Spatial-temporal patterns in distribution and feeding of juvenile salmon and herring in Puget Sound, WA

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Abstract

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This study described the distribution and feeding of juvenile salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasi*) in Puget Sound to explore the potential for resource competition among these species. We used surface townets, midwater trawls, and acoustics surveys to assess distributions of fish in surface waters, among bathymetric zones, and depth strata in the water column. Seasonal and spatial variability was evident in epipelagic biomass. Occurrence of biomass generally increased progressively during the summer and shifted to deeper depths. Despite considerable variability, spatial, temporal, and dietary overlap was observed among herring and juvenile salmon, especially for Chinook and coho salmon. Crab larvae and amphipods were important prey for most salmon species and herring. Herring were present in higher abundances than salmon and had high population-level consumption demand. If food resources are limiting, there is potential for competitive interactions among salmon and herring.

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Introduction

Estuaries provide important rearing and forage habitat for a variety of fish species and, in many cases, are considered essential fish habitat (Roni et al. 1999, NOAA-NMFS 2007). However, because estuaries also provide a variety of natural resources to human populations, they are often negatively affected by human activities, such as pollution and shoreline modification (Sarthou 1999, Simenstad et al. 2011, Cereghino et al. 2012, Morley et al. 2012). Understanding the dynamics of fish communities that utilize estuarine habitats can provide guidelines to address these concerns.

Puget Sound, a large estuary in the northwest corner of Washington State, provides rearing and foraging habitat for many fish species. It also serves as a nursery area and migratory corridor for anadromous Pacific salmon (*Oncorhynchus* spp.) populations, several of which are currently listed as threatened under the Endangered Species Act (NMFS 1999, 2007). Typically, salmon utilize nearshore, epibenthic habitats upon estuarine entry and later transition to offshore, pelagic habitats in preparation for outmigration to the ocean environment (Feller and Kaczynski 1975, Beamish et al. 1998, Duffy et al. 2010). A sizeable body of work exists on the importance of nearshore Puget Sound habitats to salmon (Meyer 1979, Fresh et al. 1981, Simenstad et al. 1982, Aitken 1998, Duffy 2003, Brennan et al. 2004, Weitkamp 2010). Salmon use of pelagic habitats in Puget Sound has not been well-characterized, although evidence suggests that these habitats offer important growth opportunities (Beauchamp and Duffy 2011). Additionally, interactions among salmon and other small pelagic fishes in Puget Sound are not well-understood, although forage fishes play an important role in the Puget Sound community (Penttila 2007).

We present data from nearly a decade of midwater trawl surveys in offshore habitats of Puget Sound. To our knowledge, this dataset is the only long-term offshore pelagic dataset that exists for Puget Sound. We combine observations from this dataset with surface townetting data in shallow habitats close to shore and acoustics data which span bathymetric zones across Puget Sound in order to assess fish distributions across Puget Sound, and discuss the potential for competitive interactions among juvenile salmon species and Pacific herring (*Clupea pallasi*).

Chapter Objectives

Chapter 1 pairs acoustics and net data to characterize patterns in vertical and horizontal distribution of epipelagic acoustic backscatter by basin over April-October in three areas (shallow shelf zones, transition zones, and deep offshore zones), link backscatter patterns to observed species distributions, and describe seasonal patterns in relative biomass as measured by three gear types: acoustic surveys, midwater trawls, and surface townets.

Chapter 2 describes spatial and temporal patterns in epipelagic diet composition of Pacific herring and juvenile salmon, quantifies diet overlaps among species, and estimates population-level consumption demand of each species over the summer growth period (July-September).

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Chapter I: Spatial-temporal distribution of juvenile salmon and forage fish in Puget Sound: seasonal habitat use

Abstract

Fishes often utilize multiple habitats over the course of their estuarine residence. Puget Sound, WA, provides epipelagic habitat to a variety of species, including declining populations of (Pacific herring, *Clupea pallasi*) and Endangered Species Act-listed Pacific salmon (*Oncorhynchus* spp). Currently, little is known about epipelagic habitat use by the fish community in Puget Sound. We used surface townetting, midwater trawling, and hydroacoustic data to characterize epipelagic fish distribution from April through October, 2011 in four basins of Puget Sound. Seasonal and spatial variability was evident in epipelagic biomass (fish and jellyfish). Biomass generally increased progressively during the summer and shifted to deeper depths. Biomass was observed more often in the offshore zone than in shelf and transition zones. Net catches indicated that herring and juvenile salmon species dominated the epipelagic fish community and exhibited considerable spatial and temporal overlap with one another. Spatial and temporal patterns in fish biomass sampled by surface townets generally reflected the patterns measured below the surface by acoustics. In July and September, when midwater trawl data were also available, acoustics and midwater trawls produced closer relative estimates to one another than to the surface townets. The spatial-temporal overlap among species and increase in biomass over the summer period create increased potential for species interactions, especially in the offshore zone.

Introduction

Pelagic communities support a wide variety of vertebrates, including planktivorous and piscivorous fishes, birds, marine mammals, and humans. Protection of habitat for these species is often an important management concern (Minello 1999, Sarthou 1999, Beck et al. 2001, Able 2005). Legislative efforts in the United States have mirrored this concern, mandating the protection and management of oceanic species that utilize open ocean and continental shelf habitats and anadromous species that use estuarine and riverine habitats for reproduction (Magnuson-Stevens Fishery Conservation and Management Act, amended NOAA-NMFS 2007). The importance of habitats to a fish species can be assessed by their presence/absence, densities, growth, or production (Searcy et al. 2007). However, determining fish distribution and habitat use at any given time can be complicated. Certain locations are more accessible to observation than others (e.g., shoreline habitats are easily delineated and sampled, whereas offshore habitats require more consideration and often specialized sampling gear). Additionally, many fish species occupy multiple habitat types (e.g., migration) or utilize one habitat in different ways (e.g., feeding shifts) over the course of their lifespans (Minello 1999, Roni et al. 1999).

In Puget Sound, WA, Pacific salmon (*Oncorhynchus* spp.) exhibit transitions from estuarine and nearshore marine neustonic- and epibenthic-feeding to offshore epipelagic-feeding behaviors before emigrating to the open ocean (Feller and Kaczynski 1975, Beamish et al. 1998, Duffy et al. 2010, Claxton et al. 2013). The timing and size at transition varies by species and life history type, as does the relative value of habitat among and within species and life history types (Meyer 1979, Simenstad et al. 1982, Aitken 1998, Roni et al. 1999). Estuarine, nearshore, and epipelagic habitats serve as important rearing areas through the early marine ontogeny of salmon (Duffy et al. 2005a, Beauchamp and Duffy 2011).

Although small-scale studies on salmon habitat use have been fairly common in nearshore habitats over the past few decades (Weitkamp 2010), few researchers have focused on relating seasonal habitat use by salmon to habitat use by other far more numerous small pelagic fishes in Puget Sound – most notably, populations of Pacific herring (*Clupea pallasi*), surf smelt (*Hypomesus pretiosus*), and sand lance (*Ammodytes hexapterus*) (Mitchell 2006, Penttila 2007, Rice et al. 2012). Assessing epipelagic habitat use within Puget Sound is an important step towards understanding resource availability and use by the pelagic Puget Sound fish community, and how these factors contribute to interspecific interactions.

This project was undertaken to characterize the distribution in epipelagic fish biomass in Puget Sound, specifically focusing on patterns in salmon and Pacific herring. We expected horizontal shifts in biomass with distance from shore and vertical shifts towards deeper depths in the water column as fish grew over the summer. Our specific objectives were to 1) characterize patterns in vertical and horizontal distribution of epipelagic acoustic backscatter by basin over April-October in three zones (shallow shelf, transition, and deep offshore), 2) pair acoustics data with net data to make inferences about the distribution of species in these areas, and 3) describe seasonal patterns in relative biomass as measured by three gear types: acoustic surveys, midwater trawls, and surface townets.

Study Area

Puget Sound is a glacially-formed estuary in northwest Washington State that encompasses 2,329 km^2 to 2,632 km^2 over tidal cycles and connects to the rest of the Salish Sea via Admiralty Inlet and, in a lesser capacity, via Deception Pass and the Swinomish Slough (Burns 1985). Puget Sound is comprised of four bathymetrically-distinct basins separated by shallow sills: Whidbey Basin, Main Basin, Hood Canal, and South Sound. While there are water exchanges and organism movement among basins, each basin is generally viewed as a discrete entity (Burns 1985). Differences in physical properties (e.g., pH, dissolved oxygen, river discharge), anthropogenic influences (e.g., pollutant load, shoreline modifications) and biological patterns (e.g., abundance of zooplankton and fish, species composition) have been reported among basins (Duffy et al. 2005b, Greene et al. 2012, Rice et al. 2012). The epipelagic zone (i.e., surface to 60 m water column depth) of Puget Sound provides a large volume of rearing habitat for juvenile salmonids and forage fishes. Several of these species are listed as threatened under the Endangered Species Act (ESA): Chinook salmon (*O. tshawytscha*, NMFS 1999), steelhead (anadromous *O. mykiss*, NMFS 2007), and Hood Canal summer chum (*O. keta*, NMFS 1999). Other species, e.g., Pacific herring populations, have experienced declines (Hayes and Landis 2004, Landis et al. 2004, Reum et al. 2011, Siple unpub. data) and age-structure collapses (Landis and Bryant 2010) or remain largely unassessed (Penttila 2007). Although these species depend on Puget Sound to complete some or all of their life cycles, little is currently understood about epipelagic habitat use in the Sound (Greene et al. 2012). In addition, there are different types of epipelagic habitat within each basin (e.g., shallow-bottom nearshore habitats vs. deeper-bottomed offshore habitats, and varying water column depths) that salmon and other forage fishes may exploit (Meyer 1979, Shepard 1981, Burns 1985, Fresh 2006, Beauchamp and Duffy 2011, Cereghino et al. 2012).

Methods

Survey design

Surface townetting, midwater trawl, and hydroacoustic survey data were collected during daylight hours between April and October 2011. The study area within Puget Sound extended from latitude 47.11° to 48.16° and longitude -122.75° to -122.26° (Fig. 1.1). Bottom depths ranged from 4 m to >280 m.

Surface townetting transects were performed monthly in Admiralty Inlet, Whidbey Basin, Central Puget Sound, and South Puget Sound by National Oceanographic and Atmospheric Administration Northwest Fisheries Science Center (NOAA-NWFSC; Greene et al. 2012). Monthly surface townet transects sampled the epipelagic waters along the 30-m isobath along shore. Depth-stratified midwater trawling was conducted in July and September in Admiralty Inlet and Central Puget Sound from the Canadian Coast Guard Ship (CCGS) W.E. Ricker (58 m length), operated by the Department of Fisheries and Oceans (DFO) Canada and the Canadian Coast Guard.

Hydroacoustic surveys were performed monthly from an aluminum Almar research vessel (7.3 m length). Monthly acoustic surveys consisted of nearshore zigzag transect segments that bracketed (both on-offshore and alongshore) a subset of the surface townet transects, followed by a cross-channel transect. Additional cross-channel transects coincided with midwater trawling by DFO. Acoustic transects were typically performed within one day of fish collections (1-3 hours for NOAA-NWFSC surface townet sites, same-day DFO sites). Each on-offshore zigzag transect typically extended over bottom depths of <50 m and was paired with a cross-channel transect perpendicular to shore over deep water across the entire basin. All transects were performed during daylight hours in wave heights of ≤1 m.

Data collection & processing

Acoustic data were collected using a BioSonics DE-6000 echosounder with a 201 kHz split-beam transducer (1 kW input power, major 3 dB beam angle 6.8°, equivalent beam angle 20.97 dB re 1 sr). The transducer was mounted on an aluminum towed body at approximately 1 m below the surface and towed at a speed of 2.2-2.7 m/s (4.3-5.2 kt). Acoustic data were obtained at a rate of 2 pings per second and pulse duration of 0.4 ms, with S_v (biomass standardized by volume sampled; S_v in dB re 1 m^{-1}, herein dB) minimum collection threshold of -65 dB to -70 dB. Data were collected to a maximum of 150 m, although bottom depths of the areas sampled often exceeded 150 m. The system was calibrated using Biosonics Visual Analyzer (Version 4.2, www.biosonicsinc.com) before April and after September with a standard tungsten carbide sphere.

All acoustic data analysis was performed in Echoview (Version 5.3.34.21868, Myriax Pty Ltd, www.echoview.com). Data files were each scrutinized for bottom identification, noise issues, and school detection. Regions of bad data, such as underwater bubbles created by turbulence, were visually identified and excluded from the analysis. An offset of 1 m from the analyst-corrected bottom was applied to eliminate bias from bottom data. In addition, we excluded data within 2 m of the transducer face. The speed of sound was assumed constant at 1486.57 m/s, given the range of salinities and temperatures found in Puget Sound over the spring-summer period (temperatures approximately 8-16°C and salinities approximately 20-31 ppt; Moore et al. 2008). An absorption coefficient of 0.0491 dB/m was used, based on pre-survey calibration. We applied a minimum analysis threshold of -65 dB to all acoustic data.

We focused on sampling epipelagic depths in the water column, because prior midwater trawling data indicated that this was the depth range used by forage fish and juvenile salmon over the study period (Beamish et al. 1998, Beauchamp and Duffy 2011). Almost all (97%) of the fish sampling (trawling, townetting) focused on water column depths shallower than 60 m. In most acoustic data files, a daytime scattering layer was apparent approximately 60 m below the surface. This layer was assumed to be primarily composed of euphausiids (Cooney 1971, Ross et al. 1982, Ohman et al. 1983), and was therefore excluded from the fish analysis. Distinction of fish biomass became ambiguous at depths greater than approximately 60 m due to the presence of the 60 m scattering layer and minimal net sampling at depths greater than 60 m. Acoustic patterns above 60 m in the water column were visually different than patterns below 60 m. Additionally, net sampling indicated that deeper water column layers were mainly occupied by non-target fishes like gadoids and spiny dogfish (*Squalus suckleyi*) during daylight. For these reasons, we limited our analysis to the upper 60 m of the water column. Acoustic backscatter within 60 m of the surface and above our -65 dB analysis threshold was assumed to be fish backscatter.

Fish were collected with surface townets monthly from April - September 2011 in all four regions. Surface townetting was performed using a Kodiak surface trawl (6.1 m wide x 3.1 m deep, 6 mm mesh cod-end) towed between two boats. These daylight tows typically covered areas as close to the shoreline as possible where bottom depth ranged from 4-54 m and lasted 10 minutes (see Greene et al. 2012 for additional details).

Midwater trawls were also performed in Central Sound and Admiralty Inlet during July and September 2011. The midwater trawl net deployed by DFO Canada (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 with a 10 cm mesh cod-end and 1 cm mesh liner for the hindmost 7.6 m of the cod-end. The net was fished at 5 kts for 20 minutes at depth from the vessel CCGS W.E. Ricker (see Beamish et al. 2000 for additional details). Midwater trawls were conducted during daylight with the headrope at 15 m depth increments in the water column (surface, 15 m, 30 m, 45 m, 60 m), with the greatest amount of effort at the surface. Trawls covered areas with bottom depths ranging from approximately 75-280 m.

Data analysis

Epipelagic fish biomass distribution from acoustics surveys

We characterized general spatial-temporal patterns of epipelagic fish distribution using echo integration of acoustic backscatter. Integrated acoustic backscatter was exported in 5 m vertical by 50 m horizontal bins for zigzag and cross-channel transects. In the event of missing GPS data, we interpolated between GPS values assuming a linear sampling track. Bottom depth served as an indicator of proximity to shore, and was used to split data into three categories: 0-50 m shallow shelf zones, 50-75 m transition zones, and >75 m deep offshore zones. Depth categories were chosen based on the range of bottom depths covered by other sampling efforts (surface townets: 4-54 m and midwater trawls: >75 m). Graphical results are presented as proportional integrated backscatter in the water column (s_A, also known as NASC, m^2/nmi^2). Model results are based on the linear form of mean volumetric backscatter (volume backscattering coefficient; s_v, m^{-1}) values for each bin.

Most (99.7%) of the variance in s_v depended on the presence/absence of biomass rather than the magnitude of biomass when present. Prior observations suggested that juvenile salmon occupied upper water column depths early in the summer and transitioned deeper in the water column over the summer growth period (Emmett et al. 2004). We tested this observation by dividing the water column into upper and lower categories: upper water column was defined as 0-30 m depth and lower water column was 30-60 m. We used generalized linear mixed-effects models with transect as a random effect to account for the lack of independence of acoustic segments along a transect, and tested for whether the presence of biomass was best predicted by month (April-October), region (Admiralty Inlet, Whidbey Basin, Central Puget Sound, South Puget Sound), zone (shelf, transition, offshore), water column depth (categorical: 0-30 m, 30-60 m), or interactions of these factors. All statistical analyses were conducted in the R Programming Environment using the vegan: Community Ecology package (Oksanen et al. 2012). Graphics were created using the PBSmapping (Schnute et al. 2012), reshape (Wickham 2007), and ggplot2 (Wickham 2009) packages.

Vertical and horizontal distribution of species caught in trawls

Acoustic data were paired with midwater trawling and surface townetting data to evaluate species-specific distribution patterns in relation to the overall distribution of biomass. Total catch for each fish species caught in the surface townetting was recorded and standardized to catch per 10 min tow. Surface townets not depth-stratified, and sampled 0-3 m of the water column. Depth-stratified midwater trawl catches were recorded by species and standardized to catch per 10 min tow. From all townet and midwater trawl samples, fork lengths (FL) to the nearest 1 mm and wet weights (WW) to the nearest 0.1 g were recorded for random sub-samples of up to 60 fish per species. Midwater trawl catches were used to generate length frequencies (FL or total length, mm) for each species by 15 m depth increments in the water column (0-15 m, 15-30 m, 30-45 m, 45-60 m; Fig. A1). Species distributions by depth increment were summarized.

Seasonal patterns in relative biomass observed by gear type

We examined patterns of relative fish abundance as characterized by different gear types (acoustics, midwater trawls, surface townets) in Central Puget Sound to infer distribution patterns of species. Acoustic data were categorized into shelf zones corresponding to the bottom depths sampled with surface townetting (<50 m) and offshore zones corresponding to bottom depths sampled with midwater trawls (>75 m). We calculated a normalized index of fish abundance (*S*) using catch anomalies:

$$S = \overline{\left(\frac{FP_m - \overline{FP_r}}{SD\left(FP_r\right)} \right)}$$

where *FP* represents values of fish abundance as observed with surface townets (CPUE), midwater trawls (CPUE), acoustics (mean S_v of all bins 0-60 m in the water column over shelf, transition, and offshore zones), acoustics (mean S_v of all bins 0-60 m in the water column within the shelf zone), or acoustics (mean S_v of all bins 0-60 m in the water column within the offshore zone); *m* is month, and *r* is the reference month (July) over which fish abundance was normalized. $SD(FP_r)$ denotes the standard deviation of FP_r. We used July as a reference month, so $\overline{FP_r}$ represents the mean of July values for each gear type.

Results

Epipelagic fish biomass distribution from acoustics surveys

The occurrence of measurable biomass was increasingly likely in sampling cells as the season progressed, with an initial significant increase in July in all bathymetric zones (shelf, p=0.002, Table 1.1; transition, p<0.001, Table 1.2; offshore, p<0.001, Table 1.3). Additionally, the occurrence of biomass became less likely in the upper water column over time, suggesting a shift towards deeper depth strata. Biomass occurrence was more frequently observed in the offshore zone ($p<0.001$), followed by the transition zone, and least frequent in the shelf zone (Table 1.4). The effect of month generally outweighed the effects of basin and water column depth; this suggests strong seasonality in the presence of epipelagic biomass.

