Regardless of origin, pink and chum salmon physiological status is positively correlated indicating that early marine factors affect hatchery and wild stocks in similar ways.

Future studies of early marine survival should focus on the critical late summer and fall period and how important energy stores are for the survival of SEAK juvenile chum salmon entering the GOA for their first winter at sea. Additionally, as more years of data are collected in the SECM program, it may be possible to predict overall marine survival of hatchery chum salmon in SEAK based on biophysical conditions in coastal waters.

In conclusion, this study identifies links between large-scale and local-scale biophysical variables and describes ecosystem dynamics specific to Icy Strait. The abundance of juvenile chum salmon in Icy Strait is related to environmental factors at the regional scale, while physiological status is related to local environmental factors. Relationships found between juvenile chum salmon physiological status and biophysical variables aid in determining when their spatial and temporal occurrence intersect the critical periods for juvenile chum salmon during early marine residency.

2.5 Figures

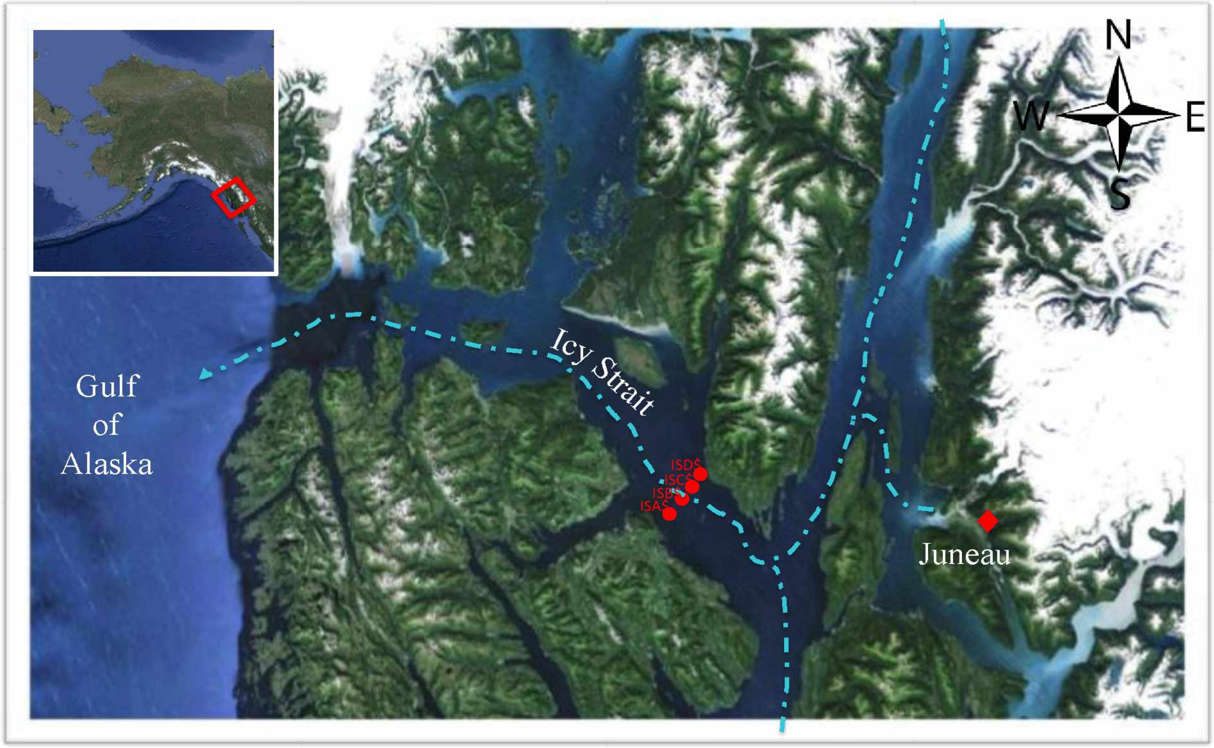

Figure 2.1 Juvenile chum salmon migration paths from inside waters of Southeast Alaska to the Gulf of Alaska.

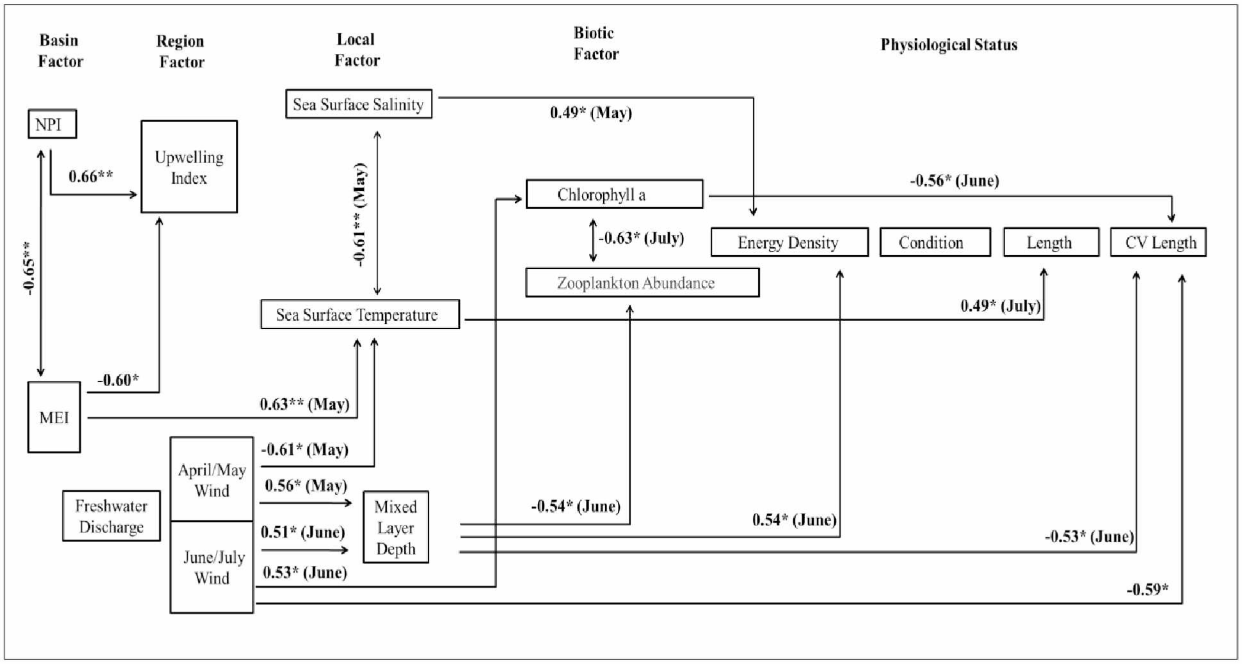

Figure 2.2 A path diagram illustrating the relationship among basin, region, local, biotic factors and physiological status indices of juvenile chum salmon in Icy Strait 1997-2013. Arrows indicate the effect of one variable on another. Correlation coefficients and the nature of the relationship are shown above path arrow. The asterisks indicate the level of significance: ***p≤ 0.001, **p≤0.010, *p≤0.05 (adapted from Fukuwaka and Suzuki, 2000).

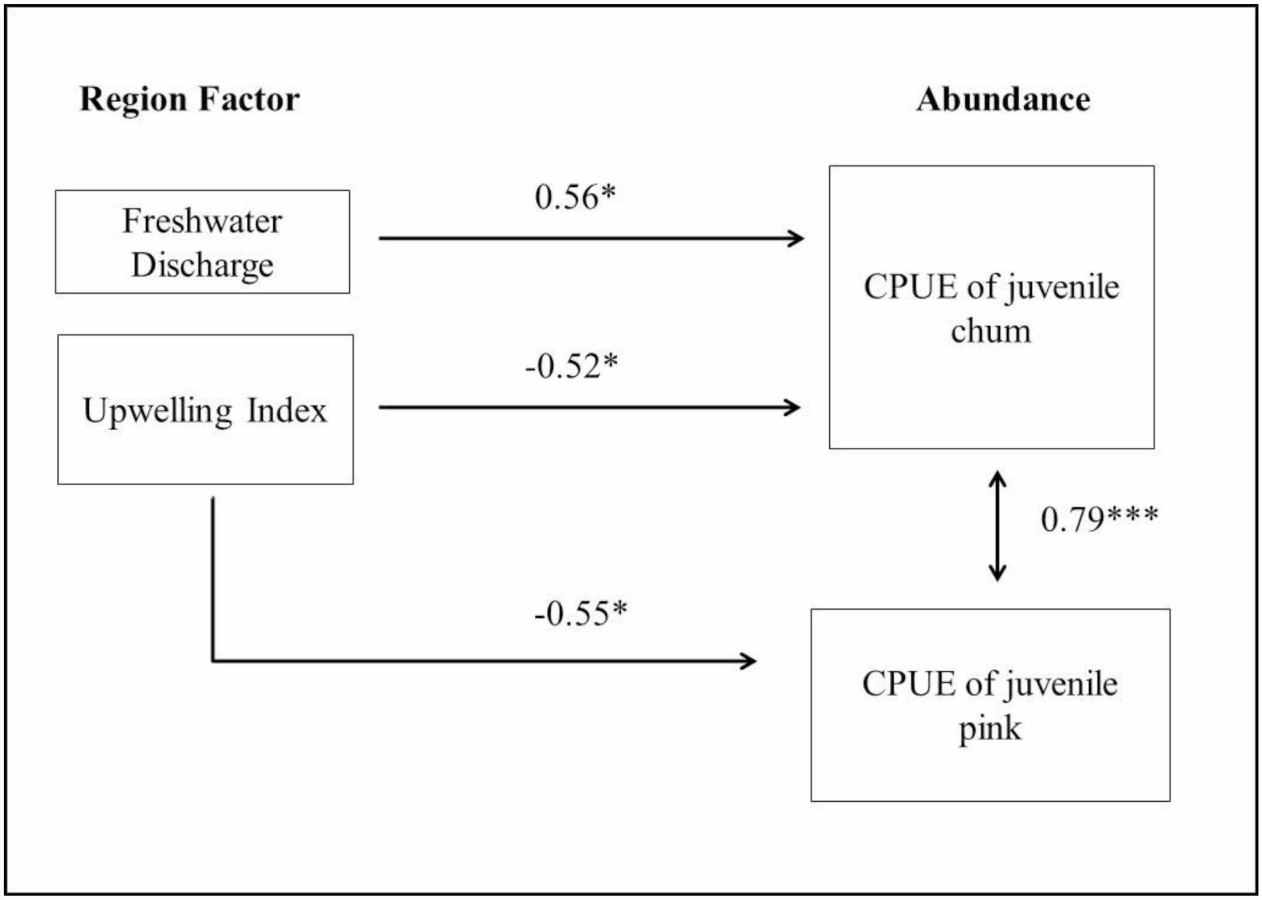

Figure 2.3 A path diagram illustrating the relationship among regional factors and the abundance of juvenile chum salmon in Icy Strait 1997-2013. Arrows indicate the effect of one variable on another. Correlation coefficients and the nature of the relationship are shown above path arrow. The asterisks indicate the level of significance: ***p≤ 0.001, **p≤0.010, *p≤0.05 (adapted from Fukuwaka and Suzuki, 2000).

