

Potential for Competition Among Herring and Juvenile Salmon Species in Puget Sound, Washington

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Keywords: spatial-temporal overlap, diet composition, diet overlap, feeding rate, consumption, competition, juvenile Pacific salmon, Pacific herring, Puget Sound

The importance of early marine life to the survival of Pacific salmon (*Oncorhynchus* spp.) is well-known (Simenstad et al. 1982, Beamish and Mahnken 2001, Beamish et al. 2004). Growth during the summer rearing period strongly influences salmon survival; juveniles must accumulate sufficient energy stores to reduce size-selective mortality processes. Faster early marine growth is associated with higher marine survival for Chinook salmon (*O. tshawytscha*; Tovey 1999, Duffy and Beauchamp 2011, Tomaro et al. 2012), coho salmon (*O. kisutch*; Beamish et al. 2004), and pink salmon (*O. gorbuscha*; Moss et al. 2005, Cross et al. 2009). However, competition among salmon species and other forage fishes has been linked to reduced growth (Cooney et al. 2001), likely because it limits availability of food resources that already vary naturally.

Puget Sound, Washington State, provides an essential early marine growth environment for Pacific salmon, including Endangered Species Act-listed Chinook salmon (NMFS 1999). Juvenile Chinook salmon that grow bigger by July of their summer in Puget Sound experience significantly higher smolt-to-adult survival (Duffy and Beauchamp 2011). Much of this growth is achieved by feeding in the offshore epipelagic zone of Puget Sound. Variability in offshore growth within Puget Sound can be ascribed to variation in feeding rate (Duffy 2009). Therefore, factors which affect feeding success, such as competition, during this critical period could influence marine survival.

We used midwater trawl data from the main basin of Puget Sound (Central Puget Sound and Admiralty Inlet) to assess spatial-temporal overlap and dietary overlap between Pacific herring (*Clupea pallasii*) and juvenile salmon. We then used bioenergetics model simulations to calculate feeding rates (proportion of the theoretical maximum consumption) for each species.

Midwater trawl operations were conducted by Department of Fisheries and Oceans Canada (DFO) on the CCGS *W.E. Ricker* during July and September/October, 2001-2011 (except in 2003 and 2010, when no trawls were conducted). The trawl net deployed by DFO (model 250/350/14 midwater rope trawl; Cantrawl Pacific Ltd., Richmond, British Columbia) was approximately 14 m deep by 30 m wide when open at depth, it had a 10-cm mesh cod-end with a 1-cm liner for the hindmost 7.6 m of the cod-end, and the towing speed was 2.6 m/s (Beamish et al. 2000). Trawl operations were conducted during daylight at pre-determined, randomly varying 15-m depth increments with the greatest amount of effort at the surface layer (0-15 m).

Counts of all fish in the trawl catch were recorded by species. Hatchery-origin salmon were identified by the presence of coded-wire tags (CWTs) or adipose-fin clips, which comprised about 80% of the total juvenile Chinook catch. Unmarked salmon (no CWT, no clip) were assumed to be wild-origin. However, a low but unknown proportion of unmarked fish were likely of hatchery origin due to incomplete marking. Fork lengths were measured to the nearest 1 mm, and wet weights (WWs) were recorded to the nearest 0.1 g for sub-samples of up to 60 fish per species.

Stomach contents for subsamples of all salmon species were identified by DFO researchers. Herring samples were frozen whole for later analysis. Invertebrate prey items for each sample were separated into broad taxonomic categories (e.g., copepods, crab larvae, euphausiids, gammarid and hyperiid amphipods). Proportional volumetric (cm³) contribution of prey was estimated using each non-empty fish stomach as an individual sampling unit. Stomach contents of frozen herring were analyzed at the University of Washington using dissecting microscopes and following the DFO taxonomic categories. Blotted wet weights of prey categories were measured using an electronic scale and recorded to the nearest 0.0001 g. Proportional wet weight (g) contribution of prey was calculated using each non-empty fish stomach as an individual sampling unit. Diet overlap between species was calculated using the Schoener index (Wallace 1981).