Because Central Basin was sampled most consistently, we used it to illustrate the distribution of biomass among depth strata in the three bathymetric zones (Fig. 1.2). Data from other regions of the Sound are included in the appendix (Fig. A2). In the shelf zone of the Central Basin, virtually all backscatter was observed in the upper 15 m of the water column until July, when some backscatter was also observed in deeper layers. From August through October, larger proportions of backscatter were observed below 15 m water depth than above 15 m. These observations are consistent with a pattern of fish shifting deeper within the water column over the study period. Additionally, the percentage of sample cells which contained no backscatter slightly (from 99.9% to 94%) decreased from April through October. While backscatter was observed in more sample cells later in the study period, total integrated backscatter did not increase, suggesting greater dispersal of backscatter later in the summer.

In the transition zone, almost all backscatter was observed at 45-60 m in April. Aside from that month, proportional backscatter in the transition zone followed a similar pattern to the shelf zone: greater proportions of backscatter were observed in the upper 15 m of the water column until July, after which most backscatter was deeper than 30 m. The decrease over time in percentage of sample cells with no backscatter (99% to 94%) was also observed in the transition zone.

In the offshore zone, the depth at which most backscatter was observed was more variable. In April, June, and October, high proportions of backscatter were observed above 30 m. In May, backscatter was almost equally distributed between the 0-15 m depth layer and the 45-60 m depth layer. In July, August, and September, the opposite was true. The percentage of offshore sample cells with no backscatter did not clearly follow the decreasing pattern observed in the shelf and transition zones. In contrast, lower percentages were observed in April (96%), July (92%), and September (95%), and high percentages (99% empty sample cells) were observed in May, June, and October. This suggests that the vertical distribution of epipelagic biomass in the offshore zone is more variable than in the shelf or transition zones. Over all zones, the percentage of sample cells with zero backscatter was lowest in July.

Midwater trawl data were available in July and September to provide inference on which species likely contributed to acoustic backscatter patterns. Catches in July suggested that herring contributed most to observed backscatter deeper in the water column. In September, Chinook and chum salmon were found throughout the water column and also contributed to observed backscatter. A large catch of juvenile spiny dogfish was observed at depth in September; spiny dogfish potentially contributed to backscatter at deeper depth strata (Nakken and Olsen 1977).

The range of variability in biomass within bathymetric zones was large: standard errors for biomass values in shelf zones ranged from 16% to 100% of mean s_v (linear form of S_v) values. Similarly, in transition zones, standard errors were 18% to 100% of mean values. In offshore zones, standard errors were 12% to 100% of mean values. On average, the standard error associated with the mean biomass of each depth layer was > 50% of the mean.

Vertical and horizontal distribution of species caught in trawls

Midwater trawl catch compositions varied by depth strata and region (Fig. 1.3) and were primarily composed of juvenile salmon species and Pacific herring. Catches in Admiralty Inlet were lower than in Central Puget Sound in both July and September overall, but this pattern varied by species: Chinook salmon catches were higher in Central Sound in both months, whereas coho salmon catches were higher in Admiralty Inlet in July and (to a lesser extent) September. Herring far outnumbered the other species in the catches. Most biomass was found in the upper 30 m of the water column, particularly in July (91% CPUE). Chinook salmon were caught at all depths sampled, but densities were highest in 0-15 m during July and 0-45 m in September. Chum salmon were observed only in the upper 15 m of the water column in July; in September, the highest densities remained in 0-15 m, but chum were found throughout the upper 45 m. In Central Puget Sound in September, a large catch of juvenile spiny dogfish was encountered at 45 m depth. Herring were caught in most of the tows in Central Puget Sound (18 out of 23) and typically in large numbers (on average, 1,483 fish in 10 minutes trawling). Herring were caught in under half the tows in Admiralty Inlet (5 out of 11), but a couple trawls contained very large quantities of herring (e.g., 10,500 fish in 10 minutes trawling). Young-of-the-year herring recruited to the trawl catches in September and contributed to the general increase in CPUE that month (Fig. A4).

Seasonal patterns in relative biomass observed by gear type

Normalized abundance in Central Puget Sound appeared to follow similar patterns of low fish densities for all gear types during spring that increased dramatically in July, then varied from July through October for all gear types (Fig. 1.4). Negative deviations were observed for all gear types from April through June. Surface townet estimates peaked in July, then declined rapidly from August to September. In contrast, midwater trawl estimates increased between July and September. Acoustics estimates were variable but, with the exception of October, all three acoustic metrics (shelf, offshore, and total) followed very similar patterns. September and October had the highest range of deviation over all months. In September, this was due to the large difference in normalized abundance relative to July for midwater trawls (high abundance in September) and surface townets (low abundance in September). In contrast to the typical coherence of the acoustics estimates, relative abundance of backscatter in the shelf zone in October was noticeably higher than offshore backscatter and total backscatter.

Discussion

Overall, we observed high spatial and temporal variability in total biomass estimates and species-specific catches. Epipelagic distributions of biomass varied horizontally among basins, vertically within the water column, and temporally over the summer period. We observed a general trend of initially low abundance across habitats from April through June, then increased abundances during the summer, and a biomass shift towards deeper depth strata within the water column. Trawl catches increased from July to September and coincided with declines in townet catches, but an increase from recruitment by young-of-year herring. Abundances as measured by all gear types declined by October.

Our results are consistent with findings that pelagic fish utilize nearshore and offshore zones to differing extents based on species, size, and life history stage (Simenstad et al. 1982, Aitken 1998, Roni et al. 1999, Jung and Houde 2003). Horizontal and vertical location of biomass in the upper 60 m of the water column varied significantly over the April-October across bathymetric zones (shelf, transition, and offshore). Acoustic backscatter was more commonly observed in the offshore zone. In the transition and shelf zones of Central Puget Sound, a shift was clearly evident in the proportion of backscatter within 15 m depth strata: biomass moved from surface layers to deeper depth strata in the water column as the season progressed. This result is consistent with observed fish movement: large juvenile Chinook salmon were found in deeper depth strata in Puget Sound over the sample period. Chinook salmon in the Strait of Georgia also shift towards deeper depths as they grow, a pattern which may be related to the onset of pelagic piscivory – i.e., a shift in foraging behavior and habitat use (Duffy et al. 2010, R. Sweeting & R. Beamish, *pers. comm.*). Similar distribution patterns of salmon have been documented in other regions (Emmett et al. 2004, Litz et al. 2013). Observations from other regions of Puget Sound were less consistent, and may reflect observed biological differences in species composition among basins (Table A1, Figs. A2 and A3, Rice et al. 2012).

Herring and salmon were often caught concurrently in trawl catches and exhibited a high degree of spatial overlap. Additionally, midwater trawl catch compositions indicated that salmon and herring were the most influential contributors to observed backscatter in the daylight epipelagic offshore zone. This spatial overlap may be important to Puget Sound salmon and herring stocks in terms of resource availability. Pacific herring share several key food items with juvenile Chinook salmon and coho salmon (see Chapter 2). If herring and juvenile salmon display substantial spatial-temporal and dietary overlap, the potential for competitive interactions is greater and may negatively affect feeding and growth or instigate a shift in the species' realized niches (Hutchinson 1959, Case and Gilpin 1974, Wilson 2010). Alternatively, their aggregated presence may reduce predation risk for the individual fish (Brock and Riffenburgh 1960) and their interactions may be predation-mediated (Mittelbach 1986, Persson 1993).

Differences between trawl and townet catches may be due to species behavior or gear limitation. We rarely observed yearling coho salmon in surface townetting catches, while subyearling chum and Chinook salmon were common. Conversely, all three salmon species were common in midwater trawl catches. Previous nearshore studies of salmon have noted that, unlike Chinook and chum salmon, coho salmon begin utilizing offshore habitats relatively quickly after their initial entrance into the estuarine environment (Conley 1977, Bax et al. 1978, Meyer 1979, Pearce et al. 1982, Hiss and Boomer 1986). Alternately, if coho salmon were present in nearshore habitats during surface townetting events, their large size may have enabled them to evade the townet, since surface townetting catches can be biased against larger fish (Bax and Whitmus 1981). The propensity for young herring to spend weeks to months in nearshore habitats before recruiting to the offshore environment (Hourston 1959, Brown et al. 1996) suggests that patterns of herring catches in townets and trawls is influenced by ontogeny and may explain the observed July peak in CPUE in townets and the later September CPUE peak in trawl catches. The concurrent decline in backscatter abundance in the shelf zone over July to September and increase in backscatter abundance from August to September in the offshore zone, although less intense than the decline in shelf townet CPUE and increase in offshore trawl CPUE, supports this hypothesis. The existence and strength of these movement patterns likely differs across Puget Sound relative to regional species composition.

The complementary use of multiple gear types for sampling epipelagic biomass enabled a composite assessment of seasonal distribution among zones and within the water column. Net sampling and acoustic sampling complement each other well; each method is subject to different biases, and using both methods simultaneously can reduce potential bias (Aglen 1996, Aglen et al. 1999). Surface townets sampled only the upper 3 m of the water column and were representative of the surface layer of the shelf zone. Midwater trawls sampled the upper 60 m of the water column but were constrained to the offshore bathymetric zone. Acoustic surveys sampled from approximately 3 m to 60 m and were able to cover all three bathymetric zones (shelf, transition, and offshore), thereby providing a linkage between the habitats sampled by townets and trawls. Trawl catches are an adequate method for assessing salmon, as demonstrated by Beamish et al. (1998), (Beamish et al. 2004). However, catches of herring in trawls were very patchy, with catches fluctuating between zeroes and thousands, likely due to their schooling nature. Since herring schools are unlikely to be distributed randomly throughout the estuarine environment and similar sizes of herring tend to school together (Pitcher et al. 1985), we would expect trawls to have difficulty characterizing herring distribution and abundance. Acoustic surveys cover a large volume of water efficiently and, as such, may more effectively assess patterns in epipelagic biomass than net sampling (especially for patchily-distributed species like herring); however, they are not species-specific. Other acoustic studies have demonstrated precise tracking of biomass patterns (Mason et al. 2005, Mehner 2006, Probst et al. 2009, Bertrand et al. 2010). A methodology which combines net and acoustic surveys is recommended as it allows for efficient and comprehensive sampling and identification of species: acoustics data can map broad-scale biomass and target areas with anomalously high densities, while net sampling can provide species composition and fish condition information (Simmonds and MacLennan 2005, Dennerline et al. 2012, Spencer et al. 2012).

Over the course of this study, we made a number of sampling assumptions. Sampled areas were assumed to represent full basin areas and catches were assumed to be representative of the fish population. Acoustic shadowing was assumed minimal, due to the low densities of observed backscatter (Zhao and Ona 2003, Simmonds and MacLennan 2005). We assumed no shifts in fish detection due to effects of species, day, area, or month and no effect of fish behavior and/or ontogeny (Midttun 1984, Ona 1990, Horne 2003). The magnitude of these assumptions may vary by species; for example, vessel avoidance behaviors by herring have been recorded during acoustic surveys (Misund 1990). Finally, while our noise threshold was appropriate for measuring backscatter from fish, it may have also included backscatter from other organisms (e.g., jellyfish, large zooplankton). Surface townets regularly caught jellyfish near the surface (Table A1, Fig. A3). Jellyfish were also caught in midwater trawls, but biomass and numerical abundance were not quantified. In other regions of Puget Sound, jellyfish have been observed from the surface down to greater than 60 m (our depth cut-off) in the water column (Moriarty et al. 2012). Jellyfish have previously been recorded on acoustics (Brierley et al. 2005); we assumed jellyfish backscatter did not contribute above the threshold (Parker-Stetter et al. 2013) and, if it did, we assumed it would be a small and consistent bias. Aggregations of euphausiids and large copepods may also not have been excluded fully, particularly at water depths approaching 60 m scattering layers, where euphausiids and copepods have previously been recorded (Cooney 1971, Ross et al. 1982, Ohman et al. 1983).

Understanding the factors that drive fish distribution and habitat use is critical to assessing and quantifying potential outcomes of species interactions within estuarine and marine communities like Puget Sound. Estuarine habitats do not exist in isolation; waters flow, nutrients transfer, and organisms move among habitats. The importance of a habitat to a fish community may be influenced by the habitats to which it is connected (Pihl et al. 2008), particularly for anadromous species like salmon which move through a variety of habitats before outmigration to the open ocean. In many systems, large-scale physical variables (e.g., climate regimes), local drivers (e.g., water temperature, river flow, stratification), and potentially predation pressure are linked to fish distributions (Recksiek and McCleave 1973, Bottom and Jones 1990, Abookire et al. 2000, Hagan and Able 2003, Jung and Houde 2003, Emmett et al. 2006, Litz et al. 2013). The mechanisms by which the distributional patterns in Puget Sound fish biomass observed through surface townetting, midwater trawling, and acoustics are linked to physical factors and predator-prey dynamics and whether these patterns are consistent over time (e.g., inter-annually, inter-decadally) are poorly understood. Identifying areas of concentrated biomass and targeting those areas for further investigation is an important step in assessing potential for competitive and predatory dynamics, as well as limitations in resources for pelagic fish (e.g., habitat, food). For example, in our work, large aggregations were regularly visually observed on echograms during acoustics surveys and often appeared to be associated with an increase in the slope of the bottom. Aggregations of zooplankton and fish species near shelf-break type bathymetry in other systems have also been observed (Munk et al. 1995, Robinson and Gomez-Gutierrez 1998, Young et al. 2001, Genin 2004) and may serve as important feeding areas for fish. These types of areas within Puget Sound would be appropriate for targeted net sampling to identify which species are contributing most to this pattern and how the local bathymetry structures competitive or predatory species interactions. Results from this study contribute to a better understanding of how pelagic fishes use habitats within Puget Sound and how presence/biomass varies spatially and seasonally by providing insight into epipelagic fish distribution over the spring-summer period. If similar biomass patterns are observed inter-annually, they could enable identification of consistent areas in terms of apparent habitat use for pelagic fishes and could thus form the basis for a directed sampling program to quantify species-specific resource use and interspecific interactions resulting from shared resources.

Table 1.1. Shelf zone: seasonality of biomass presence by depth in the upper 60 m of the water column.The output is a log odds ratio, where 0 indicates equal chance of observing or not observing biomass. The intercept represents a reference state: in this case, April, Admiralty Inlet, and the lower water column (30-60 m depth) in the shelf zone.
Generalized linear mixed model fit by the Laplace approximation (s_v ~ month + basin + water column depth + month*water column depth + (1|transect). Number of observations: 94,814; number of transects: 164.

Shelf zone (bottom depths <50 m) **Effects**	**Estimate**	**Standard Error**	**Z-value**	**Pr(>|z|)**
Intercept	-3.37	0.35	-9.71	<0.001 ***
Upper water column	-1.15	0.16	-7.02	<0.001 ***
May	-1.15	0.35	-3.28	<0.001 ***
May:Upper water column	1.07	0.22	4.81	<0.001 ***
June	-11.59	122.79	-0.09	0.92
June:Upper water column	11.18	122.79	0.09	0.09
July	1.02	0.32	3.17	0.002 **
July:Upper water column	0.69	0.18	3.9	<0.001 ***
August	0.18	0.37	0.48	0.63
August:Upper water column	0.89	0.2314	3.86	<0.001 ***
September	1.95	0.37	5.33	<0.001 ***
September:Upper water column	-0.07	0.21	-0.36	0.72
October	1.99	0.4	5	<0.001 ***

October:Upper water column	-0.4	0.24	-1.68	0.09
Whidbey Basin	-0.16	0.28	-0.58	0.56
Central Basin	-0.76	0.25	-3.1	0.002 **
South Basin	-0.39	0.33	-1.19	0.23

Table 1.2. Transition zone: seasonality of biomass presence by depth in the upper 60 m of the water column. The output is a log odds ratio, where 0 indicates equal chance of observing or not observing biomass. The intercept represents a reference state: in this case, April, Admiralty Inlet, and the lower water column (30-60 m depth) in the transition zone.
Generalized linear mixed model fit by the Laplace approximation (s_v ~ month + basin + water column depth + month*water column depth + (1|transect). Number of observations: 65,675; number of transects: 135.

Transition Zone (bottom depths between 50-75 m)

Effects	Estimate	Standard Error	Z-value	Pr(>|z|)
Intercept	-3.78	0.34	-11.21	<0.001 ***
Upper water column	-1.78	0.26	-6.78	<0.001 ***
May	-0.98	0.35	-2.78	0.006 **
May:Upper water column	1.29	0.32	4.06	<0.001 ***
June	-0.41	0.7	-0.59	0.56
June:Upper water column	2.3	0.51	4.48	<0.001 ***
July	1.78	0.31	5.74	<0.001 ***
July:Upper water column	1.08	0.27	4.04	<0.001 ***
August	0.71	0.34	2.11	0.03 *
August:Upper water column	0.96	0.29	3.32	<0.001 ***
September	2.55	0.34	7.45	<0.001 ***
September:Upper water column	-0.31	0.32	-0.98	0.33

October	0.79	0.38	2.06	0.04 *
October:Upper water column	0.37	0.3	1.21	0.23
Whidbey Basin	-0.14	0.27	-0.53	0.6
Central Basin	-0.47	0.24	-2.01	0.04 *
South Basin	0.35	0.36	0.97	0.33

Table 1.3. Offshore zone: seasonality of biomass presence by depth in the upper 60 m of the water column. The output is a log odds ratio, where 0 indicates equal chance of observing or not observing biomass. The intercept represents a reference state: in this case, April, Admiralty Inlet, and the lower water column (30-60 m depth) in the offshore zone.
Generalized linear mixed model fit by the Laplace approximation (s_v ~ month + basin + water column depth + month*water column depth + (1|transect). Number of observations: 294,962; number of transects: 118.

Offshore Zone (bottom depths >75 m)

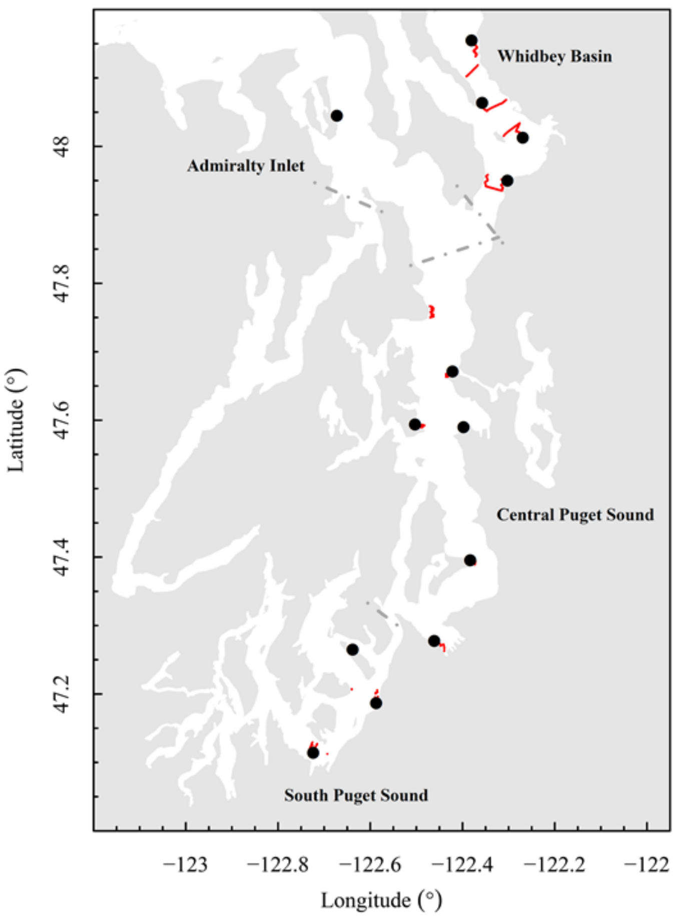
Effects	Estimate	Standard Error	Z-value	Pr(>|z|)
Intercept	-4.22	0.38	-11.2	<0.001 ***
Upper water column	-0.04	0.16	-0.24	0.81
May	-0.85	0.37	-2.32	0.02 *
May:Upper water column	0.52	0.18	2.96	0.003 **
June	0.15	0.64	0.23	0.82
June:Upper water column	-0.46	0.24	-1.92	0.06
July	2.33	0.34	6.82	<0.001 ***
July:Upper water column	-1.22	0.16	-7.66	<0.001 ***
August	1.3	0.36	3.56	<0.001 ***
August:Upper water column	-0.98	0.17	-5.77	<0.001 ***
September	2.68	0.38	7.11	<0.001 ***
September:Upper water column	-1.9	0.18	-10.83	<0.001 ***

October	0.33	0.41	0.81	0.42
October:Upper water column	-1.13	0.2	-5.75	<0.001 ***
Whidbey Basin	-0.64	0.28	-2.27	0.02 *
Central Basin	-0.47	0.26	-1.85	0.06
South Basin	-0.37	0.42	-0.89	0.38

Table 1.4. Seasonality of shelf/transition/offshore biomass presence in the upper 60 m of the water column. The output is a log odds ratio, where 0 indicates equal chance of observing or not observing biomass. The intercept represents a reference state: in this case, April, Admiralty Inlet, in the shelf zone.
Generalized linear mixed model fit by the Laplace approximation (s_v ~ month + basin + zone + month*zone + (1|transect). Number of observations: 455,451; number of transects: 166.

