

Trophic Relationships Among Juvenile Salmon During a 16-Year Time Series of Climate Variability in Southeast Alaska

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Early marine survival of juvenile Pacific salmon (*Oncorhynchus* spp.) has been linked to growth related to marine temperatures and feeding conditions during the first few months in the ocean (Mortensen et al. 2000; Farley et al. 2007; Saito et al. 2009). These relationships for juvenile salmon have been contrasted among coastal regions (Brodeur et al. 2007) and variable environmental conditions in the coastal waters of the Bering Sea (Karpenko et al. 2007; Andrews et al. 2009; Moss et al. 2009), Prince William Sound (Armstrong et al. 2008; Cross et al. 2008), and Southeast Alaska (Landingham et al. 1998; Mortensen et al. 2000; Weitkamp and Sturdevant 2008; Sturdevant et al. 2012c). However, less is known about these relationships for most juvenile salmon over an extended time series characterized by climate change (Miller et al. 2013; Orsi et al. 2013).

To address how trophic linkages and nutritional condition may shift over long-term periods of environmental change, we examined a 16-year time series in groups of warm and cold years for juvenile pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), and coho (*O. kisutch*) salmon. Trophic data included July diet composition and feeding intensity, and nutritional condition (energy density and body size) from Icy Strait (58°N, 135°W), Southeast Alaska. Typically, an $n \leq 10$ diet and $n \leq 20$ energy subsamples of average-size fish per species and year were selected from annual Southeast Coastal Monitoring (SECM) project trawl sampling in Icy Strait during daylight hours (0700-1900) between 21-31 July, 1997-2012 (Orsi et al. 2012). However, to meet sample size criteria, a few coho salmon diet and energy samples were collected from inshore and coastal stations in 1997, but no coho salmon energy samples were available in 1999. A few pink and chum salmon diet samples were supplemented from night trawls in 2004. Warm and cold years were defined by annual deviations from the long-term average of the Icy Strait Temperature Index (ISTI, mean °C, 20-m integrated water column) calculated across the months of May, June, July, and August at $n = 8$ SECM stations in Icy Strait (Fig. 1). The ISTI is significantly correlated with the climate Multivariate ENSO Index (MEI, averaged from November to March, lagged by one year; Sturdevant et al. 2012a; Orsi et al. 2013a), indicating that broad scale climate patterns can be detected in regional signals. We identified nine warm years (mean 9.6°C; range 9.3–10.3°C) and seven cold years (mean 8.8°C; range 8.3–9.0°C) in the 16-year time series (Fig. 1), although monthly anomalies were variable (Sturdevant et al. 2012b).

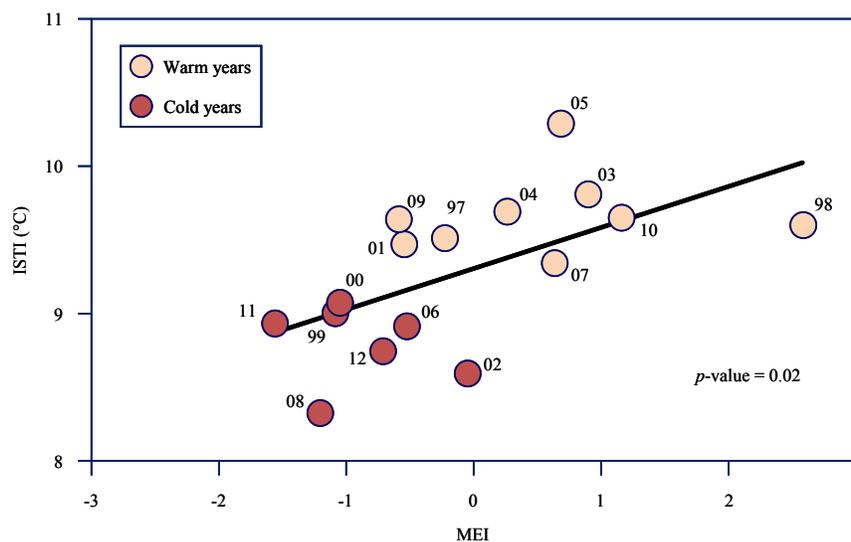


Fig. 1. Warm and cold years were categorized by anomalies of the Icy Strait Temperature Index (ISTI, °C) and correlated with the Multivariate ENSO Index (MEI, averaged from November to March, lagged by one year).