We used the Wisconsin bioenergetics model to estimate feeding rates for salmon species and herring over the July-September/October period. This model uses an energy-balance approach, where consumption over a period is fitted to observed growth, while accounting for time-varying thermal, allometric, and dietary effects on metabolic costs, and waste losses over the same period. Model inputs include the thermal experience, diet, prey and predator energy densities, and growth of the consumer. We used default physiological parameters for Chinook and coho salmon, and substituted pink salmon parameters for chum salmon. Atlantic herring model parameters were used for Pacific herring. We used water temperatures at the top of the trawl net as thermal inputs, average proportional diet composition, literature values for prey energy densities, and apparent growth (Δ WW of the mean individual from July to September).

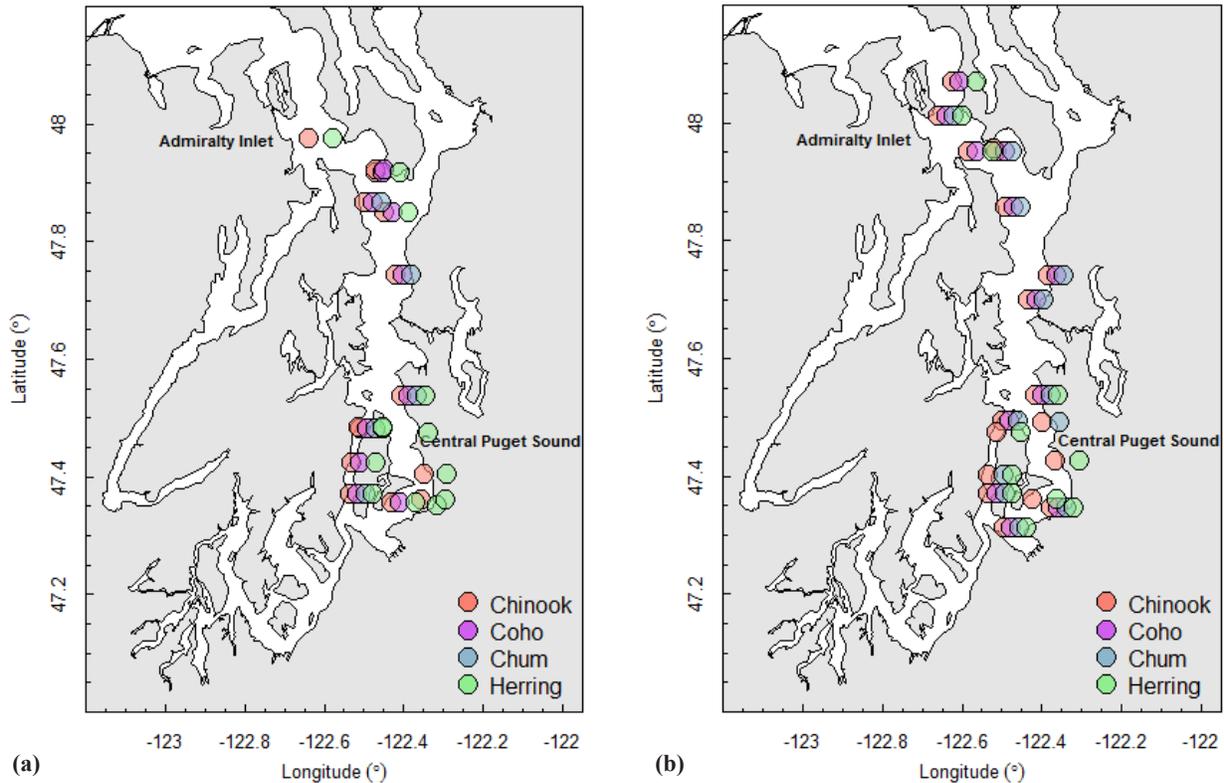


Fig. 1. Presence of Chinook, coho, and chum salmon and herring in 2011 July (a) and September (b) trawl operations conducted in the main basin of Puget Sound, Washington. Each set of dots represents one trawl operation.

Pacific herring dominated the biomass of the shallow pelagic planktivorous fish community and exhibited varying degrees of spatial and dietary overlap with juvenile Chinook, coho, and chum salmon during this critical period, thus creating potential for competition. Salmon species and herring consistently composed the majority of the catch, and they were often found together in trawl catches (e.g., 2011; Fig. 1). Over the years sampled, all four species co-occurred in 44% of trawls conducted in July, and juvenile Chinook salmon and herring occurred concurrently in 70% of trawls in July. In September/October, 23% of trawls contained all four species, and Chinook salmon and herring occurred concurrently in 42% of trawls. Most salmon and herring were found in the upper layers of the water column (0-30 m), particularly in July (Fig. 2).