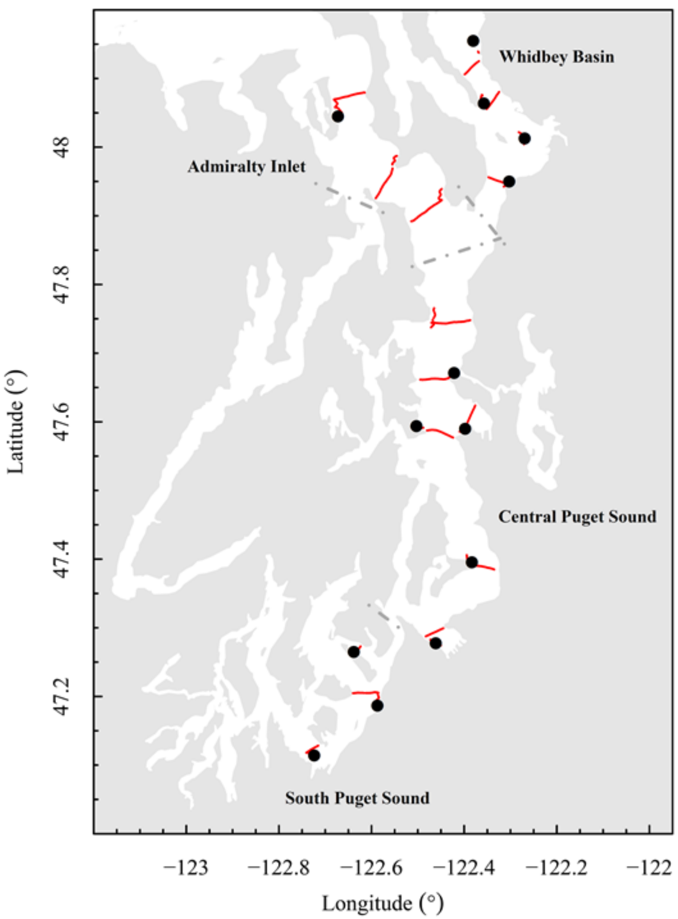
Effects	**Estimate**	**Standard Error**	**Z-value**	**Pr(>|z|)**
Intercept	-4.23	0.29	-14.46	< 0.001 ***
Transition zone	-0.01	0.14	-0.07	0.94
Offshore zone	-0.52	0.14	-3.79	< 0.001 ***
May	-0.43	0.27	-1.58	0.11
May:Transition zone	-0.73	0.18	-4.07	< 0.001 ***
May:Offshore zone	0.09	0.16	0.59	0.55
June	-0.79	0.58	-1.36	0.17
June:Transition zone	1.32	0.45	2.91	0.004 **
June:Offshore zone	1.38	0.45	3.08	0.002 **
July	1.5	0.27	5.64	< 0.001 ***
July:Transition zone	0.41	0.14	2.85	0.004 **
July:Offshore zone	0.74	0.14	5.27	< 0.001 ***
August	0.76	0.3	2.54	0.01 *

August:Transition zone	0.37	0.17	2.17	0.03 *
August:Offshore zone	0.51	0.16	3.09	0.002 **
September	1.72	0.3	5.68	< 0.001 ***
September:Transition zone	0.14	0.17	0.79	0.43
September:Offshore zone	0.37	0.16	2.27	0.02 *
October	1.41	0.34	4.22	< 0.001 ***
October:Transition zone	-0.38	0.18	-2.12	0.03 *
October:Offshore zone	-0.79	0.17	-4.55	< 0.001 ***
Whidbey Basin	-0.2	0.25	-0.8	0.42
Central Basin	-0.54	0.22	-2.48	0.01 *
South Basin	-0.24	0.29	-0.82	0.41



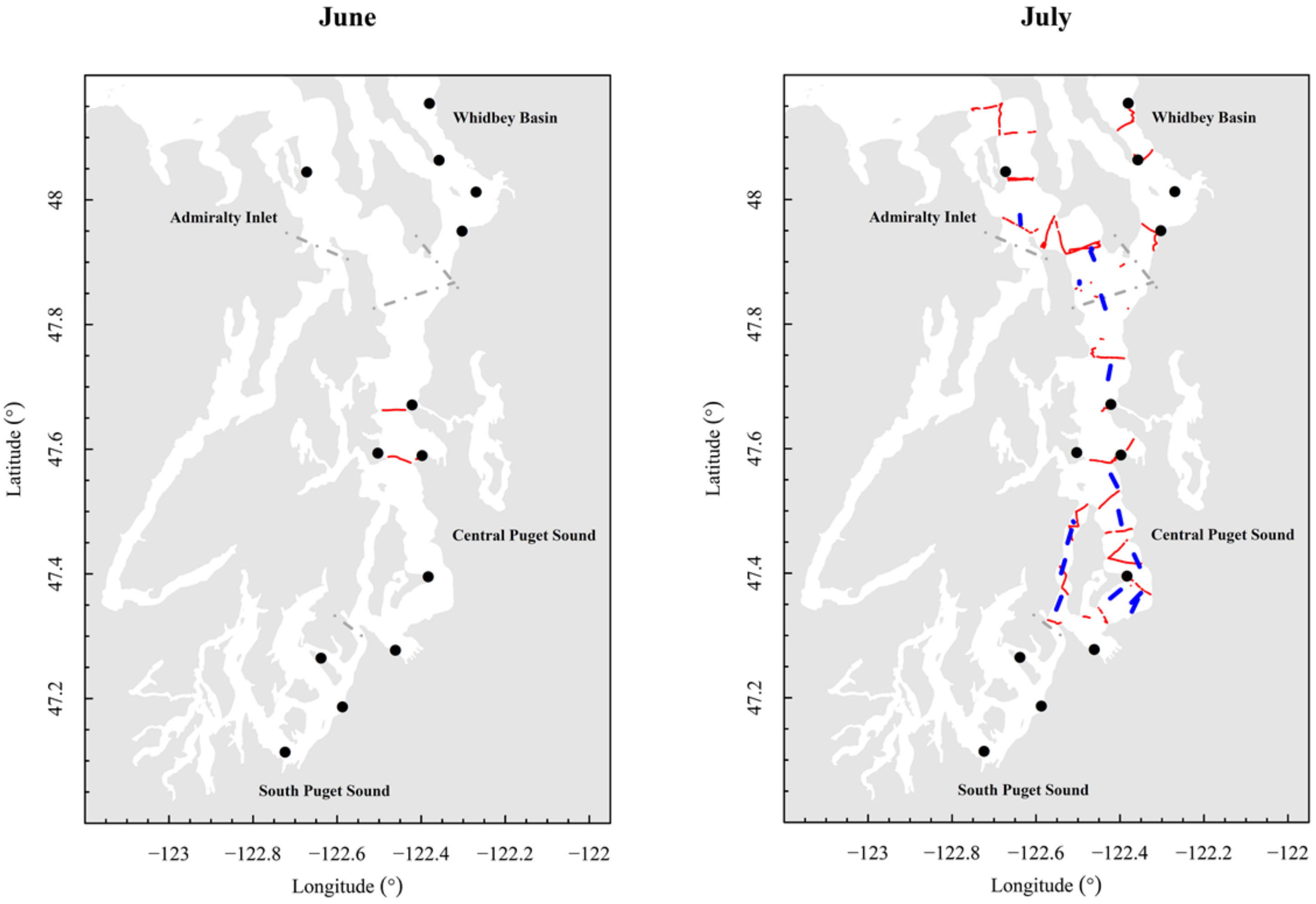
April

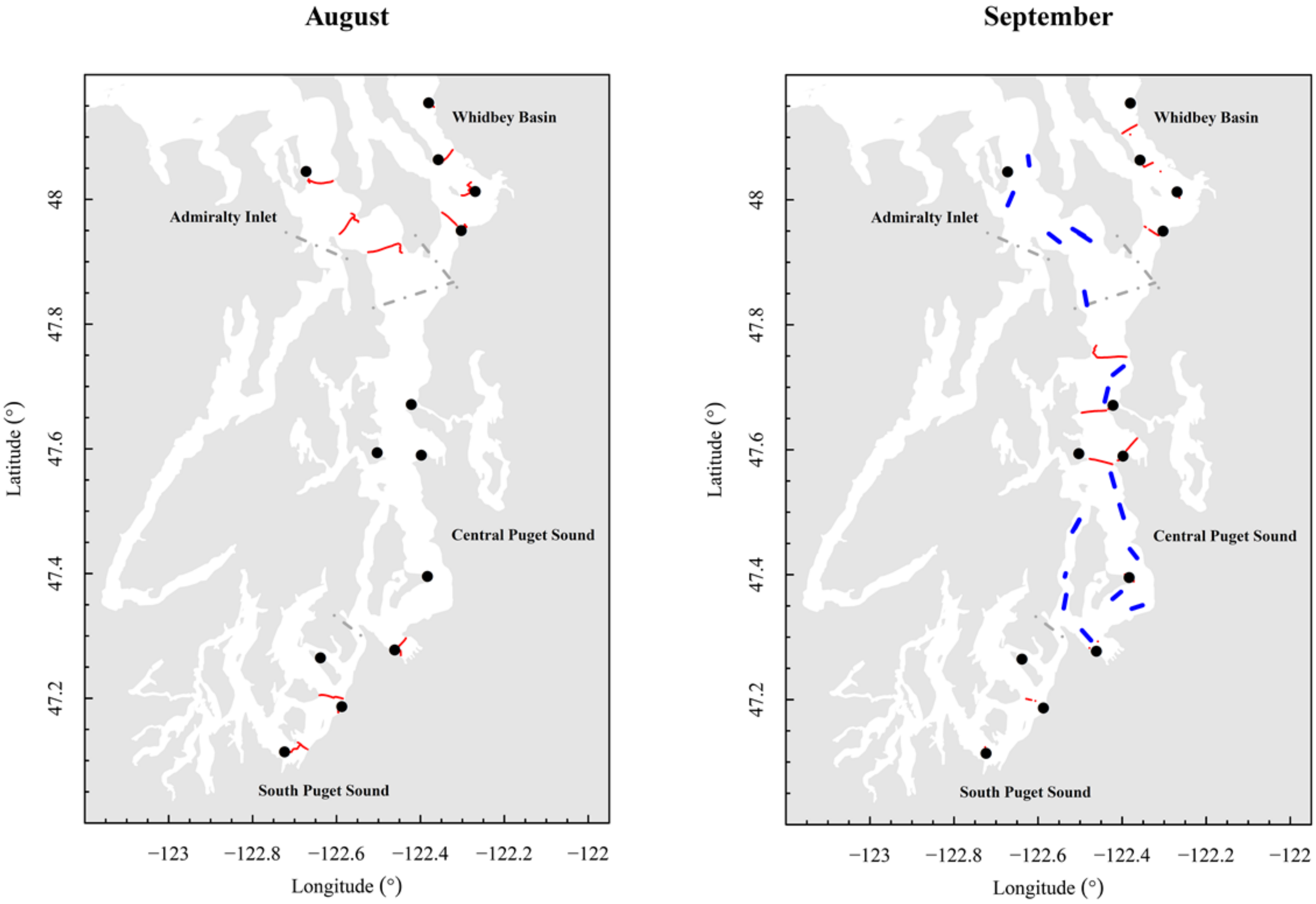
Whidbey Basin
Admiralty Inlet
Central Puget Sound
South Puget Sound
48
47.8
47.6
47.4
47.2
Latitude (°)
−123
−122.8
−122.6
−122.4
−122.2
−122
Longitude (°)



May

Whidbey Basin
Admiralty Inlet
Central Puget Sound
South Puget Sound
48
47.8
47.6
47.4
47.2
Latitude (°)
−123
−122.8
−122.6
−122.4
−122.2
−122
Longitude (°)


June
July
Whidbey Basin
Admiralty Inlet
Central Puget Sound
South Puget Sound
Latitude (°)
48
47.8
47.6
47.4
47.2
−123
−122.8
−122.6
−122.4
−122.2
−122
Longitude (°)


August
September
Whidbey Basin
Admiralty Inlet
Central Puget Sound
South Puget Sound
Latitude (°)
48
47.8
47.6
47.4
47.2
Longitude (°)
−123
−122.8
−122.6
−122.4
−122.2
−122

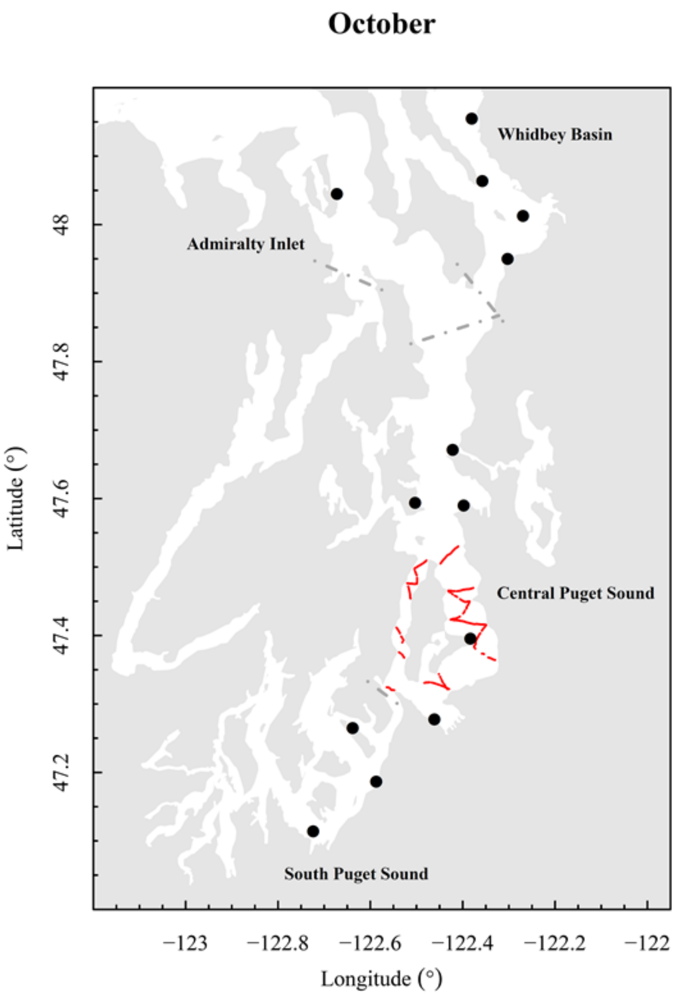


Figure 1.1. Monthly sampling effort for hydroacoustics (red lines), midwater trawls (blue lines), and surface townets (black circles). Dark grey dot-dashed lines indicate approximate separation of basins.

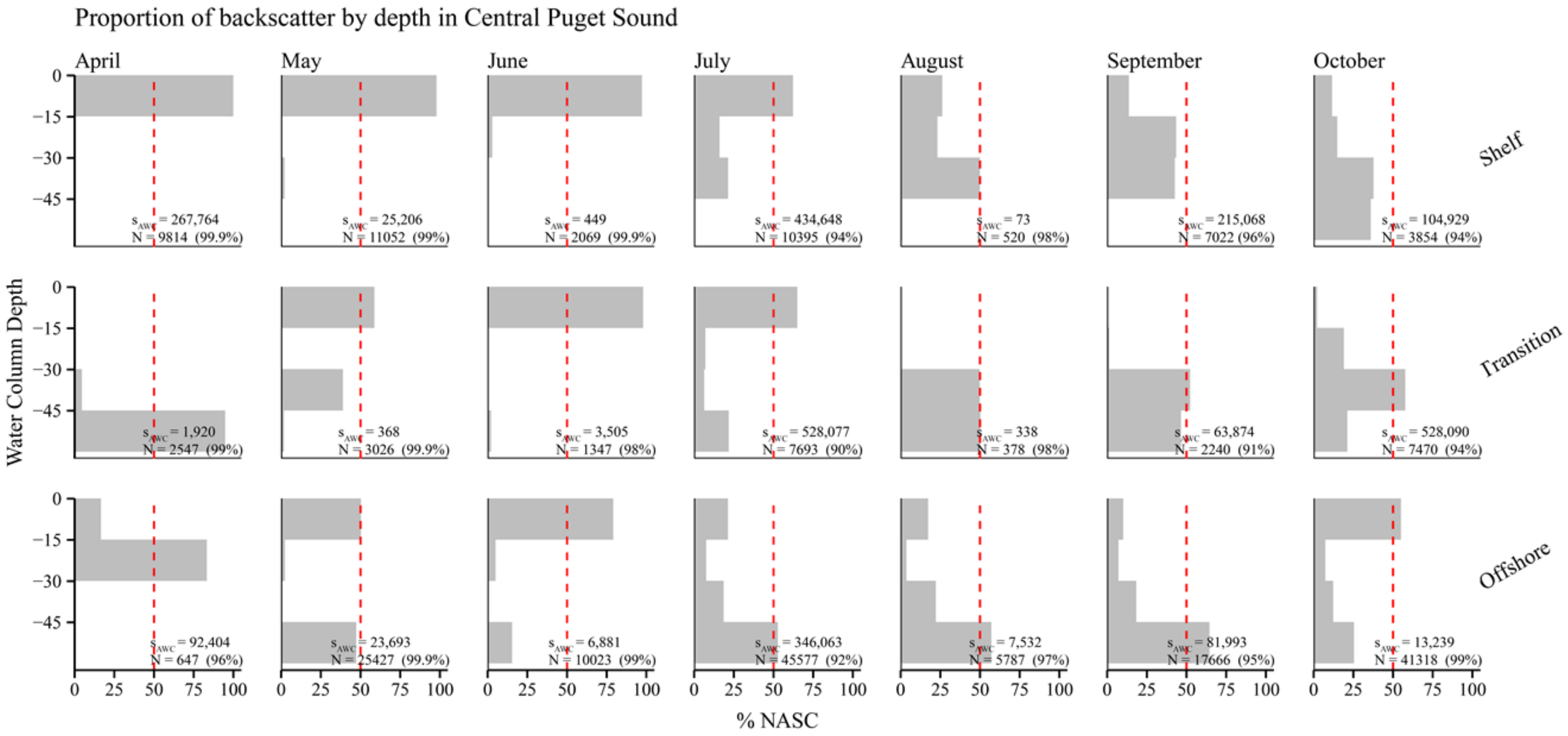


Figure 1.2. Proportional distribution of integrated backscatter (NASC) in the water column for shelf, transition, and offshore zones in Central Puget Sound. Note that axes are consistent for all plots. Results are presented as the proportion of total integrated backscatter observed within 15 m depth increments for each month and basin. The red dotted line indicates the 50% mark on each plot. Each column is a month (from April to October) and each row is a zone (ordered by increasing distance from shore). In the bottom right corner of each plot, total integrated backscatter (s_{Awc}), total number of samples (N), and percent of samples that had 0 backscatter (%) are listed.