In the laboratory, individual fish examined for diet and feeding intensity were also analyzed for nutritional condition. After the length and weight were measured (fork length, FL, mm; wet weight, g), stomach contents were removed and examined microscopically to identify prey into groups by taxa, species, and stages, when possible. Each prey group was weighed and enumerated, when possible, and the percent weight composition (% weight) was summarized by eight prey categories. Feeding intensity was described by a gut fullness index and percent body weight (% body weight = total prey wt / (fish weight – prey weight) X 100). Energy density was determined as (small) cal/g dry weight (DW) by calorimetry. We tested for species differences in feeding intensity and nutritional condition between warm and cold years using one-way analysis of variance (ANOVA), followed by Tukey's paired comparison tests when significant differences were detected. To identify trophic relationships, overall diet composition was compared among the species between warm and cold years using a multivariate ordination routine (nMDS) based on the Bray-Curtis similarities from square-root transformed percent weight data.

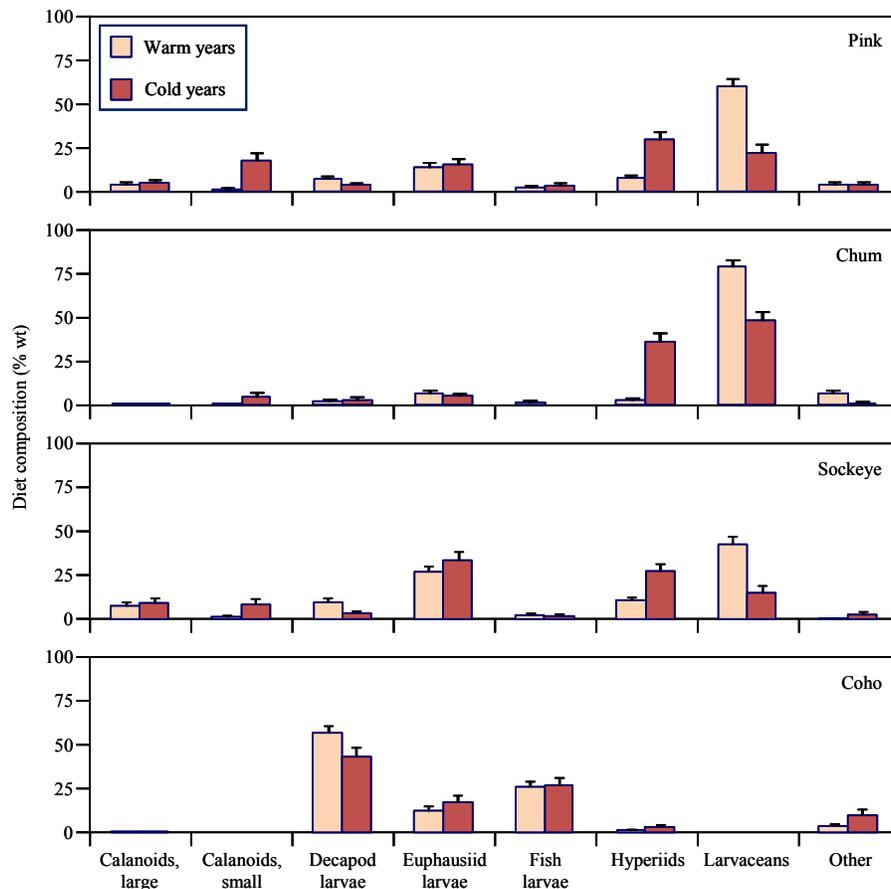


Fig. 2. Mean diet composition (percent weight, % wt) of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