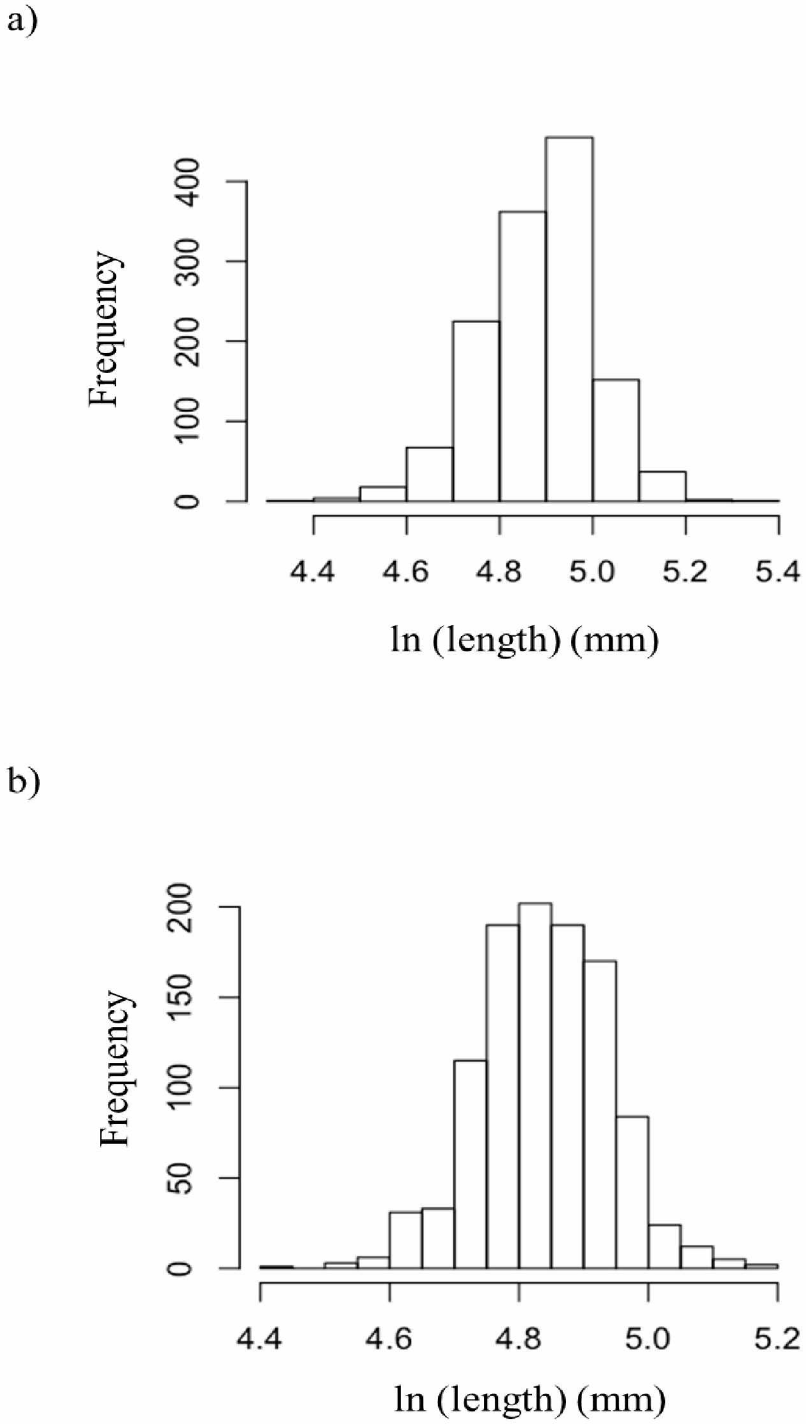

Figure 2.4 Juvenile chum salmon ln (length) (mm) distribution in a) low and b) high wind years.

2.6 Tables

Table 2.1 Biophysical variables used in this study and expected relationships with juvenile chum salmon physiological status and abundance. The time period Nov-Mar refers to the previous winter before summer data collection.

Environmental Data

Variable	Scale	Time Period	Expected Relationship
MEI	Basin	Nov-Mar	Positive
NPI	Basin	Nov-Mar	Negative
FW Discharge	Regional	Mar-May	Positive
Upwelling	Regional	Nov-Mar	Positive
Wind	Local	Apr-May, June-July	Positive
SST	Local	May-July	Positive
SSS	Local	May-July	Negative
Chl-a	Local	May-July	Positive
Zooplankton	Local	May-July	Positive

Table 2.2 Correlation coefficients between biophysical variables and physiological status variables (Res = weight-at-length residuals, Energy = energy density, Length = ln (length) CV = coefficient of variation of length) or abundance (CPUE) of chum salmon. Biophysical variables include the NPI = North Pacific Index, UI = upwelling index, MEI = multivariate ENSO index, Discharge = SEAK freshwater discharge, SSS = sea surface salinity, SST = sea surface temperature, MLD = mixed layer depth, Zoop = zooplankton volume, Chla = Chlorophyll-a concentration, Wind = Wind speeds, Pink CPUE = juvenile pink salmon abundance. P values are shown for significant correlations ($\alpha = 0.10$)

Variables	Res	Energy	Length	CV	CPUE
NPI	0.25	-0.02	0.04	-0.23	-0.22
UI	0.26	0.16	-0.01	-0.12	-0.52, p = 0.033
MEI	0.00	-0.22	0.17	0.37	-0.02
Discharge	-0.39	0.21	0.16	-0.17	0.55, p = 0.022
May SSS	0.17	0.49	-0.05	-0.29	0.38
June SSS	-0.01	0.23	-0.20	-0.11	-0.02
July SSS	0.15	0.37	-0.02	-0.07	-0.01
May SST	-0.01	-0.19, p = 0.047	0.27	0.23	-0.25
June SST	-0.03	-0.07	0.39	0.06	-0.11
July SST	0.05	-0.17	0.49, p = 0.047	-0.01	0.03
May MLD	0.03	0.32	0.22	-0.24	0.46
June MLD	-0.17	0.54, p = 0.026	0.15	-0.53, p = 0.030	0.19
July MLD	0.14	0.22	-0.17	0.04	-0.26
May Chla	0.18	0.09	0.04	-0.30	-0.05
June Chla	0.18	0.15	-0.02	-0.56, p = 0.032	-0.05
July Chla	-0.22	0.15	-0.43	-0.10	-0.19
May Zoop	-0.15	-0.28	-0.23	0.01	-0.05
June Zoop	0.34	0.01	0.09	0.30	0.22
July Zoop	0.29	-0.39	0.12	0.01	-0.20
Wind (April-May)	0.06	0.37	0.26	-0.32	0.28
Wind (June-July)	-0.41, p = 0.098	0.45, p = 0.070	0.18	-0.59, p = 0.013	0.26
Pink CPUE	-0.16	0.16	0.09	0.12	0.79, p = 0.000

2.7 References

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Chapter 3: Comparing juvenile chum salmon (*Oncorhynchus keta*) physiological status between strait and coastal ocean habitats in Southeast Alaska with implications for salmon management[1]

Abstract

We examined the differences in juvenile chum salmon physiological status between strait and coastal ocean habitats in Southeast Alaska (SEAK). We sampled juvenile chum salmon from Icy Strait, a seaward migration corridor habitat, and in the Eastern Gulf of Alaska (EGOA), a coastal ocean habitat in 2010 and 2011. Between years large basin-scale climate differences occurred, with a weak El Niño in 2010 that transitioned to a weak La Niña in 2011. In this comparison study, we found that ocean-environment conditions associated with a strong AL: lower NPI, higher MEI (warm spring SST), higher freshwater discharge and stronger coastal downwelling coincided with higher physiological status of juvenile chum salmon in the out-migrating summer as well as higher commercial harvest and hatchery survival lagged 3 years for returning adult chums in SEAK. Linear mixed effects models were used to compare juvenile chum salmon physiological status between years, habitats, and stock groups (wild vs. hatchery). Weight-at-length residuals, a measure of physiological status, were higher in 2010 compared to 2011, higher in the EGOA compared to Icy Strait, and higher in wild compared to hatchery stocks. Wild fish were shorter than hatchery fish in both years and in both habitats. Of the returning adult chum salmon to SEAK, commercial harvest and hatchery survival of age 4 fish were higher (50% and 200%) for juveniles entering the ocean in 2010 (2013 returns) compared to 2011 (2014 returns). Our results suggest differences in juvenile chum salmon physiological status in 2010 and 2011 coincided with positive and negative anomalies of the coupled ocean-atmosphere system, are linked to previous winter environmental conditions, and have the potential to be used as a predictive salmon management tool to forecast year class strength in SEAK.

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3.1 Introduction

Juvenile chum salmon (*Oncorhynchus keta*) in northern Southeast Alaska (SEAK) predominantly take a seaward migration corridor travelling from inshore waters in Icy Strait to Cross Sound and out into the Eastern Gulf of Alaska (EGOA), migrating from strait to coastal habitats (Orsi et al., 2000, 2004). The quality of rearing conditions during this stage in the nearshore and coastal habitat likely influences the growth and mortality experienced by juvenile salmon. Previous juvenile chum salmon recruitment studies have concluded that environmental processes affecting juvenile chum in nearshore and coastal habitats influence the physiological status of early life stages and subsequent marine survival (Mueter et al., 2002, 2005; Orsi et al., 2005; Moss et al., 2009; Saito, 2010). In the first summer at sea, juvenile salmon must find habitats that support the allocation of energy to somatic growth and lipid storage in order to prepare for the first winter at sea. Fluctuations in marine conditions, such as physical ocean properties, prey availability, prey quality and density-dependent factors in the early marine environment affect the physical condition of juvenile salmon and influence year class strength (Beauchamp et al., 2004; Moss et al., 2009).

Variability in the ocean processes in the Gulf of Alaska (GOA) can in part be attributed to variability in the Aleutian Low (AL) pressure system, a dominant atmospheric feature during the winter in the Northern Pacific. The AL reflects longer-term fluctuations in the atmosphere-ocean coupled system, is associated with basin-scale processes such as the El Niño Southern Oscillation (ENSO), and is measured by indices such as the North Pacific Index and the Multivariate El Niño Southern Oscillation Index (MEI; a measure of ENSO). The AL can be characterized as having strong and weak phases. An intensified or strong phase of the AL has characteristics of an El Niño event and is associated with warmer sea-surface temperatures (SSTs) in the EGOA as well as enhanced circulation, stronger cross-shelf transport, enhanced precipitation and increased discharge. More freshwater runoff and stronger cross-shelf transport aids in supplying nutrients to nearshore rearing habitats of juvenile salmon. Warmer spring SSTs are thought to increase growth and survival of salmon (Farley and Trudel, 2009). The MEI characterized 2010 as a weak El Niño year, whereas 2011 was characterized as a La Niña year with an anomalously cold winter and spring. The contrasting patterns of ocean-atmosphere processes between 2010 and 2011 could aid in understanding the influence of the marine environment on juvenile chum salmon physiological status.