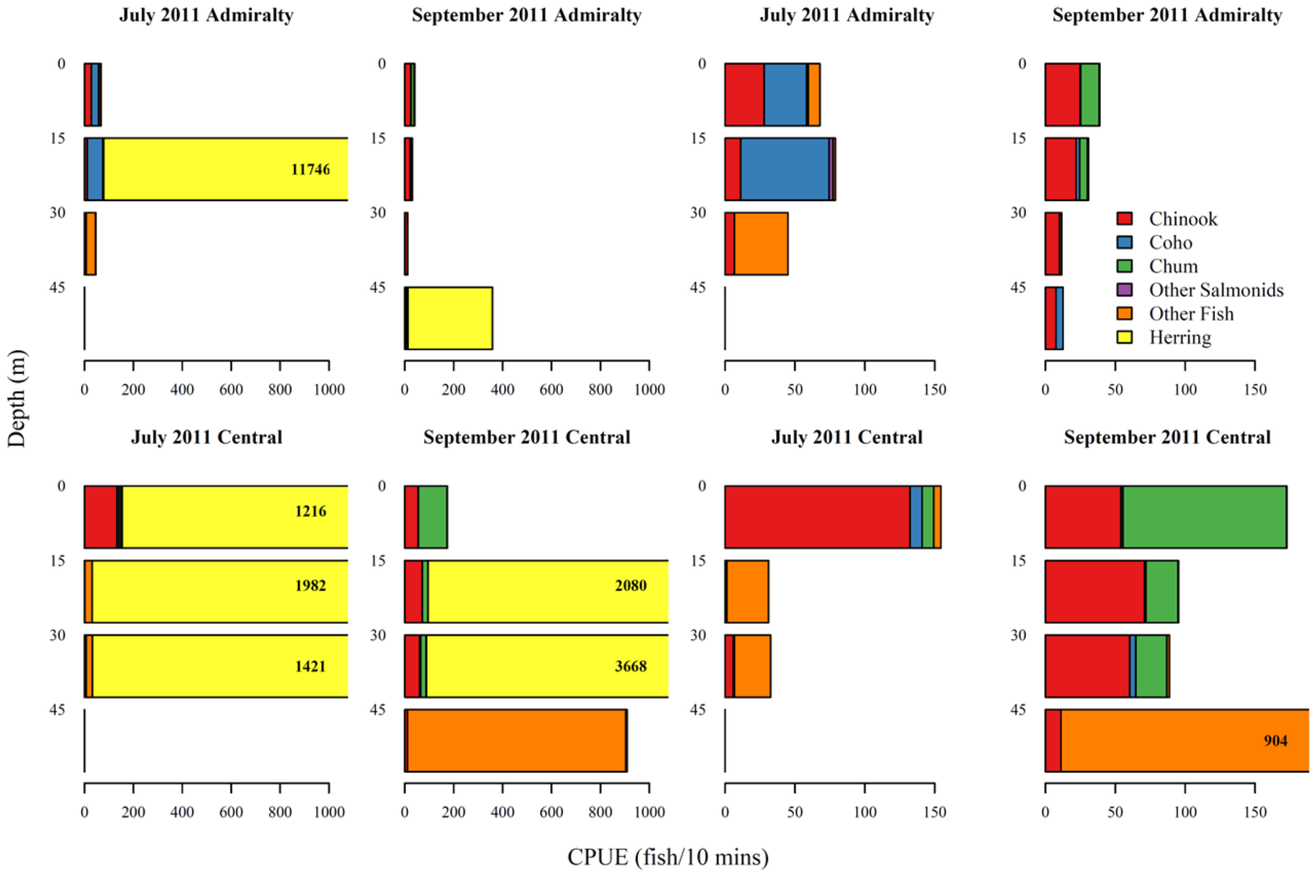


Figure 1.3. On left, midwater trawl catches of fish species, including herring, by 15 m depth increments in the water column. Bars that exceed 1000 are labeled with total CPUE (fish/10 mins) value for all species in the catch. Note that “Other Fish” at 45 m depth in September 2011 Central are all juvenile spiny dogfish. On right, midwater trawl catches of all fish species excluding herring. Bars that exceed 1750 are labeled with total CPUE values for all species (excluding herring).

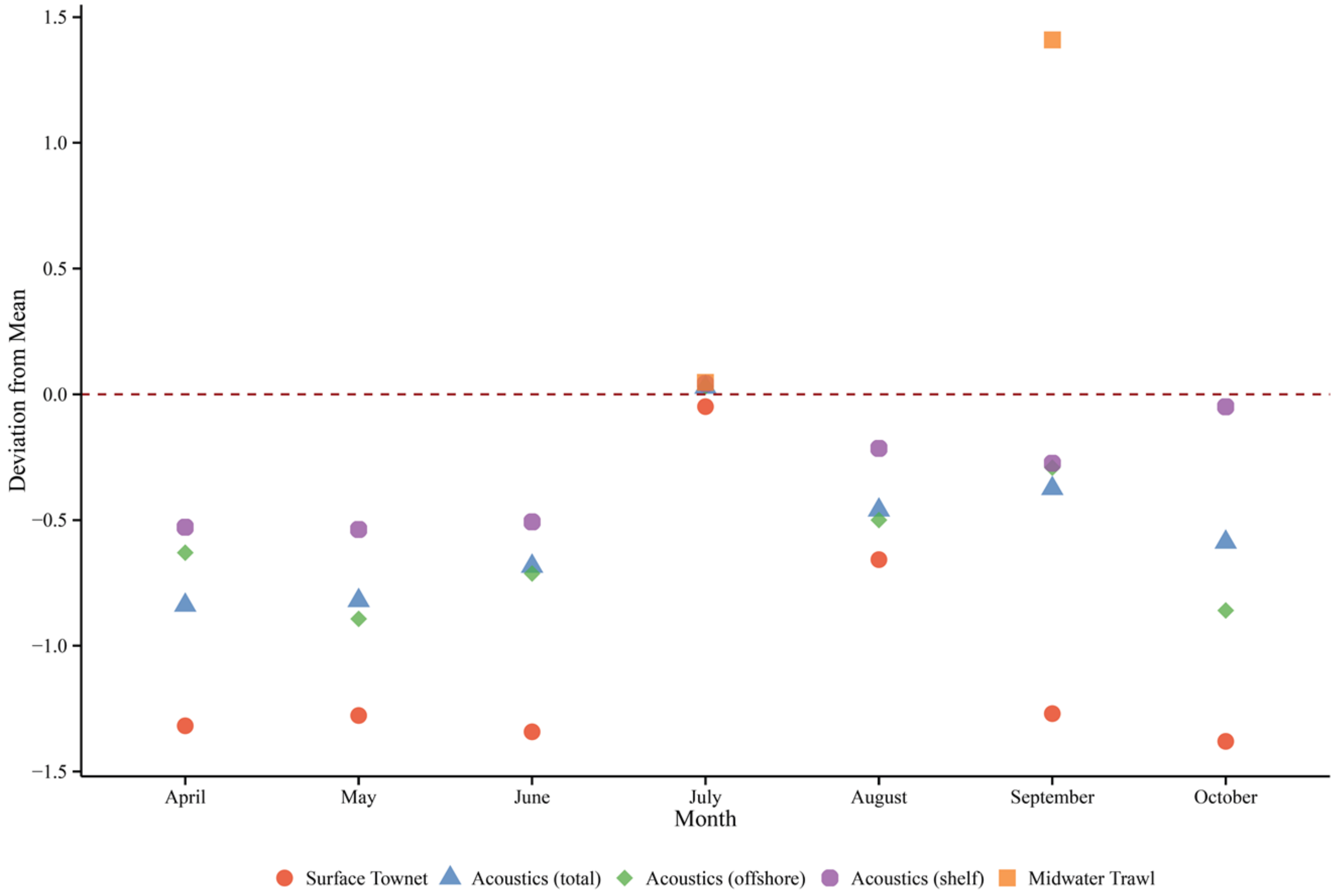


Figure 1.4. Normalized abundance (S) of fish/backscatter in Central Basin as measured by townets (fish CPUE), midwater trawls (fish CPUE), acoustics (mean S_v, shelf zone), acoustics (mean S_v, offshore zone), and acoustics (mean S_v, total). Acoustics data were categorized into shelf regions corresponding to the bottom depths sampled with surface townetting (<50 m) and offshore regions corresponding to bottom depths sampled with midwater trawls (>75 m). Normalized abundance was calculated relative to the mean in July for each gear type.

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Chapter II: Evaluating potential for resource competition between juvenile salmon and Pacific herring

Abstract

Feeding and growth of pelagic species may be dictated by resource competition. In the case of severely depleted Pacific salmon (*Oncorhynchus* spp) populations in Puget Sound, WA, competition with abundant Pacific herring (*Clupea pallasi*) during critical juvenile stages might determine growth and ultimately survivorship. We describe feeding habits of juvenile salmon and herring in Puget Sound to quantify spatial and annual variation in diet composition, describe dietary overlap, and assess the potential for competition by quantifying consumption demand by each species for shared prey. Analysis of summer stomach content data over a nine-year period in Puget Sound revealed consistent patterns of spatial, temporal, and dietary overlap. Crab larvae and amphipods were important prey for Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), and herring, whereas chum salmon (*O. keta*) ate predominantly gelatinous prey. Total demand for shared prey taxa was calculated for each population by applying bioenergetics models to data on growth, diet composition, and estimated population abundance. Because herring were much more abundant than salmon species, the population-level consumption by herring exceeded consumption by salmon, sometimes by orders of magnitude. If shared prey items are a limiting resource, there is considerable potential for herring to negatively affect salmon growth, particularly for Chinook salmon. Future work that focuses on characterizing food supply and obtaining more accurate estimates of juvenile salmon and herring growth rates over their residence period in Puget Sound is needed to better ascertain the role of competition on salmon growth and survivorship.

Introduction

The combination of trophic ontogeny and high species diversity creates the potential for complex species interactions in marine and estuarine pelagic food webs. This complexity can be manifest by a variety of competitive and predator-prey interactions among species that change across time and life history stage (Cooney et al. 2001, Willette et al. 2001, Essington and Hansson 2004, Forrester et al. 2006, Fauchald 2010). One consequence of these complex food web interactions is that the forage fish prey of higher trophic level species, such as large-bodied Pacific salmon (*Oncorhynchus* spp), might compete with juvenile stages of salmon. Walters and Kitchell (2001) termed this cultivation/depensation, implying that, at high densities, predators cultivate the food web to make it more favorable for juvenile growth and survivorship and, by extension, reduction of predator densities is accompanied by reduced juvenile survivorship due to increased interaction with competitors.

This cultivation/depensation may be an important phenomenon for severely depleted Pacific salmon populations in Puget Sound, WA. The estuarine and early marine period is important because it is a period of rapid growth by juvenile salmon (Healey 1980, Levy and Northcote 1982, Shreffler et al. 1992, Bottom et al. 2008). Moreover, survivorship during this period has a large effect on salmon populations (Simenstad et al. 1982, Beamish and Mahnken 2001, Beamish et al. 2004). Early marine growth is vital for juvenile salmon, as individuals must accumulate sufficient energy stores to reduce size-selective mortality. Faster early marine growth has been associated with higher marine survival for Chinook salmon *O. tshawytscha* (Duffy and Beauchamp 2011, Tomaro et al. 2012, Miller et al. 2013), coho salmon *O. kisutch* (Beamish et al. 2004), and pink salmon *O. gorbuscha* (Moss et al. 2005, Beauchamp et al. 2007, Cross et al.

2009). The growth achieved in this environment is often linked to later survival in the marine environment (Beamish et al. 2004, Duffy and Beauchamp 2011, Tomaro et al. 2012). For that reason, competitive interactions with other species during this life history stage can have important consequences for populations.

Pacific salmon in Puget Sound – Chinook, coho, chum, and pink salmon – use similar offshore habitats as Pacific herring (*Clupea pallasi*) during summer. Pacific herring are important prey for resident Chinook salmon (Kirkness 1948, Beauchamp and Duffy 2011), and are more abundant than juvenile salmon. Previous work has suggested considerable overlap in spatial-temporal distributions and diet among juvenile salmon species and herring (Beauchamp and Duffy 2011). Spatial, temporal, and dietary overlap between juvenile salmon and Pacific herring, combined with recent research showing a linkage between variability in feeding and variability in survival for Chinook salmon (Duffy 2009, Duffy et al. 2010, Duffy and Beauchamp 2011), suggests that competition among herring and juvenile salmon for prey resources may occur in the Puget Sound environment and could influence marine survival of salmon. However, the nature and strength of these interactions are poorly understood.

This work characterizes diet and consumption of juvenile salmon and Pacific herring in the epipelagic zone of Puget Sound over several years to explore the potential for competitive interactions among these species. Our specific objectives were to 1) identify spatial and temporal patterns in epipelagic diet composition of Pacific herring and juvenile salmon, 2) quantify diet overlap in epipelagic habitats for juvenile Chinook salmon, coho salmon, chum salmon, pink salmon, and Pacific herring, and 3) calculate and compare seasonal population-level consumption demand for each species through time.

Methods

Data collection

Diet samples of herring and salmon were collected with mid-water trawls conducted annually in Main Basin of Puget Sound (Fig. 2.1). All trawls were conducted by the Department of Fisheries and Oceans (DFO) Canada on the Canadian Coast Guard Ship (CCGS) W.E. Ricker during July and September, 2001-2011. In two years (2003 and 2010) no data were collected, and in 2004 the late summer sampling took place in October instead of September. When open at depth, the midwater rope trawl (model 250/350/14; Cantrawl Pacific Ltd., Richmond, British Columbia) was approximately 14 m deep by 30 m wide. The trawl had a 10 cm mesh cod-end with a 1 cm liner for the hindmost 7.6 m of the cod-end (for additional details see Beamish et al. 2000). Over 2001-2011, a total of 286 trawls were deployed in Main Basin with an average of 32 trawls each year. All trawls occurred during daylight hours. The average trawl duration was 20 minutes at approximately 4.5 knots (2.3 m/s) and covered 1.5 nmi. The midwater trawls were towed at varied depth strata (headrope at surface, 15 m, 30 m, 45 m, 60 m), with the greatest sampling effort directed at shallowest depths. About two-thirds of the trawls sampled the upper 30 m of the water column. Temperatures were recorded at the net for each trawl set.

Counts of all fish in each trawl sample were recorded by species. Fork lengths (FL) were recorded to the nearest 1 mm and wet weights (WW) to the nearest 0.1 g for sub-samples of up to 60 fish of each species, as available. All salmon were then processed for gut contents on board immediately after capture. Measured and weighed herring were frozen and processed for gut content analysis later in the laboratory. Salmon stomach contents were visually analyzed onboard by a single experienced individual with a 4X magnifying glass. For salmon species, proportional volumetric (cm^3) contribution of each prey category 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. For herring, blotted wet weights of prey were measured with an electronic scale to the nearest 0.001g, and the proportional wet weight (g) contribution of each prey category was calculated using each non-empty fish stomach as an individual sampling unit. For all species, invertebrates in each stomach sample were separated into taxonomic categories (e.g., copepods, crab larvae, euphausiids, gammarid and hyperiid amphipods). When possible, fish prey were identified to species and lengths were recorded.

Data Analysis

Diet composition

We described diet composition of juvenile salmon species and herring in terms of the proportional mass or volume contribution of each prey category in each stomach. This method of diet assessment is robust while also representing energetic contributions of prey (Ahlbeck et al. 2012). In graphical depictions, data are presented with individual fish as the sampling unit. For statistical analyses, fish of each species were pooled by trawl to compensate for lack of independence in fish stomachs within the collection event. When calculating dietary overlap values, we maintained taxonomic specificity where possible to represent actual overlap in prey species. However, for data visualization and for tests of differences among species and years, we combined prey categories into nine groups – alphabetically: copepods (primarily calanoid copepods), crab larvae (primarily zoea), euphausiids, gammarid amphipods, hyperiid amphipods, insects, fish, other invertebrates, and unidentified material. In addition to describing diet patterns among species and years, we qualitatively compared diets from different size classes of herring to address whether ontogenetic feeding shifts could be detected.

Proportional diet contribution of prey taxa

We tested for differences in diet composition among species, years, and months by applying multivariate analysis of diet data. We grouped diets by species and trawl set and used permutational tests of significance (PERMANOVA on arcsine-transformed data with 9999 permutations; Anderson 2001) to test for significant differences in diet composition among species, years, and months and PERMDISP to test for differences in multivariate dispersions of prey by species of consumer. These were chosen because permutational multivariate tests offer greater freedom from assumptions of data normality than non-permutational multivariate approaches (Anderson 2001, Quinn and Keough 2002). Region within Main Basin was not included as a factor because regional data were not consistently available for all species. Additional PERMANOVAs on species-specific data were performed to determine the variance attributed to month versus year effects on diet composition of each fish species. All statistical analyses were conducted in the R Programming Environment using the vegan: Community Ecology Package (Oksanen et al. 2012). Graphics were created using the PBSmapping (Schnute et al. 2012), reshape (Wickham 2007), and ggplot2 (Wickham 2009) packages.

Diet overlap values between species pairs

Diet overlap between species pairs was calculated using Schoener's overlap (Schoener 1970, as recommended by Wallace 1981):

$$1 - 0.5 \sum_{i=1}^{n} |dietN_{1,i} - dietN_{2,i}|$$

where $dietN_{1,i,}$ is the proportional mass/volume contributions of prey category i for consumer species 1 (with analogous notation for consumer species N_2). Diet overlaps were calculated at the greatest level of taxonomic specificity recorded.

Bioenergetics model individual consumption demand

Wisconsin bioenergetics model simulations (Hansen et al. 1997) were employed to estimate individual consumption rates of juvenile salmon and herring species. Previous consumption estimates generated by this model have been within 5-10% of independently generated field and laboratory estimates for juvenile Chinook salmon (Brodeur et al. 1992, Madenjian et al. 2004) and 10-14% for coho salmon (Brodeur et al. 1992, Ruggerone and Rogers 1992). We used pink salmon model parameters to model chum and pink salmon consumption, and Atlantic herring model parameters to estimate Pacific herring consumption. The model uses an energy balance approach in which total energy consumption (C) over a set time interval equals the sum of growth (G), metabolic costs (M), and waste losses (W).

$$\mathbf{C = G + M + W}$$

The primary model inputs are the initial and final body mass of the consumer (g), thermal experience (temperature experienced by the fish, °C), diet (proportions by mass or volume), and prey and predator energy densities (kJ/g wet weight) over a specified period (from the July to September/October trawl samples). Simulations using these model inputs generated estimates of individual daily consumption rate (g/d for each prey category).

Thermal inputs were the average water temperature measured at the trawl net, which reflected the fishes' thermal experience at time of capture. The model interpolated daily temperatures between July and September sampling events. Data from NOAA's Center for

Operational Oceanographic Products and Services (CO-OPS; www.tidesandcurrents.noaa.gov) oceanographic buoys were used to illustrate variation in surface water temperatures over the study period and place the model's thermal inputs in context (Fig. 2.2). This comparison revealed that temperatures obtained during the trawl surveys were generally within the temperature range measured by the buoys over the July-September sampling period.

We calculated observed diet compositions (Table A3) and used previously-published estimates for prey energy density values and indigestible fractions (Table 2.1). When data on indigestible fraction of a prey category were unavailable, we assumed 10% following Boldt and Haldorson (2002) and Cross et al. (2005). For salmon species, we used a weight-specific energy density equation (Hansen et al. 1997) for the consumers' energy density, which assumes energy density increases linearly with body mass. For herring, consumer energy density was constant over the study period at 5534 J/g.