Proportional diet compositions of juvenile salmon and herring species in July and September/October show similarity among species. Diets of Chinook and coho salmon were most similar, followed by herring, and least similar was chum salmon (Figs. 3 and 4). In July, Chinook and coho salmon and herring consumed diets consisting of large proportions of crab larvae. In September, Chinook salmon tended to eat more fish, although the overall diet composition remained diverse. Coho salmon diets in September relied on gammarid amphipods. Copepods (mainly calanoid) were important prey for herring. The post-analytically grouped “other” category was periodically important prey for chum salmon and herring. In the case of herring, this category was mainly barnacles, ostracods, polychaetes, and unidentified material. For chum salmon, this category consisted mostly of larvaceans (*Oikopleura* sp.), ctenophores, ostracods, chaetognaths, and unidentified material.

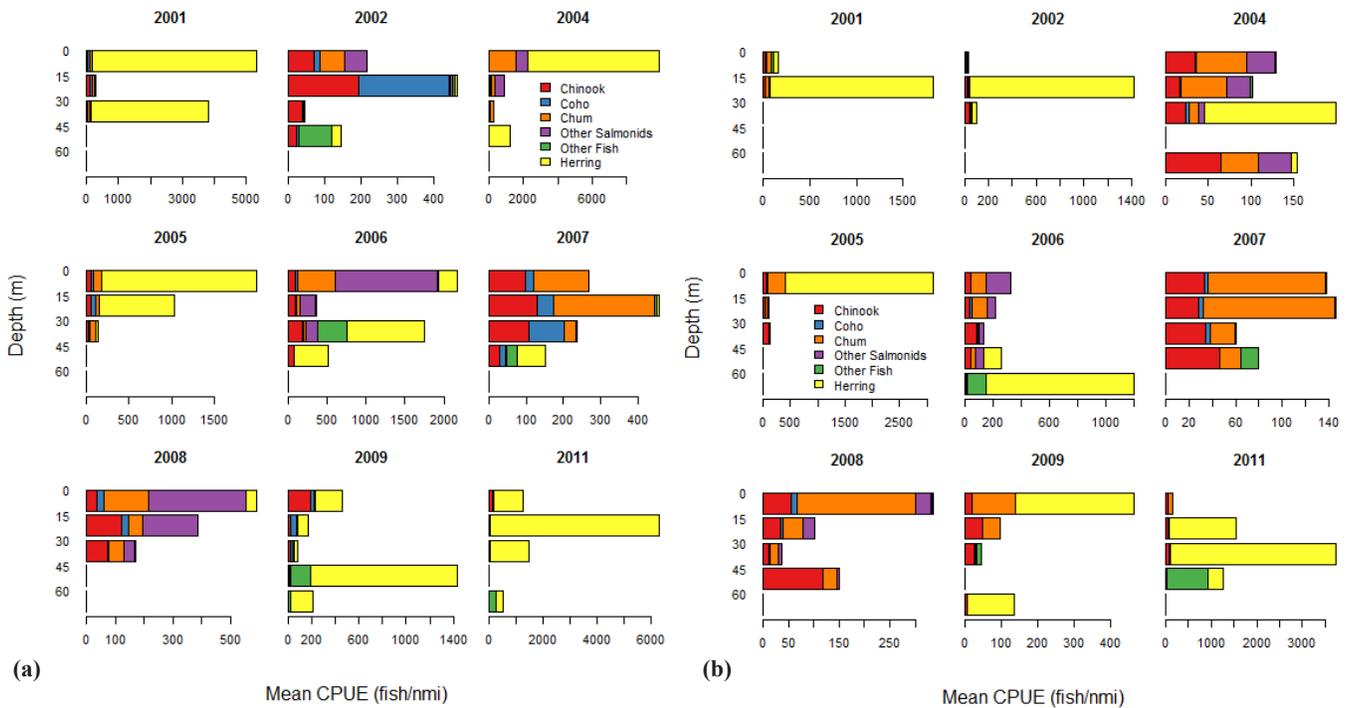


Fig. 2. Annual mean catch per unit of effort (fish/nmi) at depth strata in the water column in July (a) and September/October (b). Trawl operations conducted in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted). The category “other salmonids” includes 24 sockeye salmon (*O. nerka*), 1 steelhead (*O. mykiss*), and 112 pink salmon (*O. gorbuscha*). Note that x-axes are not constant, reflecting the large variability in catches (particularly herring) among years.