Physiological status indices can be used to understand the influence of early marine factors on energy stores and growth of a juvenile salmon (Sutton et al., 2000). Residuals from a length-weight regression can provide a quantitative measure of physiological status for each juvenile chum salmon (Jakob et al., 1996). Additionally, determining the energy content of an individual fish estimates the net energy allocated to gonad and somatic tissue growth in response to physical and biological environmental changes. Variation in the physiological status of juvenile chum salmon may help understand the difference in growth and survival by stock and identify favorable habitats for juvenile chum salmon in northern SEAK.

In this paper, we compared measures of juvenile chum salmon physiological status between two habitats in SEAK over two years and between wild and hatchery stocks. Specifically, our objectives were to 1) characterize environmental variables in strait and coastal habitats during the sample years 2010 and 2011, 2) quantify the differences in stock-specific physiological status of juvenile chum salmon between strait and coastal habitats and between 2010 and 2011, and 3) compare results to actual chum salmon production response variables in SEAK (3 year lagged adult harvest and survival).

3.2 Materials and methods

3.2.1 Study area

This study sampled strait and coastal habitats used by juvenile chum salmon during early marine residency. Two projects collected juvenile chum salmon and biophysical data: the Southeast Alaska Coastal Monitoring Project (SECM) in strait (Icy Strait) localities and the Gulf of Alaska Integrated Research Project (GOAIERP) in coastal (EGOA) localities. These sampling efforts provided spatially explicit data on juvenile chum salmon stocks during their early marine migration from Icy Strait out into the EGOA (Fig. 3.1). Juvenile chum salmon in this area predominantly take a seaward migration corridor travelling from inshore waters of Icy Strait out to the EGOA (Orsi et al., 2000, 2004). Icy Strait is located between the mainland and Chichagof Island. Icy Strait is a neritic habitat with a shallow epipelagic zone averaging 12-13 km wide and extending 250 km from inshore waters to reach the continental shelf of the EGOA. Channels such as Icy Strait in northern SEAK facilitate continuity of water properties between inshore and offshore habitats (Weingartner et al., 2009). This study area was selected because it is the primary transit corridor to the GOA for juvenile wild and hatchery chum salmon.

Seaward of Icy Strait, fish become entrained in the Alaska Coastal Current (ACC), a dominant feature in the GOA. The ACC flows counterclockwise along the GOA shelf varying seasonally, but generally flows within 40 km of the coast and northward along SEAK. Alongshore winds and freshwater discharge drive the current with seasonal variation in spring and summer due to reduced downwelling and an extension of freshwater further offshore (Stabeno et al., 2004). The outer coast sampling region extends south from Cross Sound down the coast of Western Chichagof and Baranof Islands with stations ranging from 10 km to 50 km offshore. The bathymetry in the EGOA critically influences the oceanography of the region. Deep channels direct inside waters through the Alexander Archipelago of Southeast and out to the relatively narrow (*c.* 5-10 km) continental shelf of the EGOA (Weingartner et al., 2009). Freshwater runoff from the coastal margin is transported through Icy Strait and contributes to the cyclonic, swift flow of the ACC or is entrained in eddies that transport the nutrients further offshore (Fellman et al., 2010).

In SEAK, individual hatcheries produce signature patterns of rings on the otoliths of salmon fry prior to release, making it possible to identify the specific hatchery of origin of salmon caught in the field. Thermal marks are formed during the incubation period at hatcheries by manipulating the water temperatures in order to influence the pattern of rings on the otoliths of salmon fry (Volk et al., 1999). Thermal adjustments during the incubation period alter the microstructure of the otoliths causing a dark ring to form. Most of the primary hatcheries in SEAK release chum salmon as thermally “mass” marked fish (100%) from marine net pens after several weeks of supplemental feeding.

3.2.2 Data collection

Samples were collected in Icy Strait during annual SECM surveys. Additional details of this project can be found in Orsi et al. (2000). The samples collected for this study consisted of a subset of data from the SECM project: samples of fish collected in July in Icy Strait at stations ISA, ISB, ISC and ISD in 2010 and 2011 (Fig. 3.1). Juvenile salmon samples were collected with 20-minute surface trawl hauls in daylight hours using a Nordic 264 rope trawl, fished at

~1.5 m/s for 20 minutes targeting the top 20 meters (Orsi et al., 2009). At each station, associated oceanographic measurements were taken including vertical profiles of salinity, temperature, and surface chlorophyll fluorescence (Orsi et al., 2000).

Samples in the EGOA were collected on a grid with transects extending across the continental shelf (Fig. 3.1). Oceanographic data and fish samples from 27 stations sampled in both 2010 and 2011 were used for this analysis. In 2010, stations were sampled north to south from July 3-22, while in 2011 stations were sampled south to north from July 3-18. Juvenile salmon were collected with 30-minute surface trawl hauls in daylight hours fished at ~ 3m/s targeting the top 20 meters. In 2010, the survey collected epipelagic species with a Nordic 264 rope trawl while in 2011, a Cantrawl 400 rope trawl was used (Table 3.1).

Oceanographic characteristics including salinity, temperature (°C) and chlorophyll fluorescence (μg/L) were obtained at each station using a *Seabird19Plus*. In 2010 vertical profiles were obtained at all 27 stations, whereas in 2011, vertical profiles were obtained at 20 of the 27 stations. In 2011, chlorophyll fluorescence was measured at 14 of the 27 stations (Table 3.2). Zooplankton data were not available from the GOAIERP surveys at the time of analysis. However, zooplankton was collected by the SECM project at 4 stations (IPA, IPB, IPC and IPD) from Icy Point out 65 km offshore to the shelf break in both 2010 and 2011. These stations coincided with the four northernmost stations sampled by the GOAIERP survey (Fig. 3.1), allowing us to compare zooplankton concentrations between Icy Strait and the EGOA.

Otoliths were extracted in the lab and sent to the local aquaculture association, Douglas Island Pink and Chum (DIPAC), where individuals were identified to specific stocks based on otolith patterns following Volk et al. (1984). Juvenile chum salmon without otolith thermal markings were assumed to be wild and from a mixed-stock origin.

3.2.3 Ocean environmental indices

Indices of both basin-scale and regional environmental conditions thought to influence juvenile chum salmon physiological status in SEAK were identified and compiled (Table 3.3). Basin-scale variables included the MEI, and the NPI, while regional variables included freshwater discharge and upwelling. Ocean atmosphere processes precede ocean physical properties by 1-2 months (Yeh et al., 2011) and so time periods that aligned with juvenile salmon life history characteristics during their early marine residency were chosen for each variable.

The MEI is a basin-scale variable that integrates El Niño and La Niña events with six coupled ocean-atmosphere variables: sea level pressure, zonal and meridional components of surface wind, sea surface temperature, surface air temperature and cloud cover (Wolter and Timlin, 2011). A positive MEI or El Niño event is associated with a strong AL. Previous winter ocean conditions at the basin scale are assumed to affect the early marine environment that juvenile chum salmon are exposed to (Yeh et al., 2011). Higher MEI values were expected to result in better physiological status of juvenile chum salmon. Bimonthly MEI values were obtained from the NOAA Earth System Research Laboratory (www.esrl.noaa.gov/psd/enso/mei/) and averaged over the previous winter (November - March) of each sampling year.

The NPI is defined as the area-weighted sea level pressure over the region from 30° N to 65° N and from 160° E to 140° W (Trenberth and Hurrell, 1994). The NPI is one measure of the strength of the AL, covering a low-pressure zone controlling winter storm activity in the GOA. The NPI reflects changes in the intensity of the AL in the GOA, with lower NPI values associated with a stronger AL exhibiting characteristics of coastal downwelling, higher precipitation and freshwater runoff into the GOA (Trenberth and Hurrell, 1994). Monthly NPI values (https://climatedataguide.ucar.edu) were averaged over the previous winter months, November through March, corresponding to the peak of the AL. Similar to the MEI, the winter phase of the NPI was selected to capture the effect the NPI could have on out-migration of juvenile salmon the following year. Additionally, monthly NPI values were averaged over the summer (June-August) coincides with the ocean environment juvenile salmon would encounter when migrating counter-clockwise in the outer coast shelf habitat in the GOA and could influence the survival of juvenile chum salmon.

At the regional level, mean monthly freshwater discharge in SEAK was indexed using a monthly time series based on Royer (1982), which estimates total discharge from coastal precipitation, air temperature, glacial runoff and river discharge (Royer, pers. comm., August 9, 2012; www.ims.uaf.edu/gak1/.) We averaged monthly discharge values for the spring period (March-May) to capture variability in the strength of water column stratification. The magnitude and timing of freshwater discharge, through its effects on stratification, is likely to affect primary production (Yin et al., 1997) and subsequent prey availability for juvenile chum salmon entering the marine environment.

Coastal downwelling is controlled by the AL pressures system, generating counterclockwise winds and forcing an onshore surface transport over the narrow shelf of the EGOA and downwelling along the coast. Seasonally, when the AL weakens in the summer, wind strength and downwelling intensity are relaxed and there is on-shelf movement of saline, nutrient-rich bottom water. In the winter, downwelling favorable winds support surface transport over the shelf via Ekman transport, thus mixing more nutrients into the water column in association with the ACC in preparation for spring stratification and primary production. Relaxed downwelling is measured as a daily upwelling intensity at 57^{o} N, 137^{o} W by the Bakun index (http://www.pfeg.noaa.gov/index.html). These values were averaged over the previous winter (November-March) for both years.

3.2.4 Biophysical data

Sea surface temperature (SST) and salinity (SSS) values for each station were determined by averaging the top 20 meters of 1-m binned data. Chlorophyll (Chl-a) values were restricted to surface layer (1 meter values) water for all stations. The surface layer is typically well mixed and extends from the surface to the mixed layer depth (MLD; Kara et al., 2000), which varies seasonally and between years. The MLD at the time of sampling was estimated based on a constant temperature difference criterion, T(5m)-T(MLD) = 0.2 ºC, where T(5m) and T(MLD) are values of water temperature at 5m below the ocean surface and at the bottom of the mixed layer, respectively. Zooplankton density in the EGOA and Icy Strait in July were estimated from samples obtained with BONGO nets of 333 and 505 µm mesh size that were towed in a double oblique fashion. The nets were deployed at a rate of 1.0 m/sec to a depth of 200 m or 10 m from the bottom and retrieved at a rate of 0.5m/sec. Volume filtered by the net was estimated with a flow meter and volumetric zooplankton density (ml/m^3) at each station was measured in the lab. Zooplankton densities from both mesh sizes were added for each station.