For this study, we were primarily concerned with salmon during their first summer of growth in Puget Sound (e.g., ocean-type/sub-yearling Chinook salmon) and herring. We used length frequencies in trawl catches to identify age-0 Chinook, chum, and pink salmon, and age-1 coho salmon (Fig. A4a-d). Multiple age/size classes of herring are present in Puget Sound over the summer period and size can influence diet composition. We divided herring into three size classes (FL<125 mm, 125 mm< FL< 165 mm, FL>165 mm) based on length frequencies observed in trawl catches (Fig. A4e). Over the full time series, data were usually only available for one size class (125-165 mm FL in July and FL>165 mm in September). These sizes corresponded to ages 1-3 in July; size-at-age varies by stock in Puget Sound, so size modes do not necessarily indicate single age classes (Stick and Lindquist 2009).

We assumed that growth was the change in average individual WW from July to September (referred to as "apparent growth"). We estimated apparent growth by tracking shifts in size modes from July to September/October for the Main Basin. Observed WW were used whenever possible for salmon species and herring; however, in cases where only FL was measured for a fish, WW was calculated using an equation for log-transformed FL regressed against log-transformed WW from a subsample of specimens in the trawl catches (Table A2). All fish samples were included in estimations of average individual WW (Table A4).

Calculations of population-level consumption

Individual consumption estimates from model simulations were used to derive relative population-level consumption estimates by multiplying each species' per-capita estimate by the estimated abundance of that particular species (Table 2.5). Abundances of salmon species in the Main Basin of Puget Sound were calculated from midwater trawl catches, following methods described by Beamish et al. (2000). Note that the trawl net and vessel specifications in this study were identical to those of Beamish et al. (2000).

$$A = \frac{Vmb}{mean(Vt)} \times mean(c)$$

where *A* is abundance, *Vmb* is volume of select portion of Main Basin, *Vt* is volume sampled by trawls, and *c* is the catch of the species of interest. We used an estimate of 32.1 km^3 for the volume of the Main Basin down to 60 m water column depth derived from a digital elevation model of Puget Sound (http://www.ocean.washington.edu/data/pugetsound/psdem2005.html; Parker MacCready, University of Washington, *pers. comm.*). For context, the volume estimate for the entire Main Basin was 66.1 km^3. Volume sampled by trawls was calculated by assuming the trawl opening stayed constant at 14 m x 30 m and multiplying by distance trawled. This also assumes that net catchability is constant and that all fish in front of the net are caught.

Herring catches were highly patchy and trawling data likely did not adequately represent abundance. We estimated herring abundance using two methods: abundance based on acoustic/trawl surveys reported by Stick and Lindquist (2009) for Main Basin stocks (WDFW, denoted as W), and abundance estimates calculated from spawning biomass data for Main Basin stocks (Stick and Lindquist 2009), following model procedures outlined in Beauchamp and Duffy (2011) (model, denoted as M). Stick and Lindquist (2009) recorded acoustic/trawl-based abundance estimates for age-2+ spawners; we applied the mortality rate that was used by Beauchamp and Duffy (2011) (70% annual mortality, Stick and Lindquist 2009) to back calculate age-1 abundance for these stocks. Because age-0 herring were rarely caught in the same habitats as salmon and larger herring, and age-0 herring diet composition differed from that of larger herring, we excluded age-0 herring from abundance and consumption calculations.

Results

Salmon and herring in trawls

Salmon and herring consistently composed the majority of the catch, and often occupied similar depth strata (Fig. 2.3). In even years, juvenile pink salmon contributed substantially to catches. Herring catches were variable and patchy; in some years and months, large herring catches occurred while in others very few herring were caught (e.g., July 2002 trawls caught almost no herring, while in September 2002 herring were the majority of the catch). Herring catches also varied by depth in the water column: in some years, herring catch was concentrated at the surface (e.g., July 2004), but in others herring were caught in deeper (>15 m) depth strata (e.g., July 2011). Spatial overlap was generally high among salmon and herring. In July, over all years sampled, Chinook salmon, coho salmon, chum salmon, and herring co-occurred in 44% of trawls (n=140 total trawls in July), and juvenile Chinook salmon and herring co-occurred in 70% of trawls. In September/October, 23% of trawls (n=146 total trawls in September/October) contained all four species and Chinook salmon and herring co-occurred 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. 2.3). The modal depths of juvenile Chinook salmon shifted deeper in September or October. In 2004, the trawling survey took place in October instead of September; this corresponded with abnormally large catches of salmon below 60m (Fig. 2.3b). The modal depths of herring were more variable among years and between months than juvenile salmon.

Proportional diet contribution of prey taxa

Diet composition varied among species, years, and months, but also showed considerable overlap, especially among Chinook, coho, and herring (Fig. 2.4). These factors and 2-way interaction terms were highly significant ($p<0.001$ for all) and accounted for about half (50%) of the variance (Table 2.2). Yearly sample sizes and proportional diet compositions are provided in the appendix (Table A3). Diets of Chinook and coho salmon were qualitatively most similar, followed by herring and pink salmon and, least similar, chum salmon (Fig. 2.4). In July, Chinook salmon, coho salmon, and herring diets were largely composed of crab larvae (Chinook: 20-77%; coho: 45-87%; herring: 2-100%). Chinook salmon ate more fish in September/October (2-31%), although the overall diet composition remained diverse. Gammarid amphipods dominated coho salmon diets in September (29-71%), whereas copepods (mainly calanoid) were important for herring (0-53%). Chum salmon fed on other prey categories, consisting mostly of larvaceans

(*Oikopleura* sp.), ctenophores, ostracods, and chaetognaths. Pink salmon ate a mixture of copepods, crab larvae, euphausiids, and other prey (in July, larvaceans, shrimp, ostracods and chaetognaths; in September, mainly ostracods and shrimp). For herring, other prey were mainly barnacle larvae, ostracods, and polychaetes. Small herring (FL<125 mm) tended to eat greater proportions of copepods, whereas larger herring (FL>125 mm) ate more crab larvae and hyperiid amphipods (Fig. 2.5). Proportions of crab larvae in larger herring diets typically decreased from July to September, while proportions of copepods eaten by smaller herring and euphausiids eaten by larger herring increased.

Differing amounts of diversity in diet composition over months and years were evident among species. The variance in multivariate dispersion (Table 2.3) for chum salmon was larger than that of the other species, suggesting higher diversity in diet composition over the dataset. Subsequent species-specific tests showed different contributions of year and month effects for each species (Table 2.4). Chinook salmon diet composition varied by month and year. Coho salmon diets varied more by month than by years, a pattern likely driven by the switch from crab larvae in July to gammarid amphipods in September. Chum salmon showed an opposing pattern, where diet composition varied more by year and was relatively consistent between July and September. For pink salmon, only the month effect was significant, suggesting yearly variation in diet was less important (although note that pink salmon diet composition data were available for fewer years than diet composition data of other species). For herring, the year effect was significantly more important than month on variation in diet composition.

Diet overlap values between species pairs

In general, diet overlap between species pairs was higher in July than in September (Fig. 2.6). Chinook salmon and herring had periodically high diet overlap values in July (mean 49% overlap across years, with standard deviation (SD) 23%), as did coho salmon and herring (mean 45% overlap across years, SD 28%). In September, the species of highest diet overlap with herring was chum salmon (mean 34% overlap across years, SD 16%). Of all species pairs, Chinook salmon and coho salmon consistently had the greatest amount of diet overlap across months and years (mean 65% overlap, SD 14%). Diet overlaps with pink salmon were fairly consistent across other salmon species and herring: approximately 30-50% overlap between pink and any other species in a given month and year. The species that showed highest diet overlaps with pink salmon were Chinook salmon in September (mean 53% overlap, SD 11%) and herring in July (mean 49% overlap, SD 7%). Herring diet composition data were not available in 2002 or 2005-2007.

Per-capita and population-level consumption

Bioenergetics modeling allowed us to compare sources of energy and total prey consumption by juvenile salmon and herring (Fig. 2.7). When prey biomass was converted to energy, crab larvae remained important to both Chinook and coho salmon (mean 26%, SD 9% total energy consumed for Chinook; mean 26%, SD 7% total energy consumed for coho). Fish and insects contributed high amounts of energy to Chinook salmon (fish represented on average 16% of total energy consumed, SD 10%; insects: mean 10%, SD 7%). Gammarid amphipods and fish also contributed large amounts of energy to coho salmon diets (gammarids: mean 41%, SD 7% total energy consumed; fish: mean 13%, SD 7% total energy consumed). Much of the energy consumed by chum salmon was from other prey sources (mean 28%, SD 11% total energy consumed), primarily larvaceans. Pink salmon energy sources were crab larvae and amphipods. For herring, most energy came from a mix of crab larvae, euphausiids, and hyperiid amphipods. Feeding rate (%Cmax) varied among years for all species (Fig. 2.7).

Model-based and reported abundances of herring ages ≥ 1 ranged from 23.6 million (M, 2011) to 411.7 million (M, 2001) (Table 2.5). Relative population consumption estimates ranged from 112 metric tons (2004 coho) to 103,704 metric tons (2009 M herring). The relative population consumption demand for herring was far greater than that of salmon, exceeding salmon consumption often by orders of magnitude for shared prey taxa (Fig. 2.8). For crab larvae, a prey type important to all species except chum, consumption demand by the herring population was up to 133 times greater than salmon population consumption demand. Herring consumed 1.2 to 271 times as much crab larvae as Chinook salmon, depending on year and herring abundance estimation method (W vs M). Coho salmon population consumption demand for crab larvae ranged from about a tenth of the consumption demand on crab larvae by Chinook salmon to approximately equal population-level demand, and population consumption demand by pink salmon was 1.2 to 2 times that of Chinook salmon consumption demand for crab larvae.

Discussion

The potential for interspecific competition for food among juvenile salmon and herring in Puget Sound is high, based on the substantial dietary and spatial-temporal overlap observed over multiple years. Herring consumption demand was generally much greater than that of the other species, and even all the other species' consumption demands combined. This was true regardless of abundance estimation method; herring consumed a greater amount of shared prey resources than salmon. Competition can occur when species utilize the same resources (e.g., habitat, food) and at least one of those resources is limiting (Gause 1934, Pianka 1976). Previous research suggested that food availability is limiting in Puget Sound, based on observed variability in feeding and growth linked to survival (Beauchamp and Duffy 2011). Because of the potential ability of herring to remove much greater portions of the prey base than salmon, herring may exert a large amount of competitive pressure on salmon populations. Competitive interactions among salmon species and herring have been recorded in other regions and linked to growth and survival (Sturdevant et al. 2001, Ruggerone et al. 2003, Ruggerone and Goetz 2004, Ruggerone and Nielsen 2005); competition may also contribute to observed patterns in growth and survival for Puget Sound stocks.

Trawl catches demonstrated consistent species overlap by depth in the water column and area of Puget Sound. The predominance of salmon and herring in the upper water column is consistent with observations on the coast and within other inland seas (Jaenicke et al. 1984, Pearcy et al. 1988, Waddell et al. 1992, Orsi and Wertheimer 1995, Beamish et al. 2000, Emmett et al. 2004). In some systems, juvenile Chinook salmon are spatially separated from other juvenile salmon species (Weitkamp et al. 2011) and not spatially correlated with Pacific herring (Emmett et al. 2004, Weitkamp et al. 2011). However, we did not observe spatial separation by species, and our results suggest that, within Puget Sound, juvenile salmon species and herring are using the same epipelagic habitat.

In Puget Sound, Chinook salmon, coho salmon, and (to a slightly lesser extent) herring exploit the same invertebrate prey base, and prey limitation has the potential to have greater effect in July (when diet overlap is high) than later in the year. Salmon and herring ate prey items that were generally similar to those observed in other marine areas, although proportional contributions of various prey types differed from those observed in Puget Sound (Healey 1991, Foy and Norcross 1999, Cooney et al. 2001, Norcross et al. 2001, Sturdevant et al. 2001, Schabetsberger et al. 2003). Juvenile salmon diets in Puget Sound may be distinct from the neighboring Strait of Georgia and along the Pacific coast where offshore juvenile Chinook and coho salmon are more piscivorous (Brodeur et al. 1992, Schabetsberger et al. 2003, Brodeur et al. 2007, Daly et al. 2009, Sweeting and Beamish 2009; R. Sweeting, *unpublished data*). The elevated reliance on invertebrates by Chinook and coho salmon imply that Puget Sound stocks could be particularly vulnerable to competition with other pelagic fish - like herring, which ate similar prey items to Chinook and coho salmon. Crab larvae was a particularly important prey item for Chinook and coho salmon and, while it does not play a large role in the diets of herring from other areas (Foy and Norcross 1999, Cooney et al. 2001, Norcross et al. 2001, Sturdevant et al. 2001), our results and other local studies show that Puget Sound herring consume a large amount of crab larvae (Hu 2009). Chum salmon diet composition differed markedly from the diets of other salmon species and included high contributions of gelatinous prey (larvaceans, ctenophores; Healey 1991, Arai et al. 2003).

Certain diet patterns were potentially indicative of characteristics that distinguish the Puget Sound prey field from zooplankton compositions observed in adjacent waters. The prevalence of hyperiid amphipods in chum diets is likely a reflection of their reliance on gelatinous prey; the association between gelatinous organisms and hyperiid amphipods is well-documented (Bowman et al. 1963, Harbison et al. 1977, Arai 2005, Riascos et al. 2012). However, the high contribution of gammarid amphipods in September/October diets is notable because this is not observed in neighboring systems (e.g., amphipods in Strait of Georgia coho diets are virtually all hyperiid species; Ruston Sweeting, DFO Canada, *pers. comm.*) and may reflect distinct characteristics of the Puget Sound forage base. In Hood Canal, Puget Sound, gammarid amphipods are as equally abundant as hyperiids in the water column; however, in the neighboring Strait of Juan de Fuca, hyperiids outnumber gammarids by at least a 10:1 ratio (J. E. Keister, *unpublished data*). This suggests that the forage base available to Puget Sound fish is distinct from other regions and fluctuations in prey availability may substantially influence seasonal diet composition which, in turn, likely affects the magnitude of diet overlap and potential for interspecific feeding interactions.

Patterns of diet overlap observed in Puget Sound were geographically consistent with broader areas: Chinook and coho salmon typically consume similar prey within a given geographic region (Brodeur et al. 2007, Weitkamp and Sturdevant 2008, Weitkamp et al. 2011). This suggests that comparable species interactions may be occurring across systems which are not specific to a particular environment. However, the resultant condition from these interactions varies. In some systems, overlap in resource use is ameliorated by spatial segregation of species. This does not appear to be the case in Puget Sound, where spatial overlap of salmon and herring is high. Chinook and coho salmon stocks in Puget Sound have decreased substantially over the past 30 years: a pattern which is unique to the Salish Sea when compared to adjacent regions and stocks, and consistent with the hypothesis of a cultivation/depensation mechanism wherein a reduction in salmon populations may increase potential for competitive interactions among juvenile salmon species and the more abundant herring. These potential interactions are complicated by the presence of piscivorous resident Chinook salmon that may remove substantial portions of both the juvenile Chinook salmon population and herring populations (Kirkness 1948, Beauchamp and Duffy 2011); resident predation would likely disproportionately impact the much less numerous salmon population. Abundance trends of resident salmon populations are not well characterized, but may influence the presence and strength of competitive interactions among juvenile salmon and herring in Puget Sound.

Gut content analysis is limited by diel variation in feeding and the rapidity of prey digestion (Benkwitt et al. 2009). There is evidence of diel feeding patterns for salmon and herring, based on differences in foraging effort (Brodeur and Pearcy 1987, Sturdevant et al. 2001, Schabetsberger et al. 2003), and prey compositions (Simenstad et al. 1980, Meyer et al. 1981, Shepard 1981, Darbyson et al. 2003). Because our samples were collected during daytime, our sampling methods may exclude prey taxa that were consumed during the late afternoon-evening period, when we did not sample. However, herring in Hood Canal, Puget Sound do not show strong diel differences in rate or composition of feeding (Timothy Essington, University of Washington, *pers. comm.*) and planktivorous juvenile salmon feed predominantly during the day (Armstrong et al. 2008, Duffy et al. 2010), which suggests that the effects of daylight sampling bias may be minimal. Herring guts often contained greater proportions of digested material that could not be classified into prey types than did salmon guts. Another dataset of formalin-preserved salmon and herring stomachs showed the same pattern (I. M. Kemp & C. M. Greene, *unpublished data*), indicating that the high proportions of digested material in herring guts are not simply an artifact of differences in processing methodology (i.e., frozen versus fresh). Different amounts of digested material in salmon and herring stomachs may be due to variation in feeding behavior or physiological variation in digestion. Unlike juvenile salmon, herring have the capability to utilize multiple feeding modes, allowing them to forage during both day and night (Sandstrom 1980, Gibson and Ezzi 1985, Batty et al. 1986, Batty et al. 1990, Gibson and Ezzi 1992), and their more rapid (relative to salmon) gastric evacuation rates (Brodeur and Pearcy 1987, Darbyson et al. 2003, Hallfredsson et al. 2007, Benkwitt et al. 2009) coupled with observed high amounts of digested material support the idea that herring have the potential to exert relatively higher stress on the prey base than salmon.

As is the case of any modeling effort, the Wisconsin model (Hansen et al. 1997) is only as accurate as its inputs and model parameters. We borrowed model parameters from related species (sockeye/pink salmon and Atlantic herring) for chum salmon and Pacific herring, respectively. Water temperatures from trawl sampling or from surface buoy measurements may not reflect the actual thermal regime that a juvenile salmon or herring experiences in the offshore Puget Sound, given that all these species are highly mobile and would certainly be capable of preferentially utilizing areas of higher/lower temperature (e.g., a salmon may select cooler water by moving deeper in the water column). However, growth and consumption was relatively insensitive to the variability in temperatures found in Puget Sound depths at which salmon and herring were caught over the summer period (Beauchamp and Duffy 2011) and temperature was likely secondary in importance to factors such as food availability and feeding rate.

We were limited to the use of apparent growth – the difference in average weight between sampling events – instead of a measure of true growth (e.g., scales, otoliths). Apparent growth assumes negligible size-dependent outmigration or movement among regions of Puget Sound and also negligible size-selective mortality. If fish migrate out of the system over the period of our study (July-September), and especially if larger fish migrate out of the system faster, the apparent growth metric will underestimate the actual growth that fish are achieving. Conversely, if there are size-selective pressures (e.g., predation by seabirds) that remove smaller individuals from the study region, apparent growth will overestimate the actual growth (Ricker 1969, Parker 1971, Sogard 1997). The observed interannual variability in apparent growth throughout our study may be due to actual differences in yearly growth. Alternatively, it may be due to variability in predation pressure or in fish behavior – for example, if the timing of cohorts of salmon migrating out of Puget Sound varies among years, this could also influence apparent growth patterns. Identification of the source(s) of variable growth observed in this study is needed. Scale or otolith analyses, preferably on hatchery coded-wire-tagged salmon for which size-at-release and location of release is readily obtainable, could provide fine-scale growth measurements for model inputs and would improve accuracy in consumption estimates.

We identified spatial and temporal variability in diets of small pelagic fishes feeding on zooplankton but also overlap among species on common prey taxa. We presently do not have sufficient information about the availability of zooplankton prey resources to link diet overlap between salmon species and herring to growth and ultimately survivorship. Although the existing evidence (variable feeding related to growth variation and survival in juvenile Chinook; Beauchamp and Duffy 2011, Duffy and Beauchamp 2011) is consistent with a food limitation hypothesis, gathering data on zooplankton populations in Puget Sound over the summer period would enable testing of this hypothesis and evaluation of the magnitude of food limitation.