Overall, juvenile pink, chum, and sockeye salmon were planktivorous, whereas juvenile coho salmon consumed a mixed diet of crab larvae and fish larvae (Figs. 2 and 3). Diets differed between warm and cold years only for the planktivorous species. These diets were diverse and consisted of large (≥ 2.5 mm) and small copepod (< 2.5 mm) taxa, decapod, euphausiid, fish larvae, hyperiid amphipods, and larvaceans. From warm years to cold years, planktivore prey utilization shifted from larvaceans to hyperiids and from large to small copepods, with an overall decrease in consumption of decapod larvae. Diets of the more piscivorous juvenile coho salmon consisted of fish, decapod, and euphausiid larvae. Fish and decapod larvae were prominent prey in both warm and cold years, and only minor shifts ($\leq 13\%$ weight) in prey utilization were evident; however, we did not examine fish prey species, which could vary between warm and cold years. Predation on decapod and euphausiid larvae by juvenile coho salmon is common throughout much of its range along the coasts of Washington, British Columbia, and Alaska (Brodeur et al. 2007; Sweeting and Beamish 2009; Cook and Sturdevant 2013).

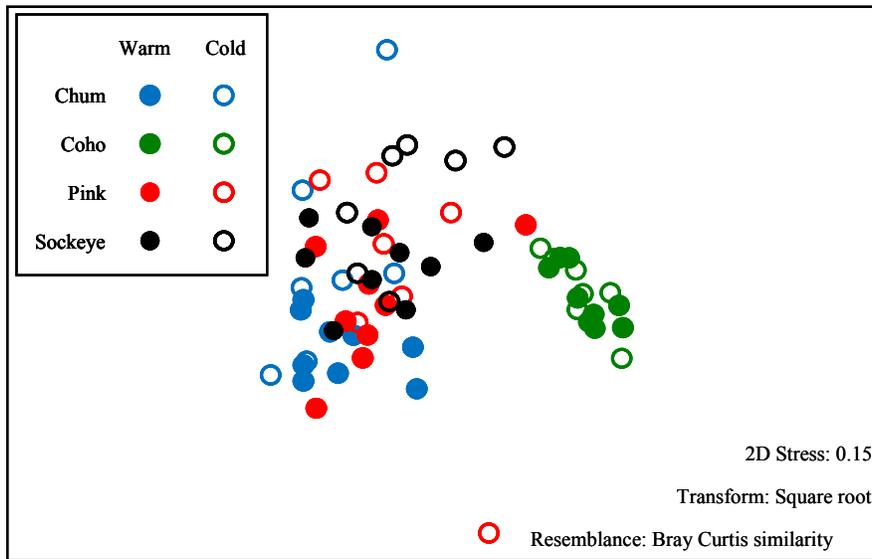


Fig. 3. Multivariate ordination of total diet composition of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012. Each symbol represents one year.

Overall, the nMDS indicated that diet differences between planktivorous pink, chum, and sockeye salmon and piscivorous coho salmon were stronger than diet differences between warm and cold years. Similarly, Sturdevant et al. (2012a) did not find a significant climate effect on adult fish predator diets between warm and cold years. Juvenile planktivorous-fish diet composition was similar to diets of juvenile salmon in the Bering Sea, Gulf of Alaska, and Puget Sound; however, fish prey was typically a much lower proportion of the diets in our samples (Boldt and Haldorson 2003; Brodeur et al. 2007; Farley et al. 2007; Bollens et al. 2010; Cook and Sturdevant 2013). A notable difference is that pteropods, a taxon linked to growth and survival for Gulf of Alaska juvenile pink salmon (Armstrong et al. 2008), contributed little to Southeast Alaska juvenile pink summer diets despite being prominent in adult pink salmon diets (Sturdevant et al. 2012a). This shift in prey composition in planktivorous juvenile salmon diets coincides with strong seasonal patterns of zooplankton composition and abundance that are related to climate in both the Gulf of Alaska and Southeast Alaska. For example, in warm years as compared to cold years in the Bering Sea, abundance of both euphausiids and the large copepod *Calanus marshallae* increased, while both hyperiid amphipods and the small copepod *Acartia sp.* (the predominant small copepod in Southeast Alaska juvenile salmon diets) decreased (Coyle et al. 2011). Similarly, climate-related monthly and interannual shifts in the timing of predominant zooplankton were suggested for conditions in Southeast Alaska (Sturdevant et al. 2012b). These shifts in predominant prey abundance suggest that planktivorous fish diets will also shift in response to changes in climate (Coyle et al. 2011) and likely explains the gradient in diet composition that we observed between warm and cold years in the nMDS results.