3.2.5 Physiological status data

In the lab, all juvenile chum salmon caught in hauls and frozen at sea were thawed and fork lengths (FL, to the nearest mm) and wet weights (to the nearest 0.1 gram) were recorded for individual fish. Length and weight measurements of juvenile chum salmon collected from all sampling stations were used to determine body condition. A length-weight regression line was fit to lengths and weights of all juvenile chum salmon collected (all stations and both years):

$$ln(W) = \alpha + \beta ln(L) \tag{3.1}$$

Where L represents juvenile chum salmon length (mm), W represents weight (mg) and α, β are regression coefficients. The regression line standardizes weights over different lengths and the residuals provide a condition index for somatic growth (Reist, 1986, Brodeur, 2004).

A subset of juvenile chum salmon caught in strait and coastal habitats (n = 20 and n = 49, respectively) were measured for energy density (joules/g wet weight) in the lab using oxygen bomb calorimetry as described in Orsi et al. (2005).

3.2.6 Analysis

The goal of these analyses was to compare juvenile chum salmon physiological status between strait and coastal habitats, two different ocean-environment years, and two different stock groups in northern SEAK in July. The specific factors considered in the analysis included: habitat (strait and coastal), year (2010 and 2011), and stock (hatchery or wild).

3.2.6.1 Biophysical variables

Due to the different sampling methods of the surveys, the water characteristics could not be compared between habitats, only between years within each habitat. Average SST and SSS measurements were compared between years and habitats. A Generalized Least-Squares (GLS) model was used to compare mixed layer depth and chl-a measurements between years and habitats while accounting for spatial autocorrelation in the data, assuming an exponential autocorrelation structure.

Zooplankton densities (ml/m^3) between habitats and years were compared using a two-way Analysis of Variance (ANOVA) model. The full model accounted for possible interaction effects between habitat and year, while a reduced model included no interaction term:

$$Ln(Zoop)_{hti} = \mu + H_h + Y_t + H_h{*}Y_t + \varepsilon_{hti} \tag{3.2}$$

Where μ is the estimated population mean, H_h represents the effect of habitat type h on zooplankton density, Y_t represents the effect of year t, and the residuals ε_{hti} are assumed to be independent normally distributed random errors with mean zero.

3.2.6.2 Physiological status variables

To measure difference in physiological status between habitats and years, we used a mixed-model approach to account for the spatial nature of the data and for possible pseudoreplication due to sampling multiple fish at each station. Linear mixed effects (LME) models were used to estimate differences in physiological status variables: *ln* (length), the weight-at-length residuals and energy densities (hereafter referred to as energy) of individual fish. The LME model included a random station effect to allow for random variability among stations after incorporating effects from possible explanatory variables. Thus the variation in weight-at-length residuals of juvenile chum salmon was attributed to 'within station' and 'between station' variation.

All indices of physiological status were compared between habitat, year and stock with the exception of energy, which was compared between habitats and years only because no stock information was available for these samples. Icy Strait stations were surveyed multiple times in July during the sampling year and so the haul number was used instead of station. The full models accounted for possible 2-way interactions while the reduced model included no interaction terms:

$$Y_{i,thj} = \alpha_t + a_k + \gamma_h + \omega_j + \alpha_t*\gamma_h + \alpha_t*\omega_j + \gamma_h*\omega_j + \varepsilon_{i,thj}$$

$$a_k \sim N(0, \sigma_a) \quad \varepsilon_{i,thj} \sim N(0, \sigma_\varepsilon^2) \qquad 3.3$$

Where the Y represents the response variables *ln* (length), weight-at-length residuals or energy; subscripts i and t represent the i^{th} stock at time t; α_t, γ_h and ω_j are fixed effects representing average annual station effects, habitat and stock, respectively; a_k is a random effect for station k assumed to follow a normal distribution with mean zero and variance σ_ε^2 representing average station-specific effects or between-station variability; and ε is the error term. Residuals $\varepsilon_{i,thj}$ are assumed to be normally distributed with mean zero and variance σ_ε^2.

Residuals encompass the deviation for fish *i* from the mean physiological status variable at station *k* in habitat *h* and year *t* and account for within-station variability.

For all LME models, if there were significant interaction terms, the datasets were separated by year or by habitat to evaluate the nature of the interaction. The non-significance of the interaction terms confirms that there was not a change in the relationship of covariates between habitats and years. Akaike Information Criterion (AICc) values were calculated for all models. The best model was defined as having the lowest AICc value. With the best model, residual diagnostics were performed to evaluate the fixed and random effect variation in the model. To evaluate the variance and normality of the model error terms, residual values were plotted against the fitted values. Quartile quartile plots were used to assess normality and variance of random effects. If the residual diagnostics revealed outliers, they were removed from the dataset. The maximum removed outliers amounted to 2% of the total samples.

3.2.6.3 Chum salmon production response variables

Physiological status of juvenile chum salmon were compared to production response varibles of commercial chum salmon harvest in SEAK and age-specific marine survial over the two study years. These response variables were lagged three years subsequent to juvenile salmon ocean entry year since most Alaska chum salmon return after three winters at sea (Orsi and Fergusson, 2009). Annual harvests of chum salmon in SEAK commerical fisheries were available from the Alaska Department of Fish and Game (Conrad and Gray, 2014) and marine survival data of hatchery chum salmon were availble from DIPAC. For commerical harvest, the total SEAK catch was used. In the case of hatchery chum salmon, age-specific marine survival data was used for age 4 (ocean-age three) fish returning in 2013 and 2014 (R. Focht, DIPAC, pers. comm., May 29, 2015).

3.3 Results

3.3.1 Ocean environmental indices

At the basin scale, the MEI characterized 2010 as a weak El Niño year, whereas 2011 was characterized as a weak La Niña with the previous winter being anomalously cold (Wolter, 2013; Fig. 3.2). All environmental indices are summarized in Table 3.3. MEI and NPI indices were inversely related, as expected. In 2010, the low NPI values, relaxed downwelling and high freshwater discharge values are characteristic of a strong AL. Regionally, the SEAK spring freshwater discharge was more than two times greater in 2010 (11804 m^3/sec) than 2011 (4532 m^3/sec). The sea-level pressure pattern seen in the NPI values support colder winter ocean temperatures and relaxed downwelling conditions in 2011 consistent with a weak AL ocean environment. The winter of 2011 had the highest relaxed downwelling values in the previous decade (2001-2011).

3.3.2 Biophysical variables

In both habitats, 2011 was warmer than 2010 and the EGOA was warmer than the strait habitat (strait- 2010: 9.46°C +/- 0.19, 2011: 9.90°C+/-0.24, EGOA- 2010: 11.51°C+/- 0.71, 2011: 12.11°C+/- 0.78). The EGOA was more saline than the strait habitat, but there were no differences in salinity between years. There was a significantly higher concentration of chl-a in 2010 compared to 2011 (GLS, $p = 0.004$) and an interaction between years and habitat (GLS, $p = 0.014$; Table 3.4). There were no significant differences in MLD between years or habitat.

For zooplankton, there was not a significant interaction effect in the model and so the interaction terms were dropped from the full model (Eq. 3.2). Zooplankton density was significantly higher in the strait habitat than in the EGOA off Icy Point (ANOVA, $p < 0.005$), and although 2011 had a higher density of zooplankton, there was no significant difference between years (Fig. 3.3).

3.3.3 Physiological status variables

The length-weight relationship for juvenile chum salmon followed the equation

$$\ln W = -11.95 + 3.10 * \ln L \tag{3.4}$$

with the residuals representing the weight-at-length residuals specific to each fish sampled. Samples were pooled from both years (N = 479 in 2010; N = 237 in 2011) and habitats (N = 510 in strait; N = 206 in EGOA).

To put in context the spatial and temporal dataset used in this observational study, the untransformed length measurements of juvenile chum salmon collected from both habitats for all available sampling months were compared. The average length of fish in July in the strait habitat was similar to the average length of fish in July in the EGOA habitat (strait = 124.24 mm, EGOA = 123.03 mm). The observation that juvenile chum salmon were similar in length in both habitats in July led us to believe that the biophysical parameters associated with these habitats could also be compared in July to assess differences in habitat characteristics.

Linear mixed effect models compared physiological status response variables between habitats, years and stocks (except for energy density) and summaries of model results are found in Table B-1. There were interactions in the linear mixed effect model for the response variable length and therefore we analyzed the habitats separately. In both habitats, there was a significant difference in the length of juvenile chum salmon between stocks (strait: $p < 0.001$, EGOA: $p = 0.05$, wild shorter than hatchery), but no significant difference between years (Fig. 3.4). There were no significant interaction effects in the full models for both habitats with the best models being the reduced model with no interaction terms (LME, Eq. 3.3; Table B-2).

For weight-at-length residuals, there was a significant difference between years (higher weight-at-length residuals in 2010 than 2011, $p < 0.001$) habitats (higher weight-at-length residuals in EGOA than Icy Strait, $p < 0.001$) and stocks (higher weight-at-length residuals of wild than hatchery stocks, $p = 0.001$; Fig. 3.5). There were no significant interaction effects in the full model (LME, Eq. 3.3; Table B-2).

For energy density, in both years, there was a significant difference between habitats with fish in the EGOA having higher energy than in the strait habitat (2010: $p = 0.004$; 2011: $p < 0.001$; Fig. 3.6). By habitat, there was a significant difference in energy density between years in the EGOA (2011 higher than 2010, $p = 0.009$) but not in the strait habitat. There was a significant interaction between habitat and year (LME, Eq. 3.3, $p = 0.037$; Table B-2). The variability among and between stations was similar in the full model with interaction terms.

3.4 Discussion

For chum salmon production response variables, juveniles that entered the ocean in 2010 compared to 2011 had higher adult returns and survival to SEAK when lagged three ocean years. Commercial harvests of chum salmon to SEAK were 10.2 M fish in 2013 and 6.5 M fish in 2014 (Conrad and Gray, 2014). Furthermore, actual marine survival of age-4 chum salmon to the DIPAC hatchery was fourfold higher for fish entering the ocean in 2010 (2009 brood year, 3.25%) compared to 2011 (2008 brood year, 0.77%). In 2013, hatchery chum salmon (those that would have outmigrated in 2010) comprised 80.5% of the commercial common property harvest

harvest, while in 2014 (those that would have outmigrated in 2011) comprised 85.3% of the total, indicating that there was higher survival for wild chum salmon from the ocean-entry year of 2010 compared to 2011 (Vercessi, 2013, 2015).

In this comparison study, we found that ocean-environment conditions associated with a strong AL: lower NPI, higher MEI (warm spring SST), higher freshwater discharge and stronger coastal downwelling coincided with higher weight-at-length residuals in the out-migrating juveniles in summer as well as higher commercial harvest and hatchery survival lagged 3 years for returning adult chums in SEAK. The link between weight-at-length residuals and adult returns was also found in another GOA study finding that hatchery juvenile pink salmon that were heavier at a given length had higher survival (Miller et al., 2012). The result that commercial harvest and hatchery survival of age-4 fish were higher (50% and 200% higher, respectively) for juveniles entering the ocean in 2010 compared to 2011 supports the concept of using physiological status data for juvenile chum salmon as a potential predictive salmon management tool to forecast year class strength in SEAK.