Our work suggests that the potential for competitive interactions among juvenile salmon and herring is present in Puget Sound. However, predicting effects of competition and other food web interactions can be complicated. If planktivorous juvenile Chinook salmon and herring depend upon the same prey resources and forage in the same areas, competitive effects such as reduced growth or niche shifts are likely (Pianka 1976, Beauchamp and Duffy 2011). A reduction in herring populations might benefit young planktivorous Chinook salmon by reducing competition; alternatively, if herring buffer against predation, declines in herring abundance could result in increased predation on juvenile Chinook salmon. Previous research has suggested complex food web interactions within Puget Sound (Harvey et al. 2012) and potential competitive interactions and prey limitation among salmon species and herring (Ruggerone and Goetz 2004, Ruggerone and Nielsen 2009, Beamish et al. 2012). Harvey et al. (2012) reports that the Puget Sound food web is driven by bottom-up forcing factors, but that several species (primarily avian) exert strong top-down pressures on forage fishes and invertebrates. Additionally, recent decades appear to have been transitional for Chinook and coho salmon, steelhead (*O. mykiss*), cod (*Gadus macrocephalus*), hake (*Merluccius productus*), and rockfish (*Sebastes* spp) in the Puget Sound food web. Management and restoration strategies for ESA-listed salmon species could be informed by accounting for how the dynamics of the entire planktivore community affect salmon growth, and how declines in the population may affect juvenile survival. This work contributes to the understanding of pelagic food webs by describing the potential for competition using simple, intuitive measures such as diet overlap and relative consumption rates of shared prey. Additional data and modeling work is needed to link the high rates of consumption of herring on prey shared with salmon to salmon growth and survivorship.

Table 2.1. Literature values for prey energy densities and indigestible fractions.

Prey Group	Energy Content (J/gWW)	Indigestible Fraction (%)	Reference	Reference Sample Area	Comments
Insect	5311	15	(Duffy 2009)*	Salmon River estuary, OR	average of salmonid adult insect prey
Fish	4649	9	(Boldt and Haldorson 2002, Duffy 2003)	WA; AK	average of juvenile salmon, herring, & sandlance
Gammarid amphipod	4646	12	(Davis 1993)*, (Duffy 2009)*	NW Atlantic	average for Gammaridea
Shrimp	4371	10	(Davis 1993)*	NW Atlantic	average of *Mysis stenoiepis* and caridean shrimp
Polychaete	1980	2	(Gray 2005)	Salmon River estuary, OR	
Euphausiid	4765	10	(Davis 1993)*	Bristol Bay	*Euphausia pacifica*
Crab larvae	2981	10	(Davis 1993)*	Bristol Bay	crab zoea
Calanoid copepod	2625	9	(Davis et al. 1998)	N. Pacific & Bering Sea	*Neocalanus cristatus*
Hyperiid amphipod	2466	13	(Davis et al. 1998)	Bering Sea	July 1992-1995
Barnacle larvae	2045	10	(Thayer et al. 1973)	Newport River estuary, NC	
Ostracod	1394	10	(Donnelly et al. 1994)	Scotia/Weddell Sea	average for *Conchoecia antipoda*, *C. belgicae*, & *C. hettacra*
Ctenophore	205	10	(Davis 1993)*	NW Atlantic	average value for mixed species, Class Tentaculata
Larvacean	3178	9	(Davis et al. 1998)	Bering Sea	appendicularians
Other/Unid	2942	10			average of other marine prey

*reference provides a summary, not original author

Table 2.2. Differences in diet composition by species, month, and year.
PERMANOVA on arcsine-transformed proportional mass/volume-based diets, 9999 permutations, Bray-Curtis dissimilarity.

	Degrees freedom	Sums of squares	Mean squares	F Statistic	R^2	Pr(>F)
Year	8	12.0	1.5	8.5	0.07	<0.001 ***
Month	1	13.3	13.3	75.1	0.07	<0.001 ***
Species	4	28.9	7.2	40.8	0.16	<0.001 ***
Year:Month	8	8.5	1.1	6.0	0.05	<0.001 ***
Year:Species	23	9.8	0.4	2.4	0.05	<0.001 ***
Month:Species	4	8.7	2.2	12.3	0.05	<0.001 ***
Year:Month:Species	23	7.6	0.3	1.9	0.04	<0.001 ***
Residuals	504	89.4	0.2		0.50	
Total	575	178.4			1	

Table 2.3. Comparisons of prey dispersions for each species.Observed p-value below diagonal; permuted p-value above diagonal.
PERMDISP and pairwise species comparisons on arcsine-transformed proportional mass/volume-based diets, 9999 permutations, Bray-Curtis dissimilarity.

	Chinook	Chum	Coho	Pink	Herring
Chinook		0.01 *	0.003 **	0.012 *	0.227
Chum	0.006 **		0.001 ***	0.95	0.056
Coho	0.001 ***	<0.001 ***		0.001 ***	0.554
Pink	0.011 *	0.951	<0.001 ***		0.011 *
Herring	0.218	0.048 *	0.556	0.007 **	

Table 2.4. Effects on diet composition of Chinook salmon (a), coho salmon (b), chum salmon (c), pink salmon (d), and Pacific herring (e) by month and year.
Pairwise PERMANOVA on arcsine-transformed proportional mass/volume-based diets, 9999 permutations, Bray-Curtis dissimilarity.

a) Chinook	Degrees freedom	Sums of squares	Mean squares	F Statistic	R^2	Pr(>F)
Year	8	7.3	0.9	5.3	0.14	<0.001 ***
Month	1	7.6	7.6	44.5	0.14	<0.001 ***
Year:Month	8	5.8	0.7	4.2	0.11	<0.001 ***
Residuals	193	33.1	0.2		0.62	
Total	210	53.7			1	

b) Coho	Degrees freedom	Sums of squares	Mean squares	F Statistic	R^2	Pr(>F)
Year	8	4.8	0.6	3.1	0.10	<0.001 ***
Month	1	12.1	12.1	63.5	0.26	<0.001 ***
Year:Month	8	3.5	0.4	2.3	0.08	<0.001 ***
Residuals	134	25.6	0.2		0.56	
Total	151	46.0			1	

c) Chum	Degrees freedom	Sums of squares	Mean squares	F Statistic	R^2	Pr(>F)
Year	8	6.6	0.8	5.3	0.22	<0.001 ***
Month	1	1.5	1.5	9.7	0.05	<0.001 ***
Year:Month	8	3.9	0.49	3.1	0.13	0.038 *

Residuals	112	17.6	0.2		0.59	
Total	129	29.7			1	

d) Pink	Degrees freedom	Sums of squares	Mean squares	F Statistic	R^2	Pr(>F)
Year	3	0.99	0.3	1.7	0.08	0.071
Month	1	0.77	0.8	3.9	0.07	<0.007 **
Year:Month	3	0.97	0.3	1.6	0.08	0.077
Residuals	45	8.97	0.2		0.77	
Total	129	22.7			1	

e) Herring	Degrees freedom	Sums of squares	Mean squares	F Statistic	R^2	Pr(>F)
Year	4	2.8	0.7	4.0	0.35	<0.001 ***
Month	1	0.3	0.3	1.9	0.04	0.112
Year:Month	4	1.5	0.4	2.2	0.19	0.014 *
Residuals	19	3.3	0.2		0.42	
Total	28	7.9			1	

Table 2.5. Estimations of salmon and herring abundance (millions) based on the volume sampled by trawling (Vnet) and the volume of Main Basin down to 60 m water column depth (32.1 km^3), modeled abundance (M) for ages-1+ herring, and reported abundance (W) for ages-1+ herring. Reported abundances were not available for 2009 or 2011.

Year	Avg distance trawled (nmi)	Avg # Chinook	Avg # Coho	Avg # Chum	Avg # Pink	Vnet (km^3)	Chinook Trawl	Coho Trawl	Chum Trawl	Pink Trawl	Herring M	Herring W
2001	1.9	76	35	110	0	1.50	1.64	0.74	2.35	0	411.7	109.9
2004	1.5	52	5	451	281	1.13	1.54	0.16	13.27	8.27	166.0	31.0
2008	1.4	73	16	138	152	1.07	2.25	0.49	4.23	4.69	168.1	74.7
2009	1.5	82	21	55	0	1.15	2.35	0.61	1.57	0	264.6	NA
2011	1.4	89	10	40	0	1.11	2.65	0.29	1.19	0	23.6	NA

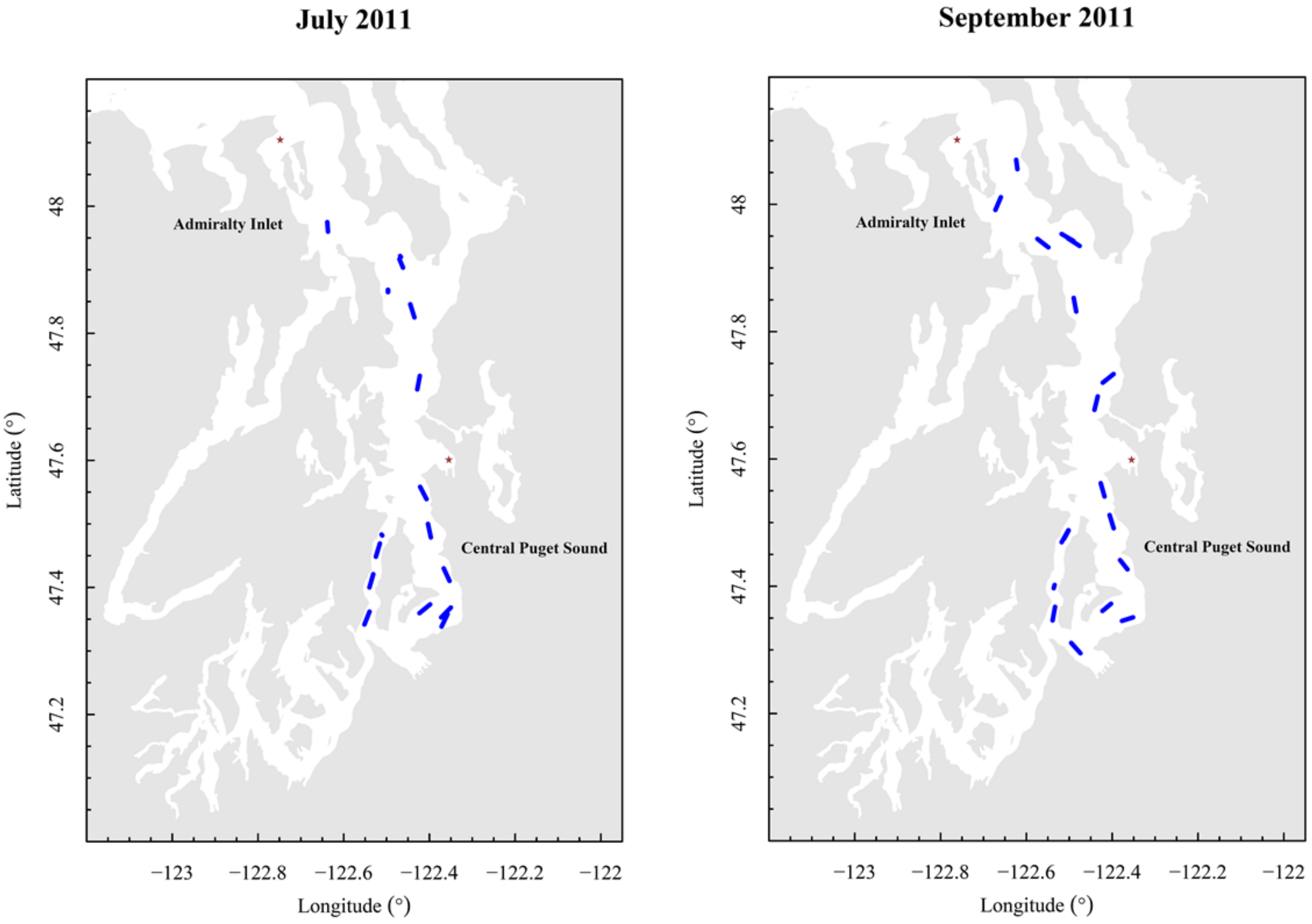


Figure 2.1. Map of study area within Puget Sound, WA. Midwater trawl tracks are indicated by blue lines and locations of buoys from which reference water temperature data were obtained are indicated by red stars. The buoy locations remained unchanged across years and trawl locations were similar to those shown here for 2011 across all years.

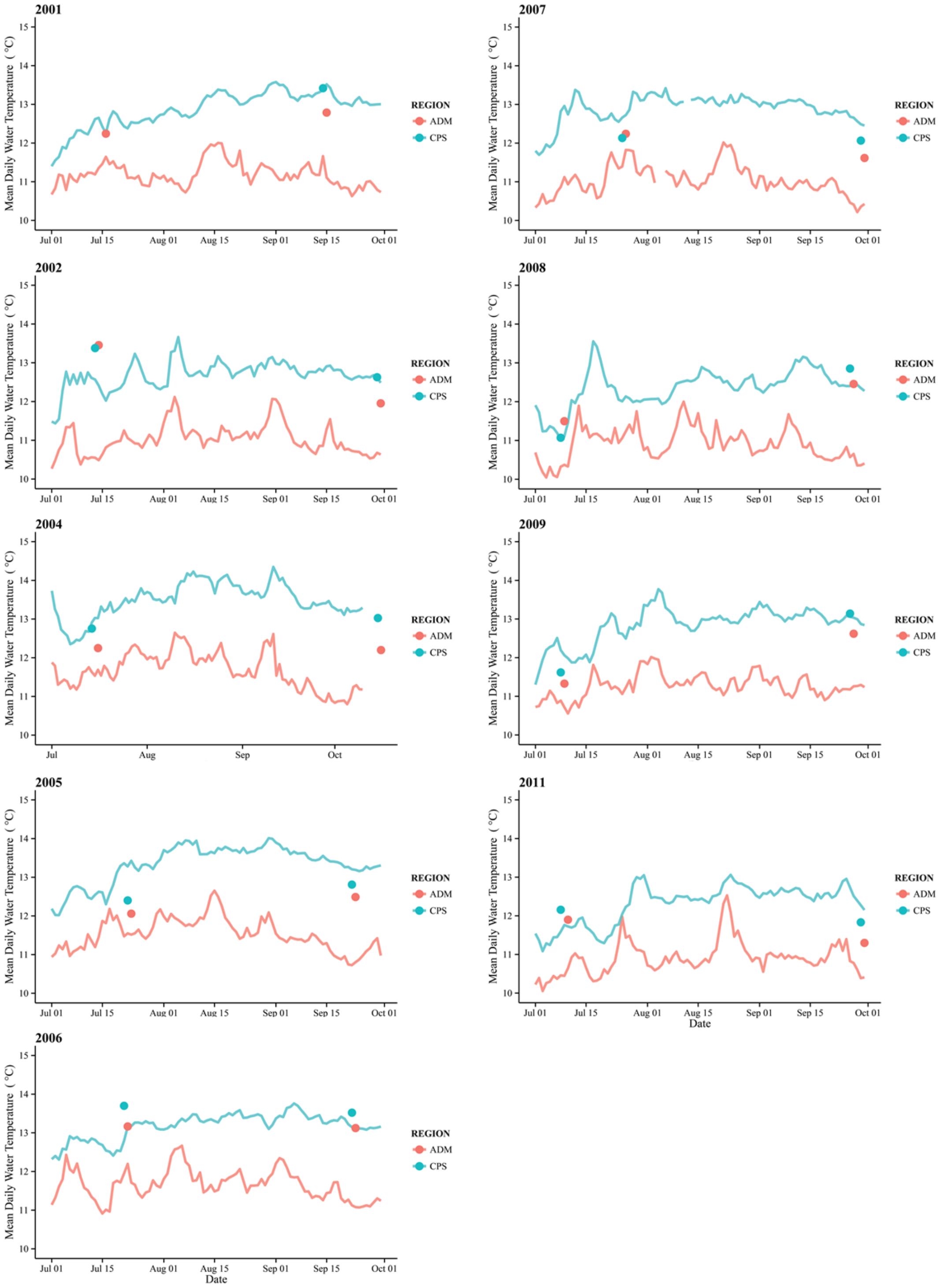
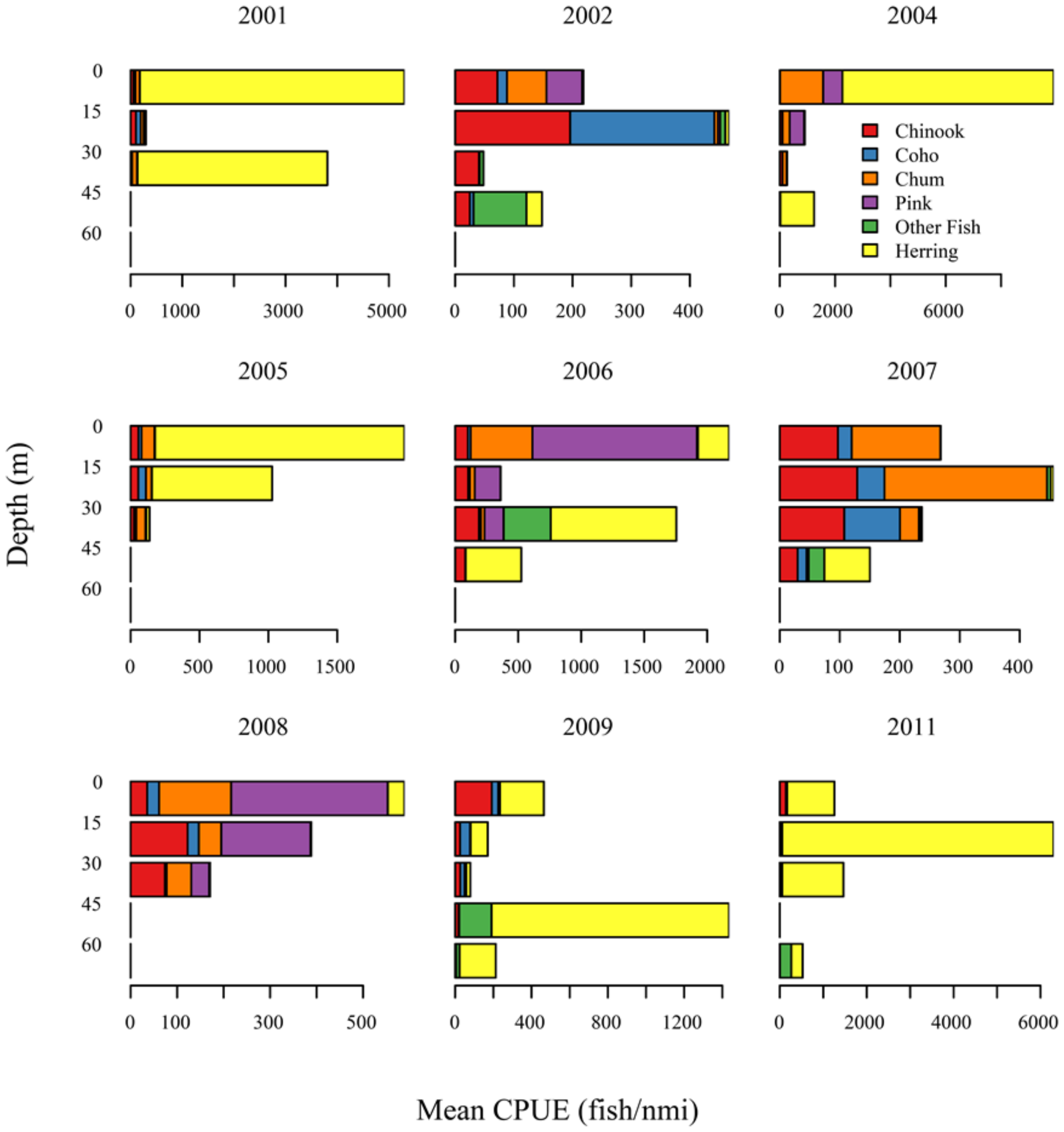


Figure 2.2. Water temperature measurements obtained from NOAA buoys (lines, surface water temperatures) and trawl measurements (points, water temperatures at net). ADM denotes Admiralty Inlet while CPS denotes Central Puget Sound. Trawl temperatures were not available for CPS 2001.