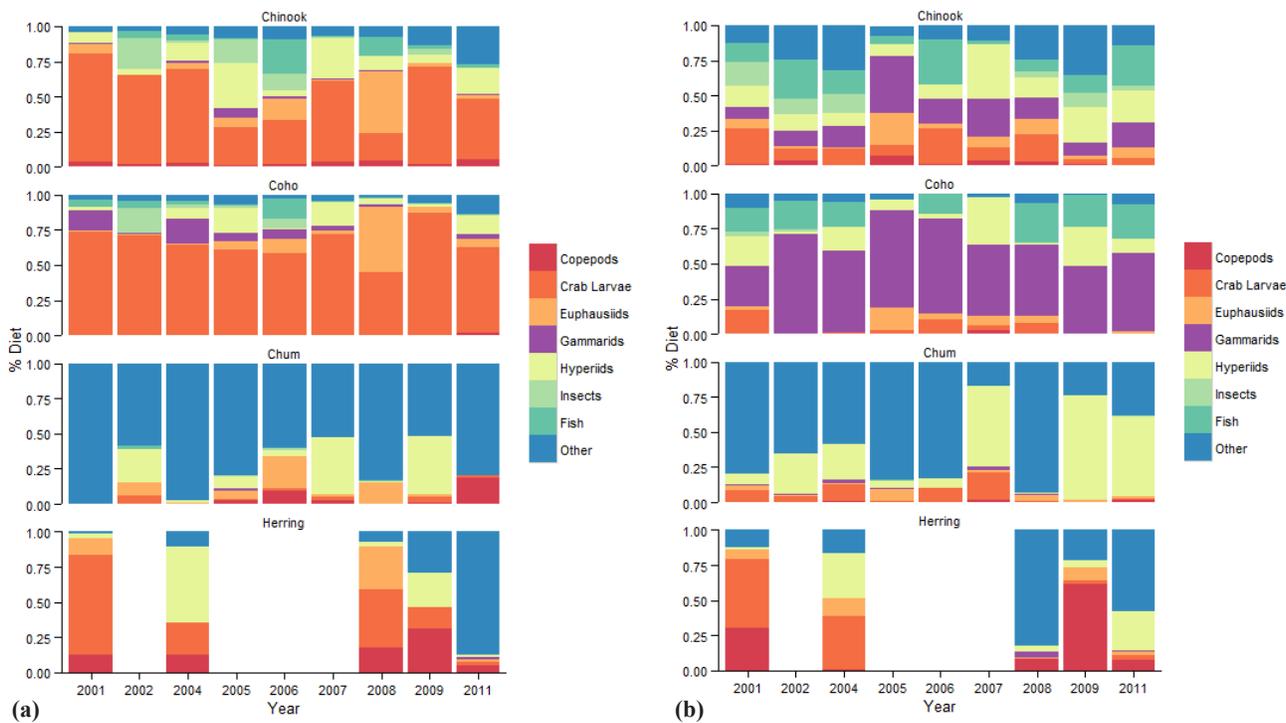


Fig. 3. Interannual comparison of the proportional diet composition by mass or volume for Chinook, coho, and chum salmon and herring in July (a) and September/October (b). Samples collected in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted).