Response variables measured could be influenced by the migration timing of stocks of juvenile salmon in northern SEAK. In Icy Strait there was a higher percentage of hatchery stocks in 2010 compared to 2011 (58% vs. 51%). The higher percentage of hatchery chum salmon in Icy Strait in 2010 compared to 2011 is consistent with the higher marine survivals reported for DIPAC age 4 fish released in 2010 (3.25%) compared to 2011 (0.77%). Conversely, in the EGOA, the proportion of hatchery juvenile chum was lower in 2010 compared to 2011 (60% vs. 70%). The difference in stock composition (hatchery/wild) between habitats in both years can be also explained by the trend for some hatchery stocks of chum salmon (i.e. DIPAC) to have peak migrations through Icy Strait in June (Orsi et al., 2005). At the time of the survey in Icy Strait (late July) the high peaks of hatchery-marked juvenile chum salmon had already migrated through Icy Strait to the EGOA.

The result that wild stocks were heavier at a given length and had shorter overall lengths compared to hatchery stocks could be due to the difference in foraging strategies between hatchery and wild fish (Sturdevant et al., 2010) or that there was a difference in migration timing of wild and hatchery fish stocks. The only indicator available to assess the difference in adult returns between hatchery and wild chum salmon was the composition of the commercial harvest in SEAK. The commercial harvest of chum salmon in 2013 (2010 ocean-entry year) had the lowest percentage of hatchery fish in the past decade (2004-2014) indicating high returns of wild chum to SEAK. High hatchery survival and a commercial catch comprising a higher percentage of wild chum salmon suggests that 2010 had favorable growing conditions for juvenile chum salmon.

Conversely, in 2011, the measured ocean environmental characteristics depicted a weak AL; higher NPI, low MEI, low freshwater discharge and relaxed downwelling coinciding with higher energy densities in the EGOA in July in 2011. Energy density measured in the summer growing season was difficult to interpret as an indicator of physiological status and subsequent production of salmon. Water temperature could also influence the allocation of energy, with fish having higher energy densities when sea temperatures are cooler (Heintz, 2009). The colder spring sea temperatures in 2011 could have influenced the growing conditions for juvenile chum salmon previous to collection in July. The contradiction between energy density and the other response variables suggests that measurements of physiological status were affected by different mechanisms specific to the fish life history at the time and location of collection.

When comparing habitats, the low weight-at-length residuals in the strait habitat compared to the EGOA may be the result of juvenile chum salmon not allocating energy to lipid stores, but to avoiding predation or maintaining basic body functions corresponding to being at an earlier developmental stage in the strait habitat. These results contradict those of a similar previous study in SEAK where condition (measured as condition factor K) was found to be higher in stocks in the strait habitat compared to coastal habitat (Orsi et al., 2001). Our result that fish in the EGOA were heavier for their length could indicate that the coastal habitat intersects the right time in a juvenile chum salmon's life for energy to be allocated to lipid storage rather than somatic growth. This physiological transition coincides with the early ocean life history of chum salmon, which grow rapidly in spring and early summer in strait and coastal habitats, then later occupy the EGOA in the late summer and fall as they need to store energy and overwinter.

In general, conditions associated with a strong AL, as seen in 2010, are thought to be better for the production of salmon in the GOA (Mundy, 2005). The high freshwater discharge observed in 2010 supports a previous study examining chum salmon in SEAK that found spring freshwater discharge was a promising positive correlate of survival and harvest (Orsi and Fergusson, 2009). Higher downwelling values, as seen in 2010, support a companion study finding a positive correlation between the abundance of juvenile chum salmon in SEAK and downwelling intensity (Chapter 2).

Low freshwater influx, as observed in 2011, could have decreased the levels of bioavailable iron, primarily sourced from freshwater rivers in SEAK, and subsequently prevented offshore transport to stimulate primary production in outer shelf waters (Martin and Gordon, 1988; Wu et al., 2009). Waite and Mueter (2013) found that positive spring chl-a concentration anomalies were associated with lower spring SST and increased upwelling (relaxed downwelling) in the EGOA, characteristics of a weak AL. However, in spite of the cool SST and relaxed downwelling conditions in the spring of 2011, satellite-derived chl-a anomalies were much lower in the spring and particularly in the fall of 2011 compared to 2010 (Waite and Mueter, 2013). Similarly, *in situ* chl-a values were significantly lower in the EGOA in July 2011 than in July 2010, despite higher chl-a values in the strait habitat in 2011. The shallow MLDs, low chl-a concentrations, and low freshwater discharge rates as seen in 2011 in the EGOA, could have negatively influenced the timing of stratification and amount of primary production, creating a match-mismatch situation for prey resources and juvenile salmon in the EGOA for this year.

Although the relationship was not significant, there were higher densities of zooplankton in 2011compared to 2010 which could explain the low primary production in 2011 in the EGOA resulting from grazing pressure by zooplankters effectively limiting the overall production of primary producers (Strom, 2001). Because the production of zooplankton biomass lags primary production by 1-2 months (Cooney, 1988), the sampling design for this study might not capture the true habitat characteristics for each sampling year. These observations suggest that the mechanisms driving productivity can vary over relatively small spatial and temporal scales.

In conclusion, differences in juvenile chum salmon physiological status in 2010 and 2011 coincided with positive and negative anomalies of the coupled ocean-atmosphere system as well as chum salmon harvest and survival lagged three ocean years. These differences suggest that the use of previous winter environmental conditions at both the basin and regional scale and juvenile chum salmon physiological status have potential to be used as predictive tools for forecasting salmon year class strength in SEAK.

3.5 Figures

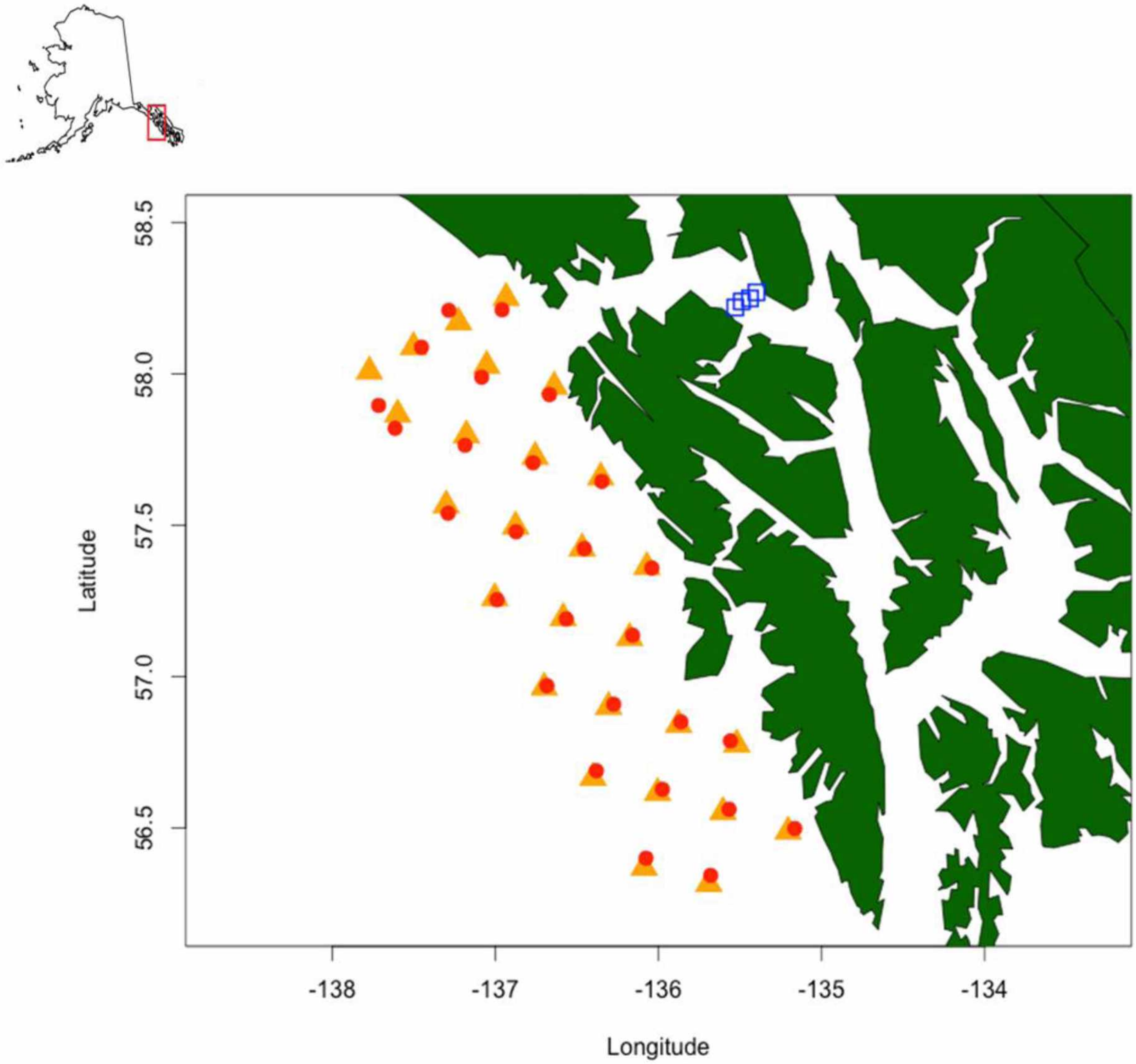

Figure 3.1 Map of sampling stations in the Eastern Gulf of Alaska (EGOA) and Icy Strait. EGOA stations are represented by red circles (2010) and orange triangles (2011). Icy Strait stations are represented by blue open squares (2010 and 2011).