a) Mean catch per nautical mile trawled in July



b) Mean catch per nautical mile trawled in September/October

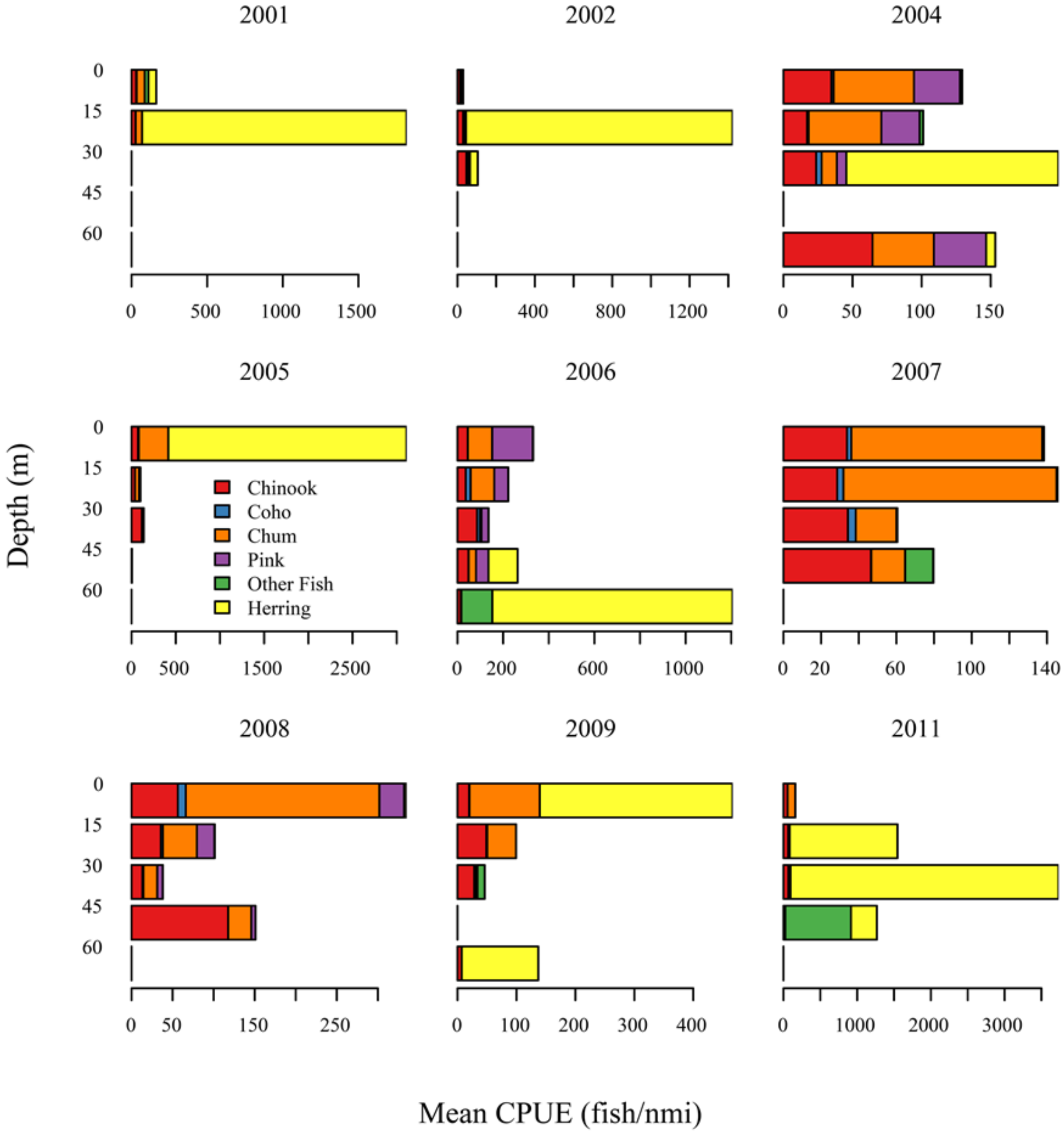
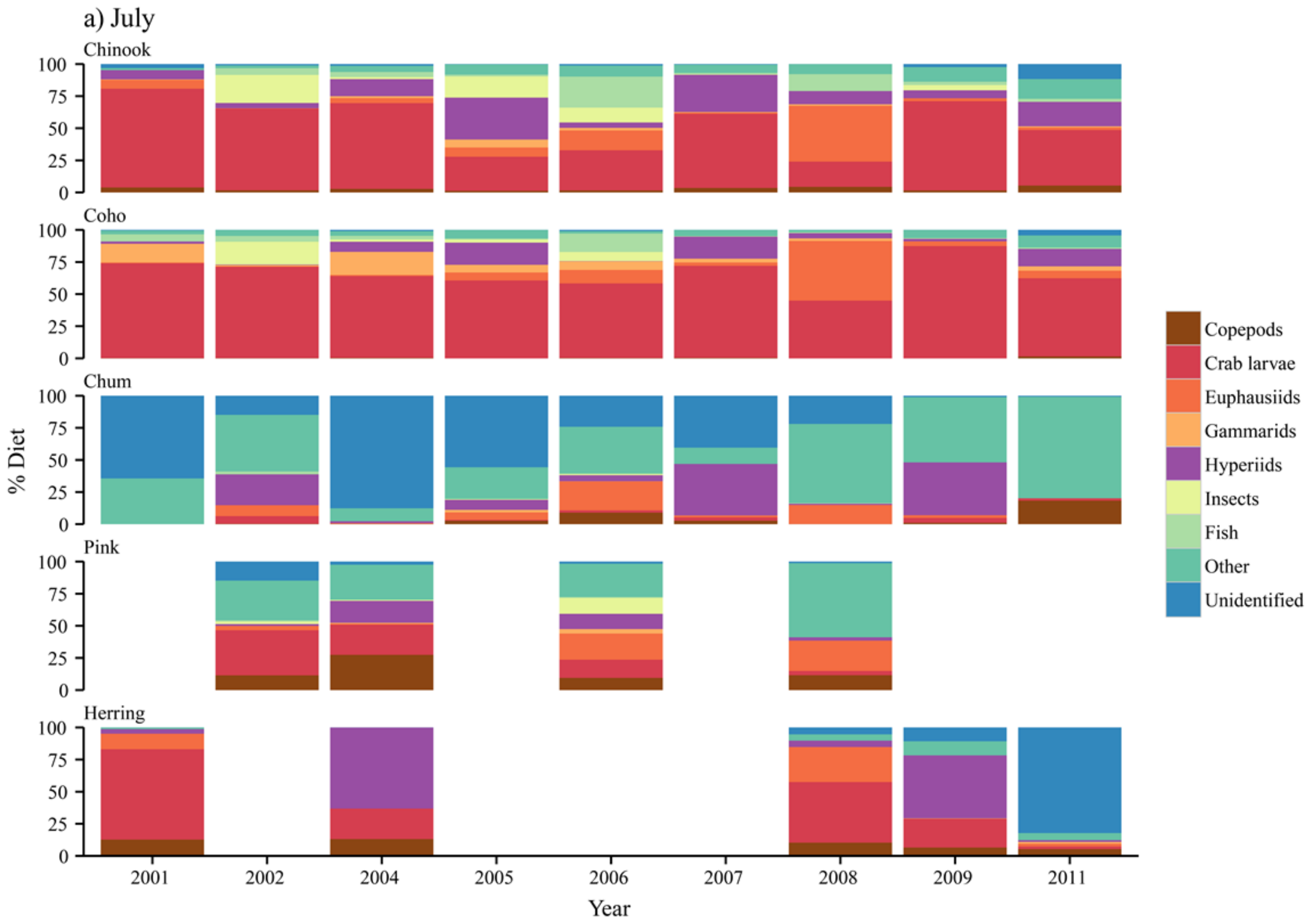


Figure 2.3. Mean catch (fish per nautical mile) by 15 m depth increments over 9 years of midwater trawl sampling in July (a) and September/October (b). Note varying scales of x-axes.


a) July
Chinook
Coho
Chum
Pink
Herring
100
75
50
25
0
% Diet
2001
2002
2004
2005
2006
2007
2008
2009
2011
Year
Copepods
Crab larvae
Euphausiids
Gammarids
Hyperiids
Insects
Fish
Other
Unidentified

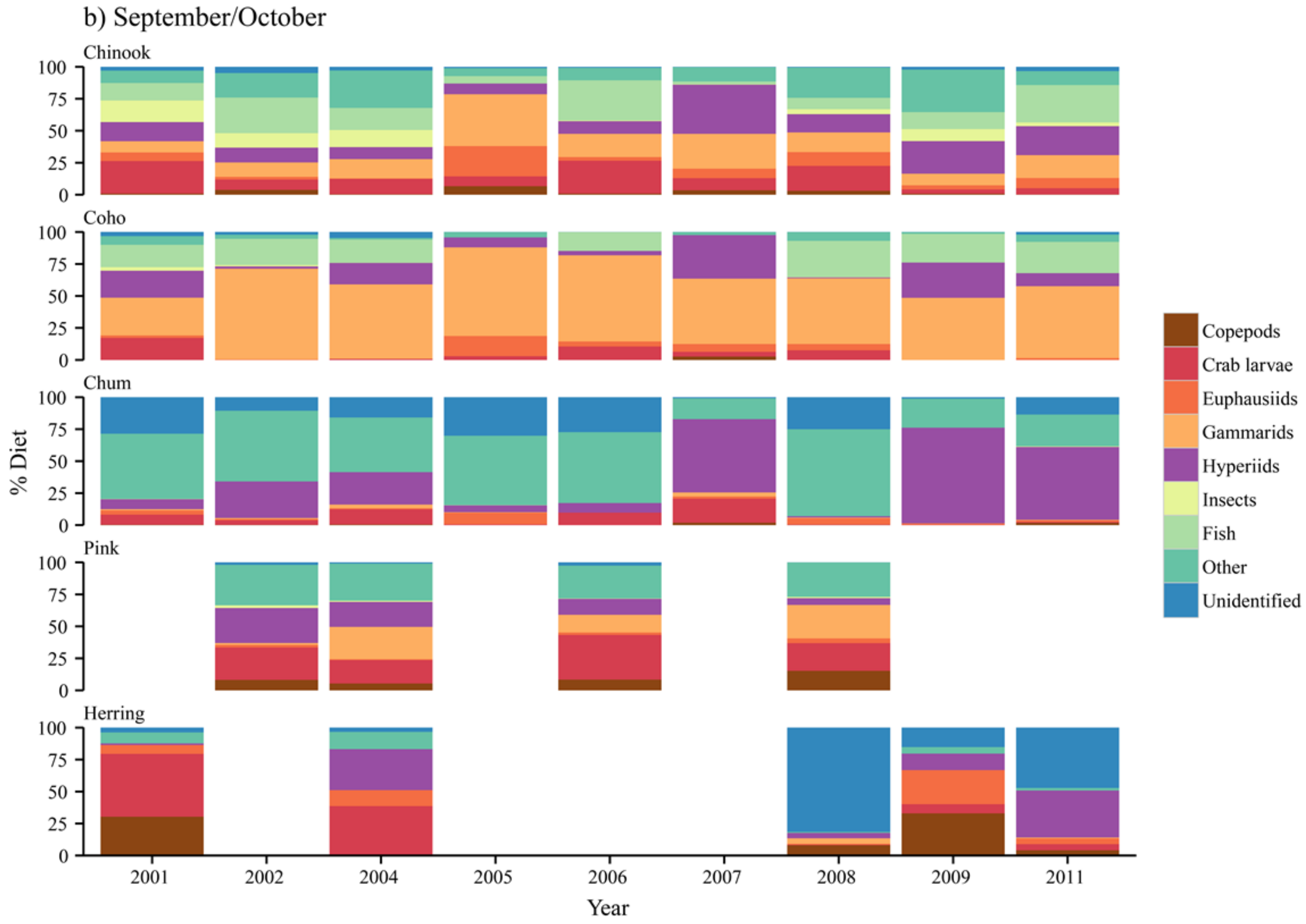


Figure 2.4. Proportional contribution of prey taxa in salmon (calculated based on volume) and herring (calculated based on mass) diet compositions in July (a) and September/October (b) in the Main Basin. Other prey were a miscellaneous mix for Chinook, coho salmon, and herring. Other prey for pink salmon included larvaceans, shrimp, ostracods, and chaetognaths. Other prey for chum salmon were larvaceans and ctenophores.

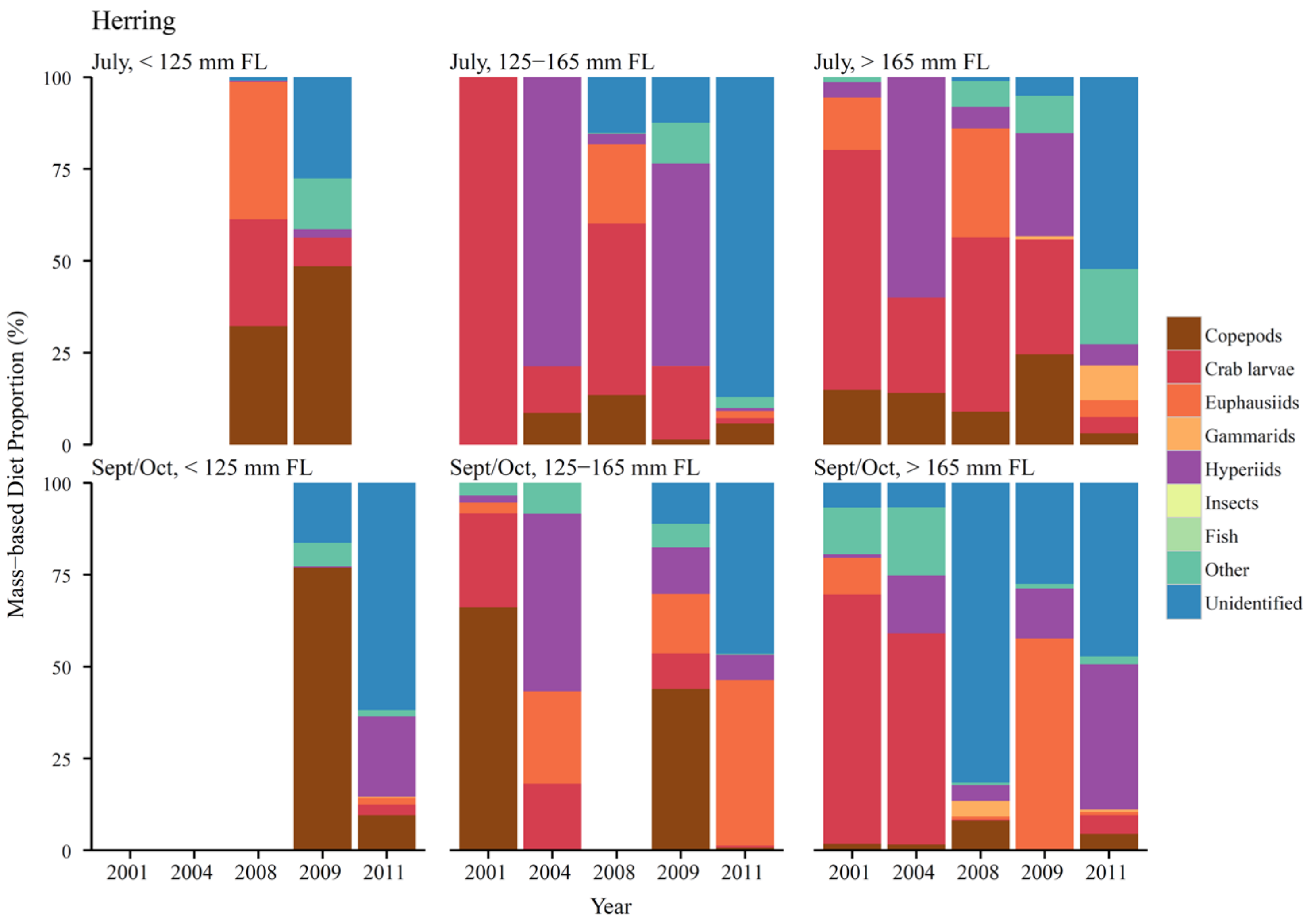


Figure 2.5. Proportional mass-based diet compositions for three size classes of herring. Size classes increase from left to right; July is represented in the upper set of panels and September/October in the lower set of panels.

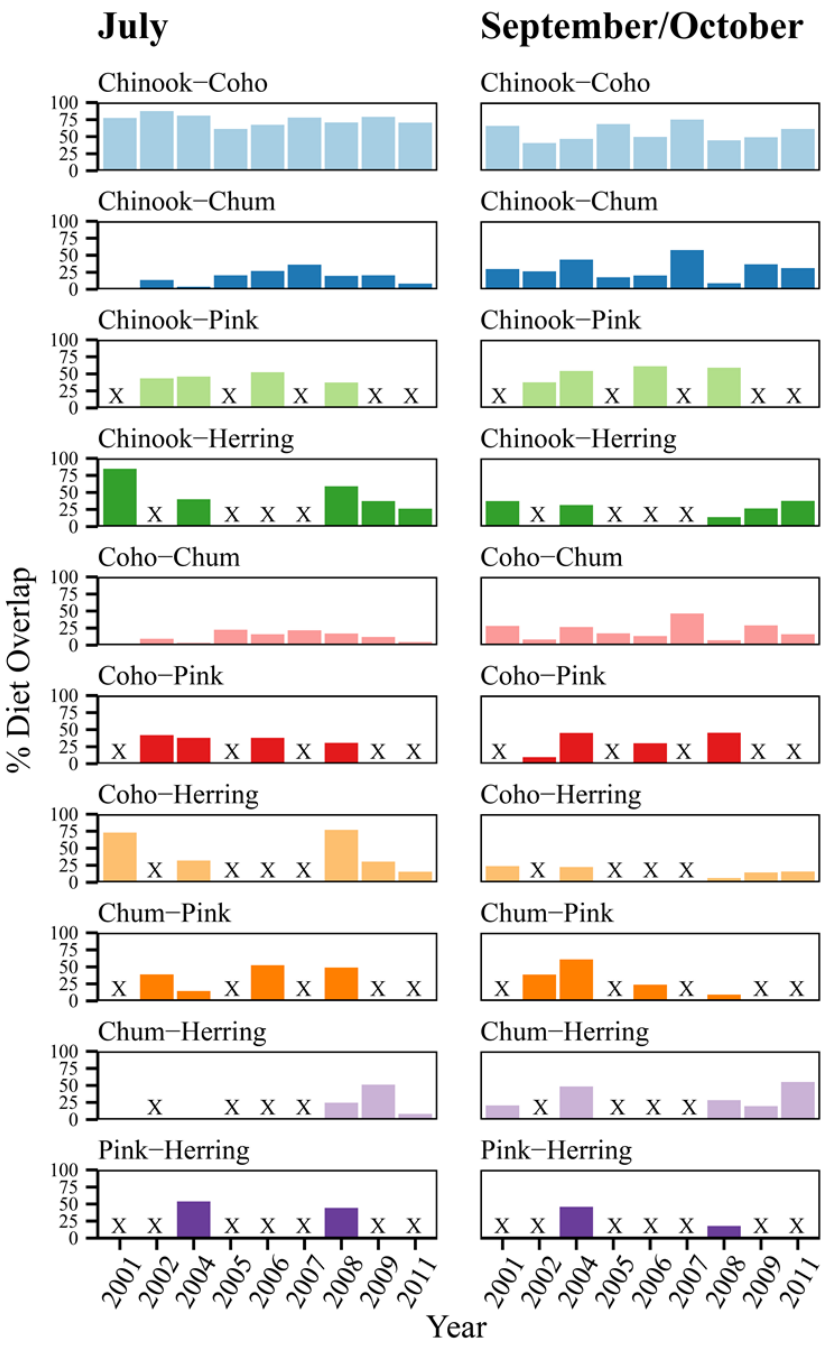


Figure 2.6. Diet overlap between species pairs in Main Basin in July (left) and September or October (right). Each row represents one species pair. Years for which data were not available are marked with an X.