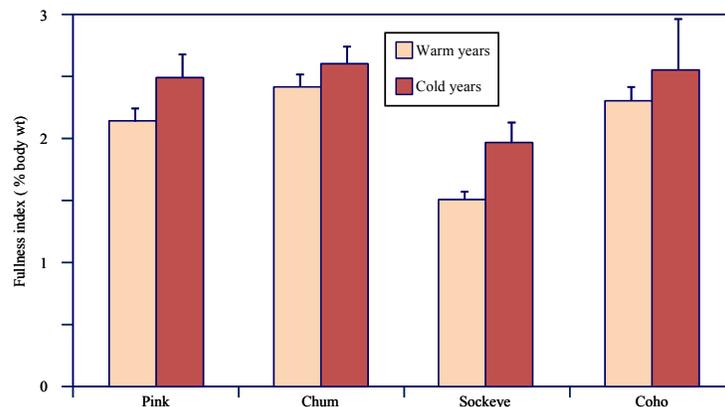


Fig. 4. Mean feeding intensity (stomach fullness index, % body weight) of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

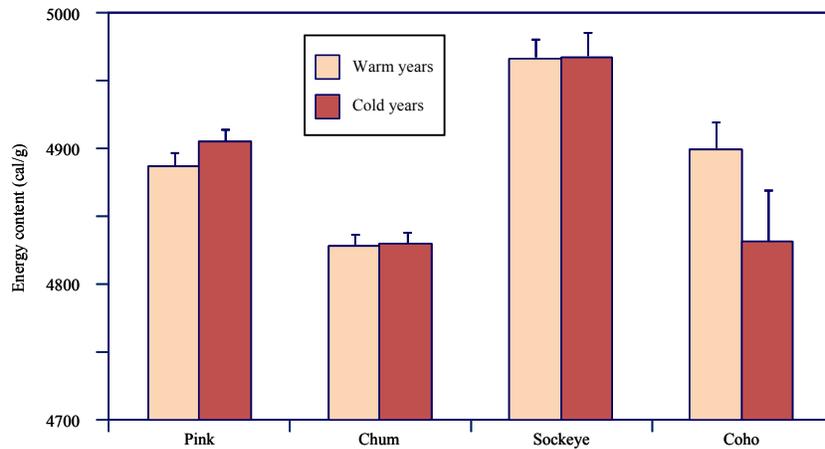


Fig. 5. Mean energy density (cal/g dry weight) determinations of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

Like diet composition, differences in feeding intensity and juvenile salmon nutritional condition were more common between species than between warm and cold years (Figs. 4–6). Feeding intensity and energy density differed significantly ($p < 0.001$) between salmon species, but only species size differed between warm and cold years. Sockeye salmon had the lowest prey percentage of salmon body weight and chum salmon had the highest. This might have resulted from differences in their primary prey species (euphausiids vs. oikopleurans; Fig. 2) or from differences in salmon body size, as prey percentage of body weight decreases with size (Fig. 6; Sturdevant et al. 2008). The percent body weight for all species increased slightly from warm to cold years. Energy density was lowest in chum salmon and highest in sockeye salmon, and only coho showed a decreasing trend from warm to cold years. These species-specific inverse patterns of feeding intensity, size, and energy density may reflect differences in trophic linkages; low energy, rapidly-digested larvaceans predominated in chum salmon diets in July compared to high energy crustaceans, such as euphausiids, observed in sockeye salmon diets (Landingham et al. 1998; Boldt and Haldorson 2003; Sturdevant et al. 2008). In addition, species differences in diel feeding periodicity and prey-specific evacuation rates have been shown for juvenile salmon in Southeast Alaska. Pink salmon fed intensively on euphausiid larvae mainly early and late in the day in August and September, coinciding with the diel migration of euphausiids, whereas chum salmon fed on oikopleurans throughout the day (Sturdevant et al. 2004). Nonetheless, chum salmon maintained a high daily ration by feeding on this low-energy prey due to rapid digestion and intensive feeding (Sturdevant et al. 2004, 2008). These differences suggest that salmon feeding intensity is affected not only by prey availability but by prey type, prey digestibility, and the salmon’s diel feeding rhythms (Benkwitt et al. 2009; Bollens et al. 2010).