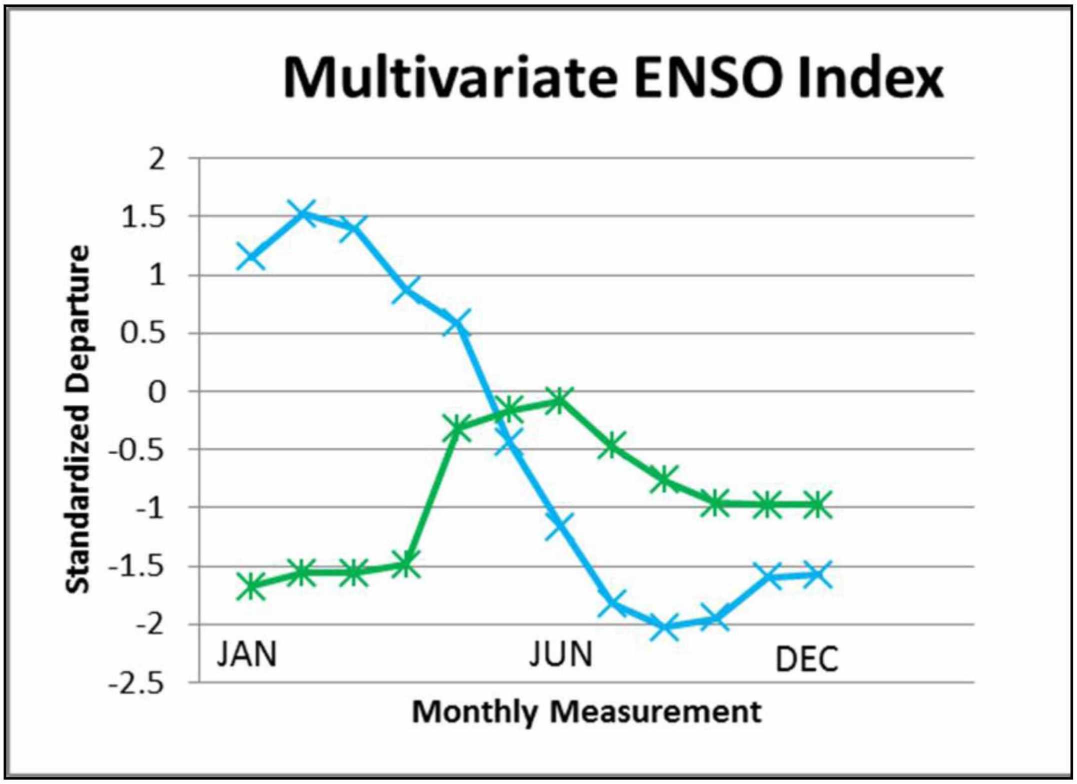

Figure 3.2 Comparison of the standardized departures from the mean monthly measurements of the multivariate ENSO index for 2010 (blue) and 2011 (green) (Wolter, 2013, data source: www.esrl.noaa.gov/psd/enso/mei/).

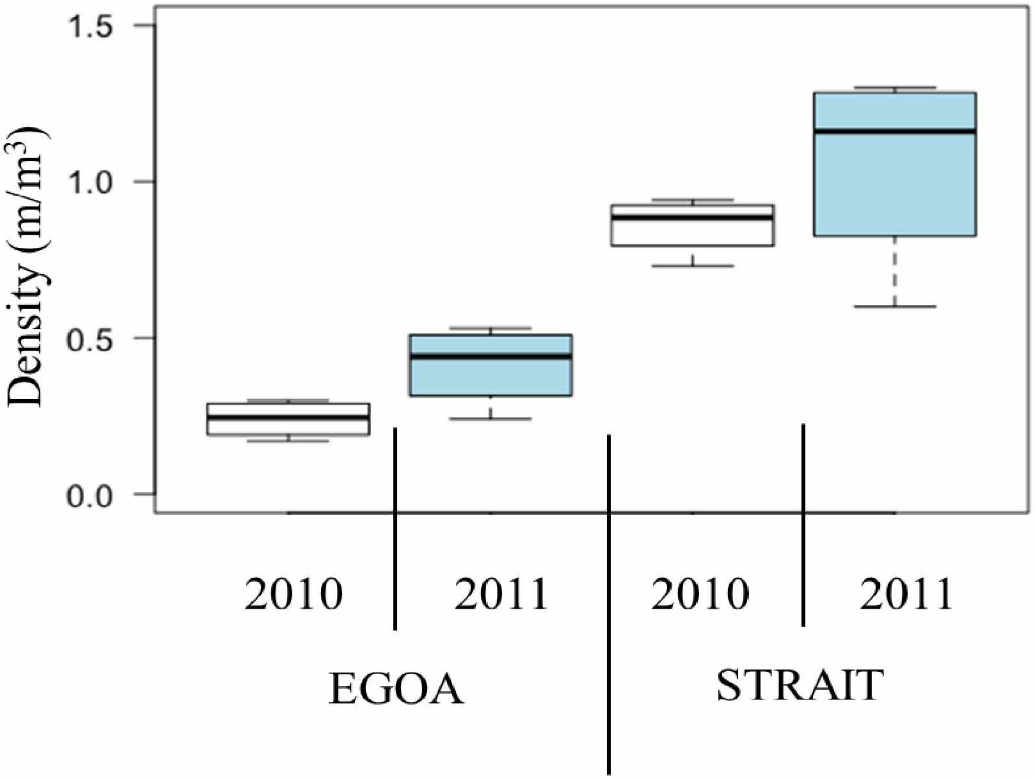

Figure 3.3 A boxplot depicting the differences in zooplankton density (ml/m^3) between year and habitat. The boxplot shows median, interquartile range and individuals outside of the interquartile range.

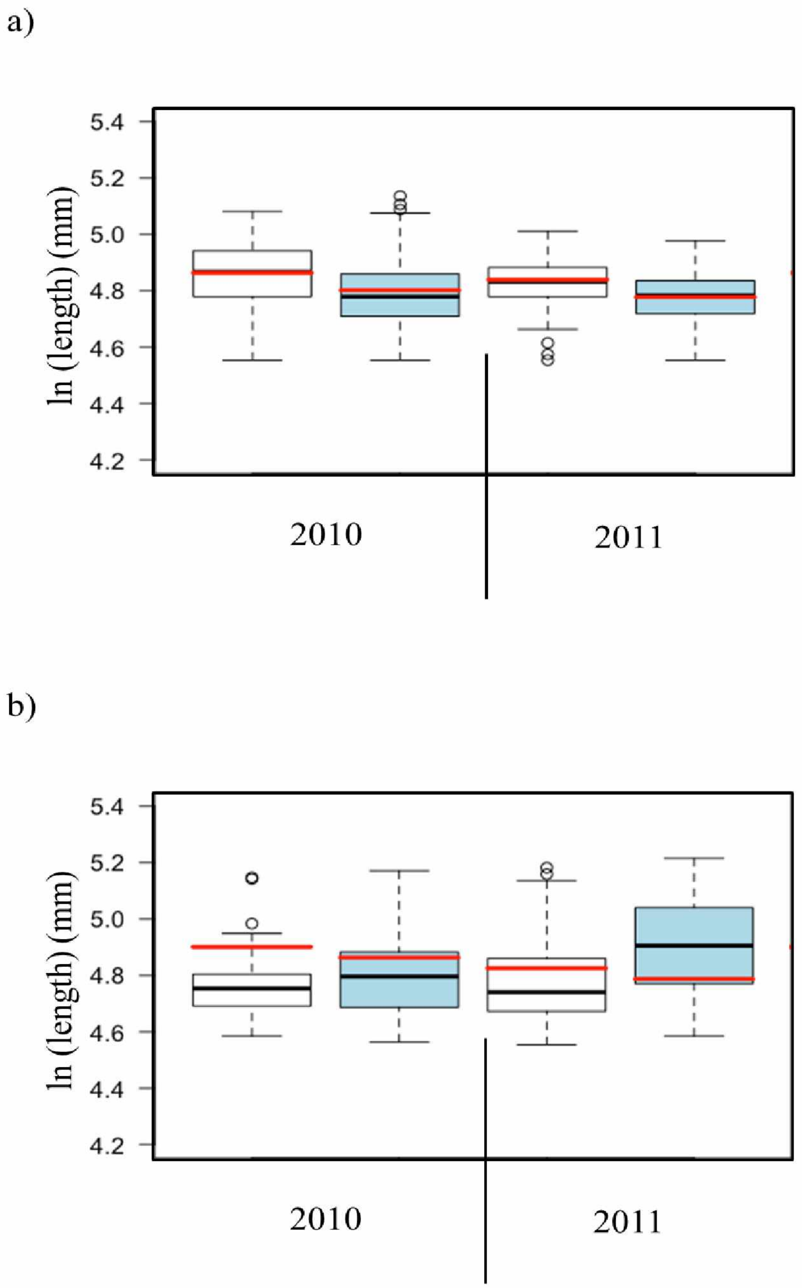

Figure 3.4 Boxplots of ln(length) of juvenile chum salmon in both habitats a) Icy Strait and b) EGOA. The boxplots depict the median and upper and lower quartiles and individuals outside of the interquartile range of the raw data not accounting for a station effect for year and stock. Blue boxes indicate wild stocks and clear boxes indicate hatchery stocks. The red line represents the modeled mean after accounting for a station effect. Outliers were removed from the data to estimate the means.

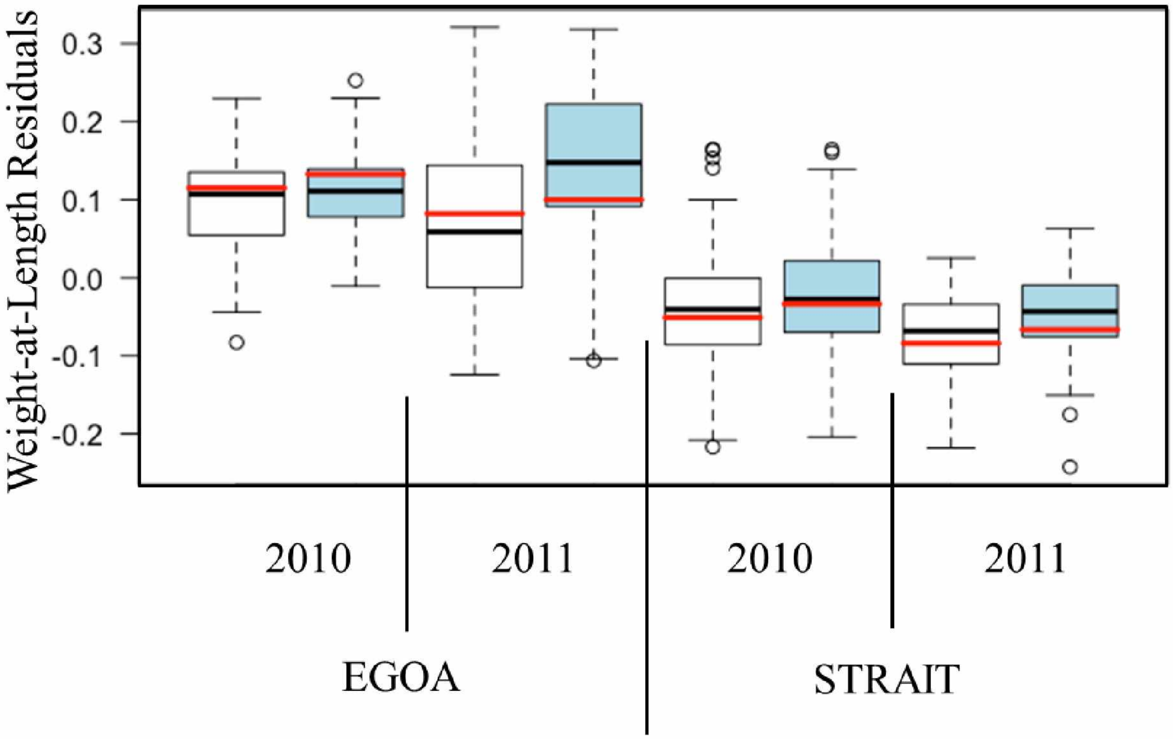

Figure 3.5 A boxplot of juvenile chum salmon weight-at-length residuals. The boxplot depicts the median and upper and lower quartiles and individuals outside of the interquartile range of the raw data not accounting for a station effect. The red line represents the modeled mean after accounting for a station effect. Blue boxes indicate wild stocks and clear boxes indicate hatchery stocks. Outliers were removed from the data to estimate the means.