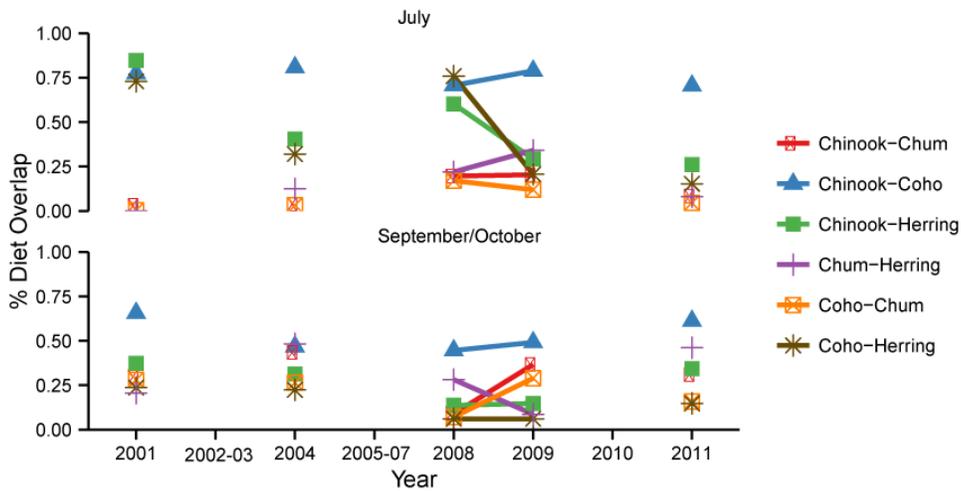


Fig. 4. Seasonal and interannual variation in diet overlap for each species pair in July (top panel) and September/October (bottom panel). Samples collected in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted).

In general, diet overlap between species was higher in July than in September (Fig. 4). Chinook and coho salmon had the greatest amount of diet overlap for both months and across years. Additionally, Chinook and coho salmon diet relationships with the other species appeared similar. Feeding rates varied interannually for all salmon species (Fig. 5). Interannual variability in herring feeding is more difficult to assess, given the lack of a consistent time series. Herring were separated into approximate age classes by size; age-1 herring was the only age-class that we were able to sample consistently over the years from July to September.

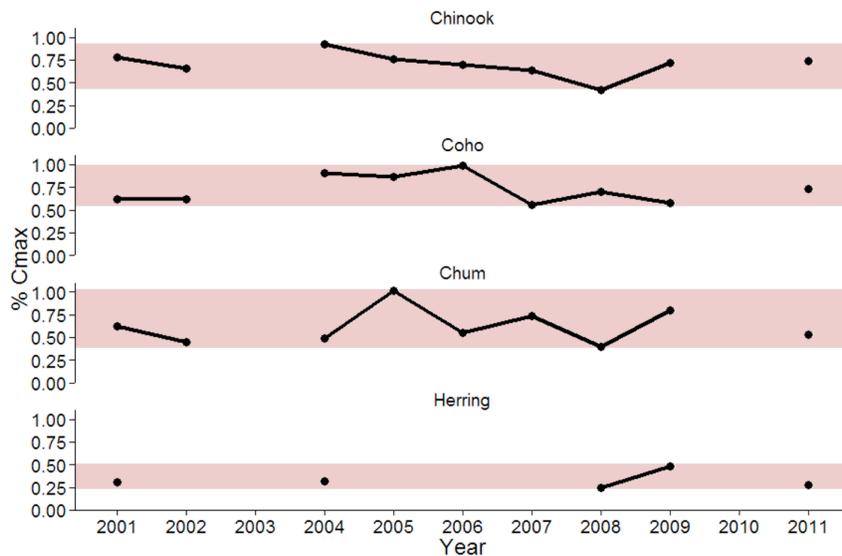


Fig. 5. Interannual variability in feeding rates of age-0 Chinook, coho, and chum salmon, and age-1 herring collected in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted). Feeding rate ($\%C_{max}$) is expressed as the percentage of the theoretical maximum consumption based on bioenergetics simulations for each species.

During the summer growth period in Puget Sound, juvenile salmon and herring exhibit generally high spatial-temporal overlap and variable but often high dietary overlap. Because of their greater population biomass, herring have the potential to remove substantially more of the prey base than do salmon. These observations, paired with previous research linking variable feeding rates and growth to variable survival for Chinook salmon (Beauchamp and Duffy 2011), are consistent with

the hypothesis that competition influences feeding over the summer growth period, thereby affecting marine survival rates of Puget Sound Chinook salmon. Our results suggest that any assessment of marine carrying capacity will need to account for the population and feeding dynamics of all major daylight planktivores in Puget Sound.

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