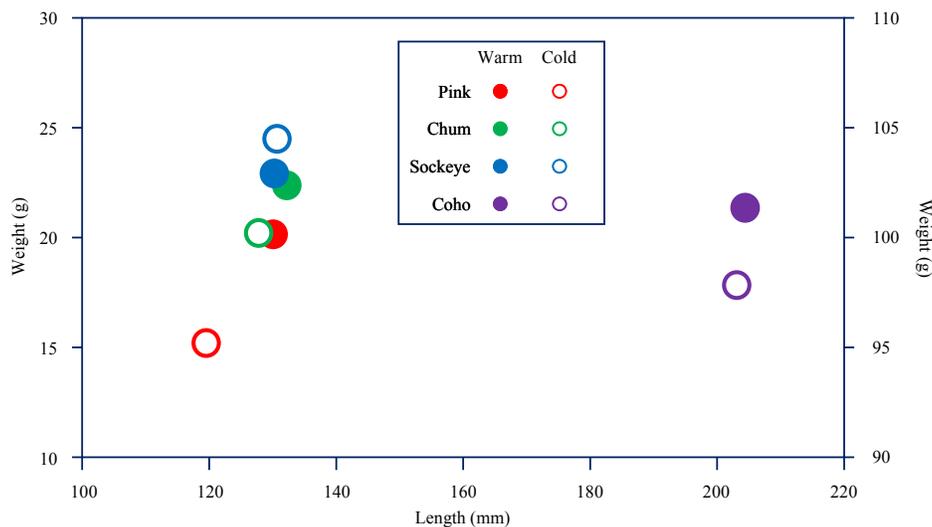


Fig. 6. Mean size (weight, g, and fork length, mm) of juvenile pink, chum, sockeye (left axis), and coho (right axis) salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

For juvenile pink, chum, and coho salmon, both length and weight were significantly ($p < 0.01$) greater in warm years; in contrast, sockeye salmon were significantly ($p < 0.01$) smaller in warm years (Fig. 6). This counter-intuitive result may be caused by an influx of high numbers of earlier-emigrating, small (age-0) sockeye in warm years (Heard et al. 2013). As size is directly influenced by growth related to water temperature, size could also be indirectly driven by prey availability (delayed plankton bloom in cold years), size-selective predation (smaller fish more likely to be eaten; Mortensen et al. 2000; Farley et al. 2007; Moss et al. 2009; Sturdevant et al. 2013), and differences in life history patterns.

In summary, juvenile salmon adapt their feeding to regional and local prey conditions mediated by habitat, physical environment, climate, and competitive interactions (Brodeur et al. 2007). While comparisons of the breadth and scope of salmon diet and condition among seasons and locales are important, the utility of our time series lies in the systematically-collected samples from a single migratory corridor in northern Southeast Alaska that is being comprehensively examined for biophysical, trophic, and climate linkages (Orsi et al. 2004, Fergusson et al. 2010; Orsi et al. 2012; Sturdevant et al. 2012a, b, c; Orsi et al. 2013). Our preliminary analysis of long-term juvenile salmon feeding ecology indicates a stable feeding gradient among the species with relatively little effect of climate on nutritional condition, and thus these co-occurring juvenile salmon are adapted for the current level of climate change experienced at this locale (on average, a 1°C temperature difference in the upper 20-m water column between warm and cold years). In Southeast Alaska, climate change may be more likely to affect life history parameters such as out-migration timing (Orsi et al. 2013; Sturdevant et al. 2013). Further analysis with this data set will include (1) adding additional years to the dataset as they become available, (2) analysis of interannual feeding patterns to identify years of particularly high influence, (3) examining prey selection from zooplankton prey suites, and (4) addition of juvenile Chinook salmon results to the time series.

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