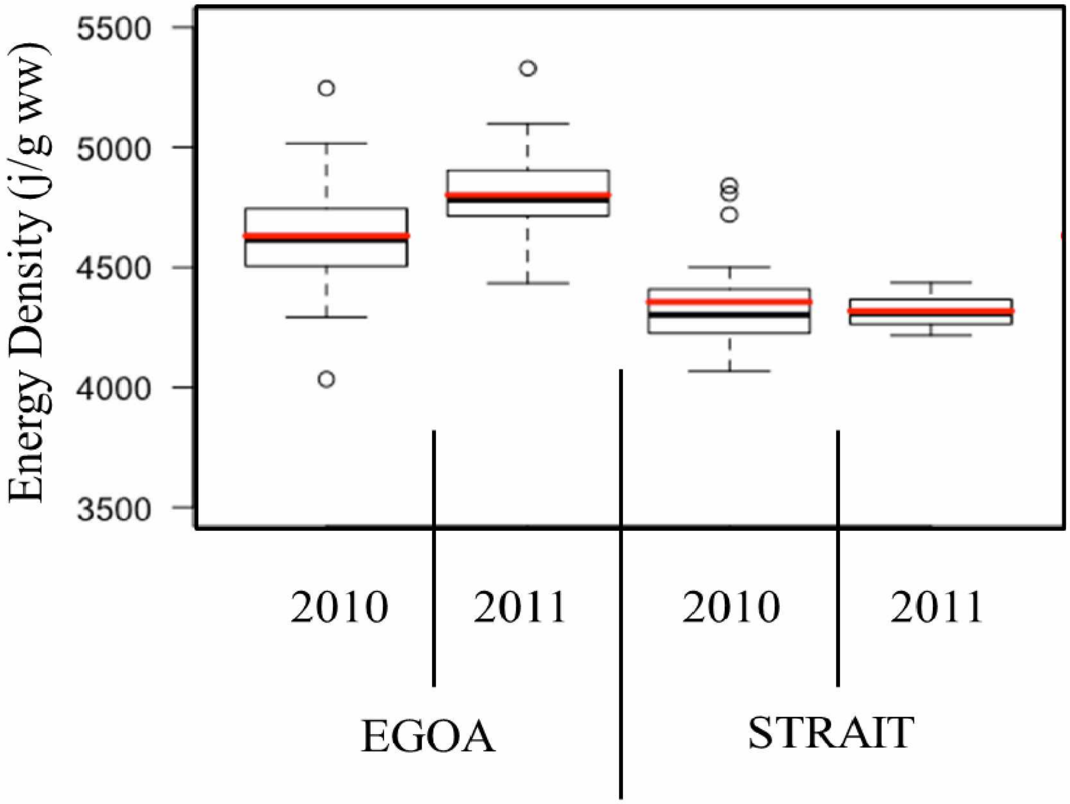

Figure 3.6 A boxplot of juvenile chum energy density (j/g ww). The boxplot depicts the median and upper and lower quartiles individuals outside of the interquartile range of the raw data not accounting for a station effect. The red line represents the modeled mean after accounting for a station effect. Outliers were removed from the data to estimate the means.

3.6 Tables

Table 3.1 Differences in trawl sampling effort in the Eastern Gulf of Alaska for July of 2010 and 2011.

Trawl Sampling Effort	2010	2011
Trawl date	7/4-7/20	7/3-7/17
Grid Direction	N->S	S->N
Number of hauls	27	27
Trawl gear	Nordic	Cantrawl
Trawl Dimensions (m, WxH)	20x20	40x30
Head Rope Spread (m^2)	400	1200
Trawl Speed (m/s)	2.8	3.4
Trawl time (min)	30	30
Distance (m)	302,400	367,200
Volume of Water (m^3)	120,960,000	440,640,000

Table 3.2 Eastern Gulf of Alaska oceanographic characteristics measurements obtained from stations in 2010 and 2011.

	Year	Characteristic	# of stations sampled
EGOA	2010	Temperature	27
	2011	Temperature	20
	2010	Salinity	27
	2011	Salinity	20
	2010	Chlorophyll	27
	2011	Chlorophyll	14
Strait	2010	Temperature	4
	2011	Temperature	4
	2010	Salinity	4
	2011	Salinity	4
	2010/2011	Chlorophyll	4

Table 3.3 Possible ecosystem indices as drivers for juvenile chum salmon physiological status compared between 2010 and 2011. The Nov-Mar time period is the winter prior to the ocean year.

Environmental Data				
Variable	Scale	Time Period	2010	2011
MEI	Basin	Nov-Mar	1.23	-1.60
NPI	Basin	Nov-Mar	1006.49	1011.13
FW Discharge (ft^3/sec)	Regional	Mar-May	4,531.76	11,804.26
Upwelling	Regional	Nov-Mar	-140.99	-79.72

Table 3.4 Generalized least-squares model generated means for chlorophyll concentration (μg/L) and mixed layer depth (MLD). Data is from stations sampled in Icy Strait and the Eastern Gulf of Alaska in July of 2010 and 2011.

Habitat	Characteristic	Year	# of stations	Model Mean
Strait	Chlorophyll	2010	4	2.10
	Chlorophyll	2011	4	4.11
	MLD	2010	4	6.21
	MLD	2011	4	6.16
EGOA	Chlorophyll	2010	27	2.52
	Chlorophyll	2011	14	1.69
	MLD	2010	27	9.20
	MLD	2011	20	6.39

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Conclusions

This thesis provides insight into the early marine residency of juvenile chum salmon in SEAK. This study identified links between large-scale and local-scale biophysical variables, as well as described the ecosystem dynamics specific to Icy Strait. Correlations suggest that previous winter basin-scale processes could 'set up' the local water characteristics of Icy Strait in the following spring. Generally, the abundance of juvenile chum salmon in Icy Strait is related to environmental factors at the regional scale. Variables that describe a strong Aleutian Low marine environment were connected to higher juvenile chum salmon abundance. Physiological status was also related to local environmental factors. The relationships found between juvenile chum salmon physiological status variables and biophysical variables aid in determining when their spatial and temporal occurrence intersects the critical early marine periods for juvenile chum salmon.

To further understand the early marine experience of juvenile chum salmon of northern SEAK, a second study examined the differences in hatchery and wild juvenile chum salmon physiological status between two habitats in SEAK over two years representing positive and negative anomalies of the coupled ocean-atmosphere system. In this comparison study, we found that ocean-environment conditions associated with a strong AL: lower NPI, higher MEI (warm spring SST), higher freshwater discharge and stronger previous winter coastal downwelling coincided with higher physiological status of juvenile chum salmon in the out-migrating summer as well as higher commercial harvest and hatchery survival lagged 3 years for returning adult chums in SEAK. Our results suggest differences in juvenile chum salmon physiological status in 2010 and 2011 coincided with positive and negative anomalies of the coupled ocean-atmosphere system, are linked to previous winter environmental conditions, and have the potential to be used as a predictive salmon management tool to forecast year class strength in SEAK.

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Appendix A: Pairwise correlation results

Table A-1 Pairwise correlation coefficients and corresponding p-values (italicized) for biophysical variables (NPI = North Pacific Index, UI = upwelling index, MEI = multivariate ENSO index, DIS = SEAK freshwater discharge, SSS = sea surface salinity, SST = sea surface temperature, MLD = mixed layer depth, Zoop = zooplankton volume, Chla = Chlorophyll-a concentration, and AM/JJ Wind = April/May and June/July Wind speeds).

	NPI	UI	MEI	DIS	M SSS	J SSS	Ju SSS	M SST	J SST	Ju SST	M MLD	J MLD	Ju MLD	M Chla	J Chla	Ju Chla	M Zoop	J Zoop	Ju Zoop	AM Wind	JJ Wind
NPI		*0*	*0.01*	*0.28*	*0.26*	*0.22*	*0.41*	*0.4*	*0.97*	*0.76*	*0.41*	*0.97*	*0.89*	*0.5*	*0.66*	*0.08*	*0.63*	*0.53*	*0.55*	*0.93*	*0.16*
UI	0.66		*0.01*	*0.51*	*0.37*	*0.17*	*0.33*	*0.7*	*0.24*	*0.26*	*0.91*	*0.81*	*0.18*	*0.48*	*0.96*	*0.09*	*0.7*	*0.42*	*0.99*	*0.96*	*0.54*
MEI	-0.65	-0.6		*0.53*	*0.52*	*0.75*	*0.93*	*0.01*	*0.42*	*0.62*	*0.5*	*0.99*	*0.89*	*0.66*	*0.99*	*0.1*	*0.97*	*0.76*	*0.74*	*0.22*	*0.96*
DIS	-0.28	-0.17	-0.16		*1*	*0.62*	*0.55*	*0.49*	*0.87*	*0.38*	*0.19*	*0.86*	*0.48*	*0.97*	*0.07*	*0.71*	*0.42*	*0.92*	*0.55*	*0.2*	*0.31*
M SSS	-0.29	-0.23	-0.17	-0		*0.04*	*0.02*	*0.01*	*0.03*	*0.03*	*0.05*	*0.36*	*0.3*	*0.41*	*0.06*	*0.79*	*0.17*	*0.33*	*0.83*	*0.16*	*0.28*
J SSS	-0.31	-0.35	0.08	-0.13	0.51		*0*	*0.76*	*0*	*0*	*0.59*	*0.18*	*0.8*	*0.31*	*0.39*	*0.69*	*0.86*	*0.64*	*0.72*	*0.67*	*0.32*
Ju SSS	-0.21	-0.25	-0.02	-0.16	0.55	0.88		*0.76*	*0*	*0*	*0.71*	*0.12*	*0.81*	*0.29*	*0.21*	*0.74*	*0.92*	*0.4*	*0.61*	*0.83*	*0.55*
M SST	-0.22	-0.1	0.63	-0.18	-0.61	-0.08	-0.08		*0.1*	*0.33*	*0.05*	*1*	*0.35*	*0.33*	*0.52*	*0.2*	*0.2*	*0.98*	*0.94*	*0.01*	*0.83*
J SST	0.01	0.3	0.21	0.04	-0.54	-0.79	-0.66	0.41		*0*	*0.54*	*0.47*	*0.49*	*0.26*	*0.97*	*0.85*	*0.73*	*0.37*	*0.66*	*0.6*	*0.9*
Ju SST	0.08	0.29	0.13	0.23	-0.52	-0.78	-0.76	0.25	0.86		*0.25*	*0.13*	*0.6*	*0.62*	*0.55*	*0.62*	*0.99*	*0.66*	*0.66*	*0.45*	*0.73*
M MLD	-0.22	0.03	-0.18	0.33	0.47	-0.14	-0.1	-0.48	0.16	0.3		*0.83*	*0.5*	*0.79*	*0.33*	*0.7*	*0.18*	*0.99*	*0.39*	*0.02*	*0.58*
J MLD	0.01	-0.06	-0	0.05	0.24	0.34	0.39	0	-0.19	-0.38	0.06		*0.86*	*0.65*	*0.19*	*0.37*	*0.92*	*0.02*	*0.04*	*0.76*	*0.04*
Ju MLD	-0.04	0.34	-0.04	0.18	-0.27	0.07	-0.06	0.24	0.18	0.14	-0.18	-0.05		*0.83*	*0.44*	*0.29*	*0.35*	*0.53*	*0.62*	*0.99*	*0.51*
M Chla	0.2	0.2	-0.13	-0.01	0.24	0.29	0.3	-0.28	-0.32	-0.15	-0.08	0.13	0.07		*0.62*	*0.29*	*0.59*	*0.41*	*0.72*	*0.7*	*0.63*
J Chla	-0.12	0.01	-0	-0.48	0.5	0.24	0.35	-0.18	-0.01	-0.17	0.27	0.36	-0.22	0.15		*0.98*	*0.68*	*0.89*	*0.7*	*0.53*	*0.04*
Ju Chla	0.46	0.46	-0.44	-0.1	-0.07	-0.11	-0.1	-0.35	0.05	-0.14	-0.11	0.25	0.29	0.3	-0.01		*0.49*	*0.01*	*0.06*	*0.67*	*0.98*
M Zoop	-0.13	-0.1	-0.01	0.21	-0.35	-0.05	0.03	0.33	0.09	-0	-0.34	0.03	0.24	-0.16	0.12	-0.19		*0.57*	*0.49*	*0.33*	*0.74*
J Zoop	-0.17	-0.21	-0.08	-0.03	0.25	0.12	0.22	0.01	-0.23	-0.12	0	-0.54	-0.16	-0.24	-0.04	-0.63	0.15		*0.08*	*0.62*	*0.4*
Ju Zoop	0.16	-0.01	-0.09	-0.16	-0.06	0.09	0.13	0.02	-0.12	0.12	-0.23	-0.51	-0.13	0.1	0.11	-0.49	0.18	0.44		*0.87*	*0.2*
AM Wind	-0.02	-0.02	-0.32	0.33	0.36	-0.11	-0.06	-0.6	0.14	0.2	0.57	0.08	-0	-0.12	0.18	0.12	-0.25	-0.13	0.04		*0.11*
JJ Wind	-0.36	-0.16	-0.02	0.26	0.28	0.26	0.16	-0.06	0.03	-0.09	0.15	0.51	0.17	-0.14	0.53	0.01	0.09	-0.22	-0.33	0.41	

Table A-2 Pairwise correlation coefficients and corresponding p-values (italicized) for physiological status variables (Res = weight-at-length residuals, Energy = energy density, Length = ln (length) CV =coefficient of variation of length).

	Res	**Energy**	**CPUE**	**Length**	**CV**
Res		*0.322*	*0.388*	*0.300*	*0.0305*
Energy	0.256		*0.179*	*0.097*	*0.207*
CPUE	-0.224	0.342		*0.196*	*0.103*
Length	0.267	0.416	0.330		*0.294*
CV	0.264	-0.322	-0.409	-0.270	

Appendix B: Linear mixed effects model results

Table B-1 Linear mixed effects model results for ln (length) (mm), weight-at-length residuals and energy density values (j/g ww). Significant variables are shown in bold p-values.

Model					Error	
	Coefficients	SE	DF	p-value	σ_a	σ_ε
Weight-at-length Residuals						
$WL\ residuals_{i,thj} = \alpha_t + \gamma_h + \omega_j + \alpha_t*\gamma_h + \alpha_t*\omega_j + \gamma_h*\omega_j + \varepsilon_{i,thj}$					0.04	0.1
Year	-0.04	0.01	677	**0**		
Habitat	-0.16	0.03	25	**0**		
Stock	0.02	0.01	677	**0**		
Energy						
$Energy_{i,th} = \alpha_t + \gamma_h + \alpha_t*\gamma_h + \varepsilon_{i,th}$					25.4	212
Year	169.75	63.99	44	**0.01**		
Habitat	-276.73	67.56	27	**0**		
Year:Habitat	-206.59	104.26	44	**0.05**		
Ln (Length)						
Strait						
$Ln(Length)_{i,tj} = \alpha_t + \omega_j + \alpha_t*\omega_j + \varepsilon_{i,tj}$					0.05	0.1
Year	-0.02	0.03	21	0.407		
Stock	-0.06	0.01	480	**0**		
EGOA						
$Ln(Length)_{i,tj} = \alpha_t + \omega_j + \alpha_t*\omega_j + \varepsilon_{i,tj}$					0.14	0.1
Year	-0.07	0.06	21	0.232		
Stock	-0.04	0.02	172	**0.05**		

Table B-2 Linear mixed-effects model comparisons for weight-at-length residuals (WL residuals), length and energy using Akaike information criterion (AICc). The best model is in bold. DF = degrees of freedom and Δ AICc is the difference in the AICc value of the two models

Model	DF	Δ AICc
<u>Weight-at-Length Residuals</u>		
1) $WL\ residuals_{i,thj} = \alpha_t + a_k + \gamma_h + \omega_j + \alpha_t * \gamma_h + \alpha_t * \omega_j + \gamma_h * \omega_j + \varepsilon_{i,thj}$	9	23.2
2) $\boldsymbol{WL\ residuals_{i,thj} = \alpha_t + a_k + \gamma_h + \omega_j + \varepsilon_{i,thj}}$	6	
<u>Energy</u>		
5) $\boldsymbol{Energy_{i,th} = \alpha_t + a_k + \gamma_h + \alpha_t * \gamma_h + \varepsilon_{i,th}}$	6	12.6
6) $Energy_{i,th} = \alpha_t + a_k + \gamma_h + \varepsilon_{i,th}$	5	
<u>Length</u>		
Icy Strait		
1) $Ln(length)_{i,tj} = \alpha_t + a_k + \omega_j + \alpha_t * \omega_j + \varepsilon_{i,tj}$	6	1.1
2) $\boldsymbol{Ln(length)_{i,tj} = \alpha_t + a_k + \omega_j + \varepsilon_{i,tj}}$	5	
EGOA		
1) $Ln(length)_{i,tj} = \alpha_t + a_k + \omega_j + \alpha_t * \omega_j + \varepsilon_{i,tj}$	6	1.8
2) $\boldsymbol{Ln(length)_{i,tj} = \alpha_t + a_k + \omega_j + \varepsilon_{i,tj}}$	5	

Table B-3 Linear mixed effects model results and raw data results for a) mean length (mm), b) weight-at-length residuals and c) energy density values (j/g ww) by habitat, stock and year. Error terms related to station variability are shown for each model.

a)

<table>
<tr><th colspan="7">LENGTH</th></tr>
<tr><td colspan="3">$Ln(Length)_{i,tj} = \alpha_t + \omega_j + \varepsilon_{i,tj}$</td><td colspan="4">Error</td></tr>
<tr><td colspan="3">*(habitats evaluated independently)*</td><td>σ_a</td><td>0.13</td><td>σ_ε</td><td>0.10</td></tr>
<tr><td>Habitat</td><td>Stock</td><td>Year</td><td>Model Mean</td><td>SE</td><td>Actual Mean</td><td>SE</td></tr>
<tr><td rowspan="4">EGOA</td><td rowspan="2">Hatchery</td><td>2010</td><td>134.42</td><td>0.05</td><td>117.88</td><td>0.02</td></tr>
<tr><td>2011</td><td>124.59</td><td>0.04</td><td>121.08</td><td>0.02</td></tr>
<tr><td rowspan="2">Wild</td><td>2010</td><td>129.67</td><td>0.05</td><td>118.64</td><td>0.02</td></tr>
<tr><td>2011</td><td>120.06</td><td>0.04</td><td>134.67</td><td>0.03</td></tr>
<tr><td></td><td></td><td></td><td>σ_a</td><td>0.05</td><td>σ_ε</td><td>0.10</td></tr>
<tr><td rowspan="4">STRAIT</td><td rowspan="2">Hatchery</td><td>2010</td><td>129.36</td><td>0.02</td><td>129.61</td><td>0.01</td></tr>
<tr><td>2011</td><td>126.59</td><td>0.02</td><td>124.66</td><td>0.01</td></tr>
<tr><td rowspan="2">Wild</td><td>2010</td><td>121.35</td><td>0.02</td><td>120.30</td><td>0.01</td></tr>
<tr><td>2011</td><td>121.35</td><td>0.02</td><td>119.26</td><td>0.01</td></tr>
</table>

Table B-3, continued
b)

WEIGHT-AT-LENGTH RESIDUALS						
Model			Error			
$WL\ residuals_{i,tjh} = \alpha_t + \omega_j + \gamma_h + \varepsilon_{i,tjh}$			σ_a	0.044	σ_ε	0.066
Habitat	Stock	Year	Model Mean	SE	Actual Mean	SE
EGOA	Hatchery	2010	0.12	0.015	0.10	0.009
		2011	0.08	0.013	0.07	0.013
	Wild	2010	0.13	0.015	0.11	0.009
		2011	0.10	0.013	0.14	0.019
STRAIT	Hatchery	2010	-0.05	0.012	-0.04	0.005
		2011	-0.08	0.014	-0.02	0.006
	Wild	2010	-0.03	0.012	-0.07	0.007
		2011	-0.07	0.014	-0.05	0.007

Table B-3, continued
c)

ENERGY DENSITY					
Model		Error			
$Energy_{i,th} = \alpha_t + \gamma_h + \alpha_t * \gamma_h + \varepsilon_{i,th}$		σ_a	25.42	σ_ε	211.79
Habitat	Year	Model Mean	SE	Actual Mean	SE
EGOA	2010	4631.98	44.75	4631.88	53.17
	2011	4801.74	45.74	4801.28	43.01
STRAIT	2010	4355.25	50.62	4355.86	48.4
	2011	4318.42	68.76	4317.03	22.8

Appendix C: IACUC approval

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Institutional Animal Care and Use Committee

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Fairbanks, Alaska 99775-7270

February 8, 2011

To: Franz Mueter, Ph.D

Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [192445-3] Surviving the Gauntlet: A comparative study of the pelagic, demersal, and spatial linkages that determine groundfish recruitment and diversity in the Gulf of Alaska ecosystem

The IACUC reviewed and approved the New Project referenced below by Designated Member Review.

Received: February 8, 2011

Approval Date: February 8, 2011

Initial Approval Date: February 8, 2011

Expiration Date: February 8, 2012

This action is included on the February 16, 2011 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.