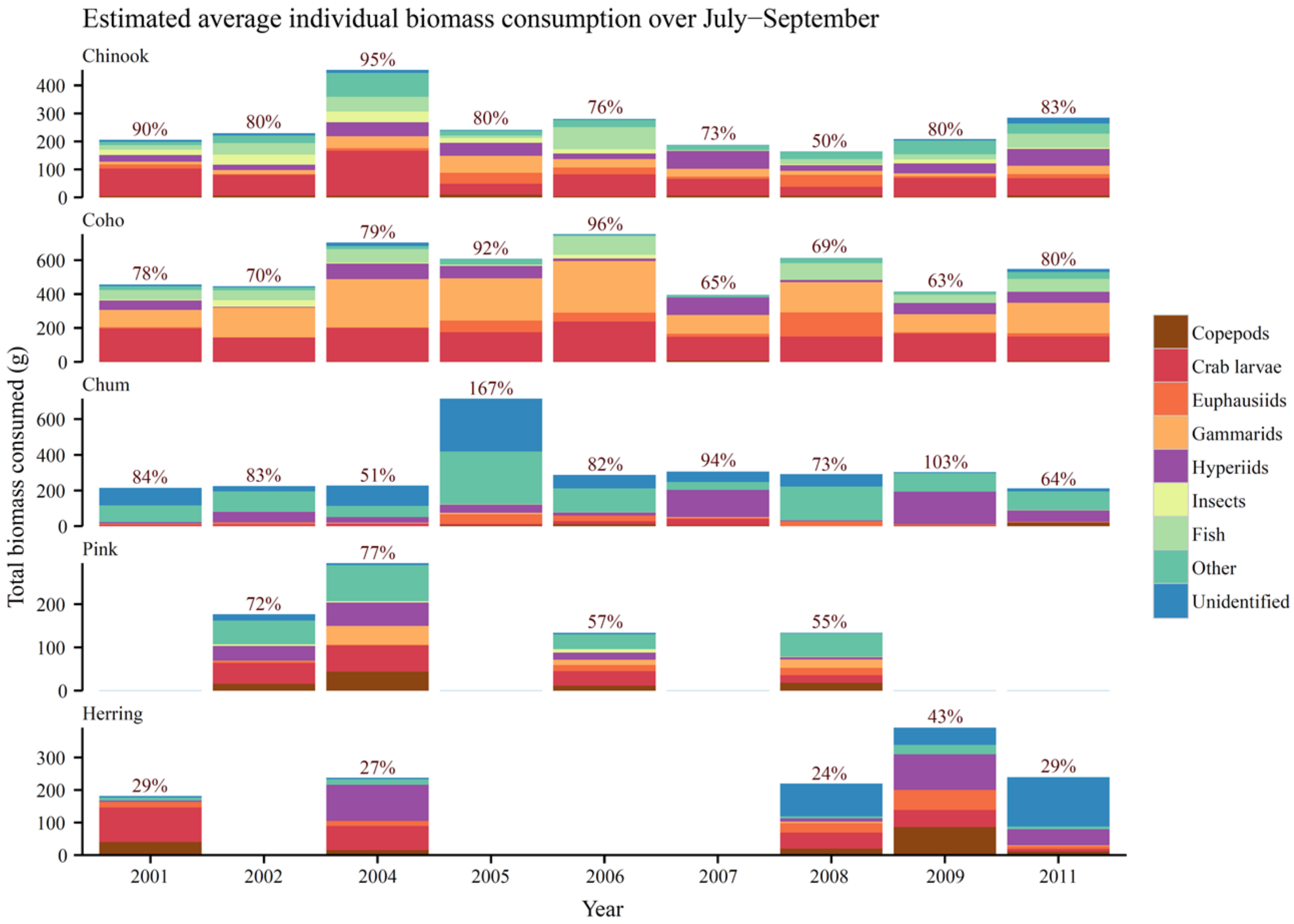


Figure 2.7. Estimated total biomass (g) consumed by the average individual of each salmon species and herring in Main Basin over time. Feeding rate (%Cmax) is labeled above each bar. Note varying scales of y-axes.

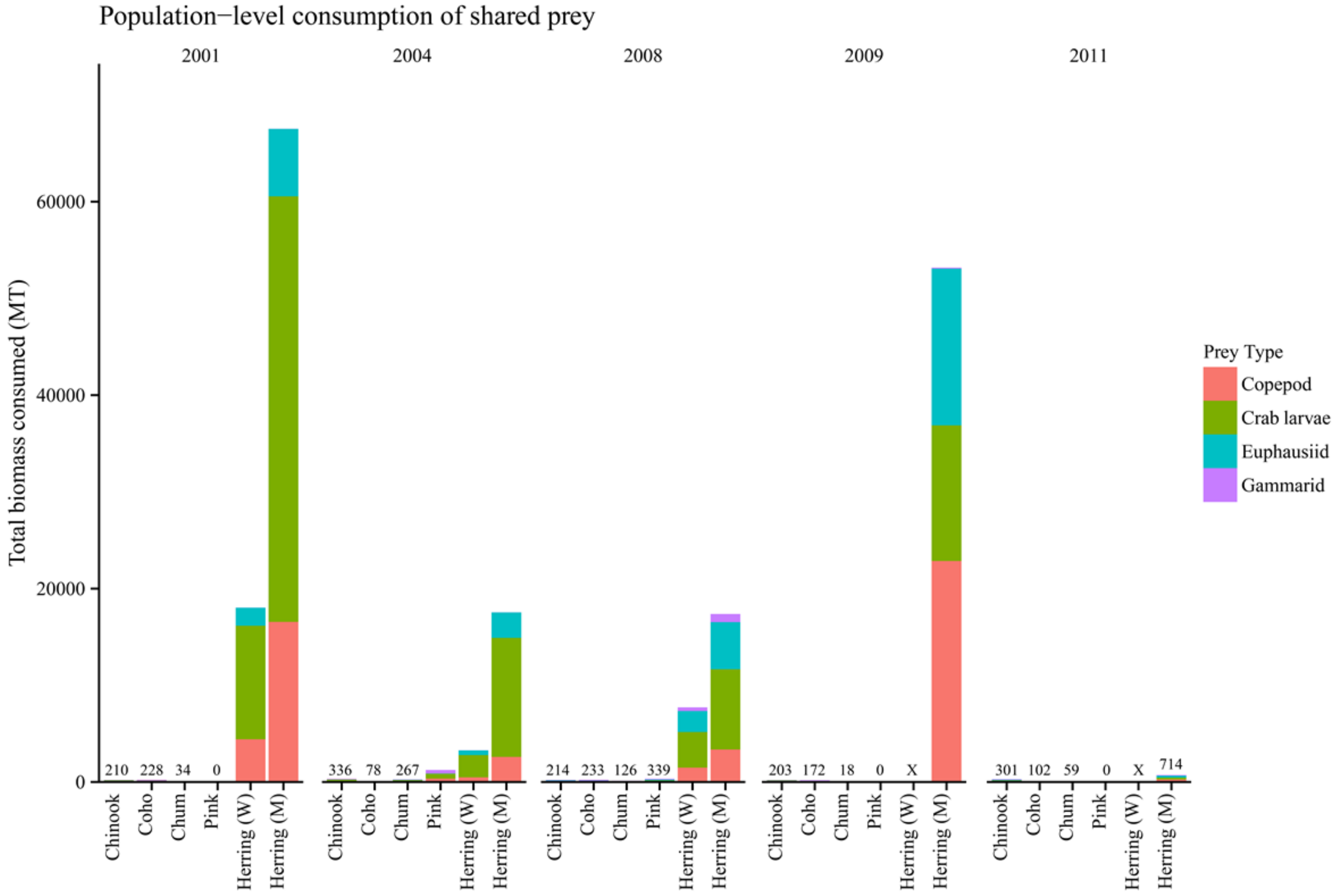


Figure 2.8. Estimated consumption demand of shared prey types (copepods, crab larvae, euphausiids, gammarid amphipods) for salmon and herring populations based on abundance estimates in Table 2.5. X indicates years where data were not available.

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Appendix A

Table A1. Numbers of tows and counts of species caught in surface townetting sampling events. Basins are denoted by abbreviations: CPS=Central Puget Sound, WHID=Whidbey Basin, SPS=South Puget Sound, AI=Admiralty Inlet. Other fish included gadids, river lamprey, sculpin, shiner perch, northern anchovy, unknown fish, and one midshipman.

Month	Basin	N tows	Chum	Chinook	Coho	Steelhead	Herring	Sand lance	Surf smelt	Three-spine stickleback	Other fish	Jellies
April	CPS	3	0	0	0	0	0	0	0	0	7	2
	WHID	2	14	0	0	0	0	0	23	5	3	0
	AI	1	0	0	0	0	0	0	0	0	0	0
May	CPS	5	0	0	0	0	1	26	0	0	3	128
	WHID	4	3	0	0	1	0	2	3	4335	1	23
	SPS	3	0	5	0	0	606	0	0	0	1	51
	AI	1	0	0	0	0	3	0	0	0	0	6
June	CPS	2	6	3	2	0	0	0	0	1	0	71
	WHID	4	340	280	20	0	13	0	702	254	15	237
	SPS	3	977	200	6	0	4	0	0	0	3	67
	AI	1	11	0	0	0	0	0	0	0	2	42
July	CPS	5	1469	44	41	0	18	0	0	5	0	338
	WHID	4	14	16	4	0	17	0	336	302	8	1236

	SPS	3	391	151	0	0	1	0	0	0	1	163
Aug	AI	1	1	0	0	0	0	0	0	0	0	33
	CPS	5	13	135	1	0	684	0	0	0	1	237
	WHID	4	1	15	0	0	0	0	1	151	0	173
	SPS	3	34	123	0	0	2	0	0	2	1	147
Sept	AI	1	1	0	0	0	0	0	0	0	0	1
	CPS	5	5	5	0	0	4	0	29	4	0	110
	WHID	4	0	5	0	0	12	14163	1	27127	1	6
	SPS	3	1	18	0	0	4	0	1	0	0	74
Oct	AI	1	0	1	0	0	0	0	0	0	0	12
	CPS	5	0	2	0	0	0	0	0	0	1	139
	WHID	4	0	0	0	0	1	0	4	3841	3	15
	SPS	3	0	2	0	0	0	0	0	2	0	58

Table A2. Length-weight regressions for salmon species and herring calculated from observed fork lengths (FL) and wet weights (WW) of species in midwater trawl catches.

Species	**Equation**	**R^2**
Chinook	$WW = 3.97 \times 10^{-6} * FL^{3.2}$	0.98
Coho	$WW = 6.38 \times 10^{-6} * FL^{3.1}$	0.97
Chum	$WW = 4.22 \times 10^{-6} * FL^{3.2}$	0.98
Pink	$WW = 5.83 \times 10^{-6} * FL^{3.1}$	0.99
Herring	$WW = 3.02 \times 10^{-6} * FL^{3.2}$	0.98

Table A3. Number of samples and average diet composition of herring (1+, mass-based proportion) and salmon (volumetric proportion) by month and year for Chinook (Chk), coho (Coh), chum (Chu), and pink salmon, and Pacific herring (Herr). Prey taxa are abbreviated as follows: Barn=barnacle, Cal=calanoid copepod, Cten=ctenophore, Crab=crab larvae (primarily zoea), Euph=euphausiid, Gam=gammarid amphipod, Hyp=hyperiid amphipod, *Oik*=larvacean (*Oikopleura*), Ostr=ostracod, Poly=polychaete, Shr=shrimp, Ins=Insect, Unid=unidentified material.

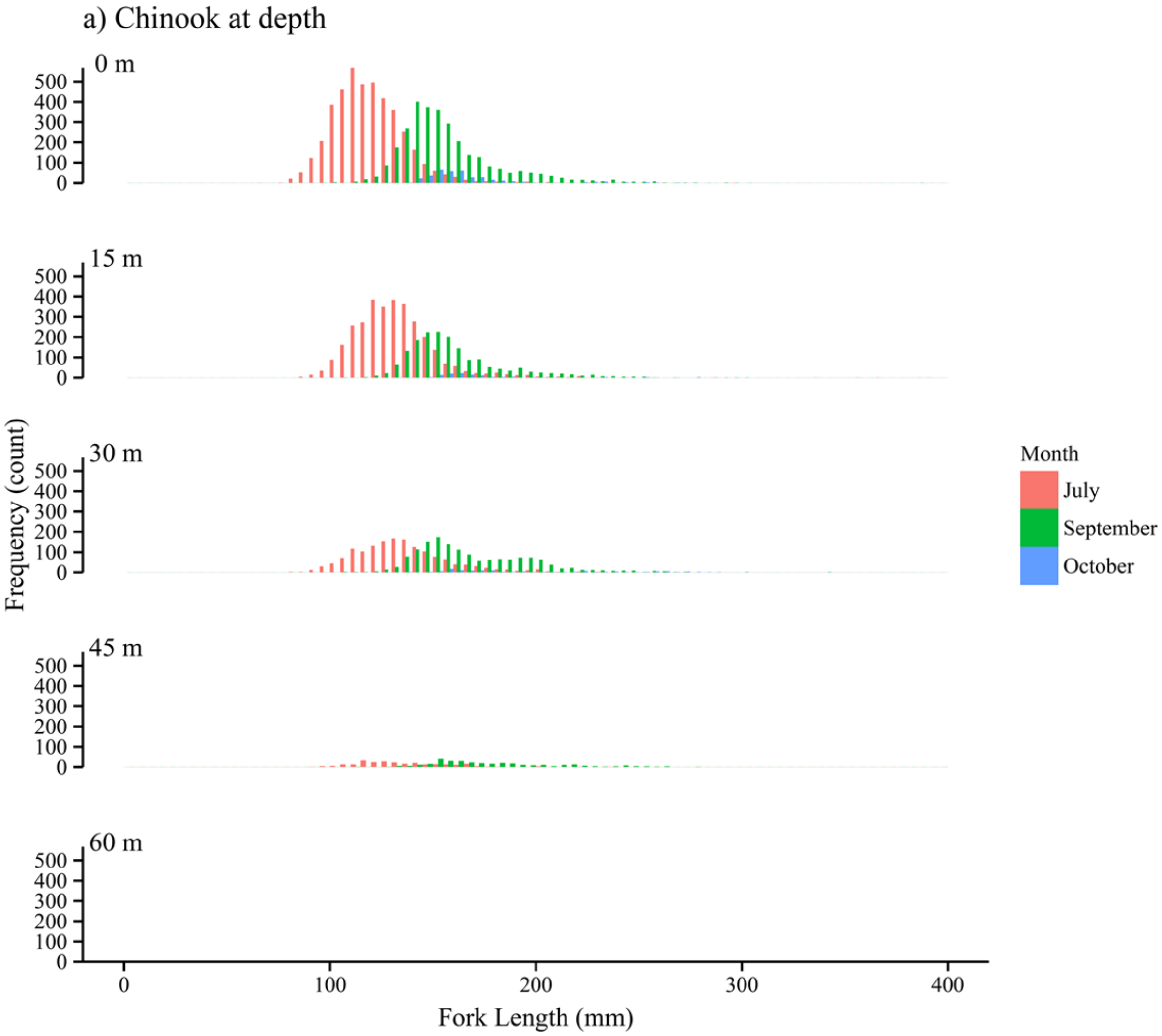
Date	Spp	N	Barn	Cal	Cten	Crab	Euph	Gam	Hyp	*Oik.*	Ostr	Poly	Shr	Ins	Fish	Other	Unid
7/01	Chk	32	0.000	0.039	0.000	0.769	0.069	0.005	0.072	0.000	0.000	0.013	0.003	0.000	0.000	0.000	0.031
7/01	Coh	101	0.000	0.002	0.000	0.738	0.006	0.146	0.018	0.000	0.017	0.001	0.000	0.000	0.055	0.012	0.004
7/01	Chu	21	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.343	0.000	0.000	0.000	0.000	0.000	0.000	0.643
7/01	Herr	7	0.000	0.128	0.000	0.703	0.122	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000
9/01	Chk	149	0.004	0.010	0.000	0.254	0.066	0.088	0.149	0.003	0.029	0.020	0.033	0.169	0.137	0.008	0.029
9/01	Coh	56	0.000	0.000	0.000	0.172	0.020	0.295	0.211	0.008	0.061	0.000	0.000	0.029	0.174	0.000	0.031
9/01	Chu	106	0.000	0.003	0.348	0.079	0.033	0.010	0.078	0.000	0.085	0.003	0.035	0.002	0.000	0.039	0.284
9/01	Herr	9	0.000	0.304	0.000	0.491	0.069	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.037
7/02	Chk	78	0.004	0.017	0.000	0.637	0.001	0.001	0.040	0.000	0.008	0.006	0.004	0.219	0.051	0.000	0.010
7/02	Coh	72	0.000	0.001	0.000	0.711	0.006	0.008	0.004	0.000	0.047	0.000	0.000	0.178	0.044	0.000	0.000
7/02	Chu	27	0.000	0.004	0.033	0.059	0.085	0.000	0.241	0.033	0.000	0.000	0.000	0.000	0.022	0.374	0.148
7/02	Pink	21	0.000	0.114	0.000	0.352	0.033	0.000	0.014	0.190	0.026	0.000	0.000	0.019	0.010	0.093	0.148
9/02	Chk	225	0.013	0.038	0.000	0.080	0.021	0.113	0.116	0.000	0.039	0.055	0.017	0.113	0.279	0.067	0.048
9/02	Coh	19	0.000	0.000	0.000	0.000	0.005	0.708	0.018	0.000	0.026	0.000	0.000	0.011	0.205	0.005	0.021
9/02	Chu	57	0.000	0.002	0.479	0.037	0.010	0.008	0.286	0.025	0.023	0.000	0.002	0.000	0.000	0.025	0.105
9/02	Pink	54	0.000	0.081	0.000	0.254	0.020	0.015	0.273	0.013	0.161	0.000	0.110	0.020	0.002	0.031	0.019
7/04	Chk	188	0.000	0.028	0.000	0.668	0.039	0.015	0.133	0.000	0.006	0.018	0.019	0.016	0.040	0.004	0.014
7/04	Coh	107	0.000	0.004	0.000	0.637	0.009	0.179	0.079	0.000	0.029	0.000	0.003	0.018	0.028	0.006	0.008
7/04	Chu	123	0.000	0.002	0.004	0.000	0.007	0.000	0.015	0.072	0.000	0.000	0.000	0.000	0.000	0.024	0.876
7/04	Pink	103	0.000	0.274	0.000	0.234	0.008	0.007	0.171	0.091	0.089	0.000	0.035	0.008	0.000	0.058	0.023
7/04	Herr	6	0.000	0.132	0.000	0.238	0.000	0.000	0.631	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10/04	Chk	104	0.075	0.004	0.000	0.120	0.004	0.151	0.094	0.000	0.132	0.040	0.018	0.134	0.172	0.028	0.028
10/04	Coh	22	0.000	0.000	0.000	0.009	0.000	0.582	0.168	0.000	0.014	0.000	0.000	0.000	0.182	0.000	0.045
10/04	Chu	83	0.001	0.005	0.049	0.119	0.008	0.028	0.254	0.161	0.167	0.000	0.028	0.000	0.000	0.020	0.158

10/04	Pink	107	0.000	0.054	0.000	0.183	0.007	0.252	0.195	0.048	0.209	0.000	0.027	0.009	0.000	0.007	0.008
10/04	Herr	8	0.000	0.008	0.000	0.378	0.125	0.000	0.321	0.000	0.056	0.000	0.000	0.000	0.000	0.078	0.033
7/05	Chk	162	0.007	0.013	0.000	0.266	0.072	0.062	0.326	0.002	0.008	0.000	0.019	0.165	0.014	0.044	0.002
7/05	Coh	90	0.000	0.000	0.000	0.607	0.061	0.060	0.173	0.000	0.052	0.002	0.001	0.024	0.008	0.012	0.000
7/05	Chu	56	0.000	0.027	0.018	0.007	0.058	0.020	0.079	0.000	0.073	0.008	0.005	0.006	0.000	0.143	0.556
9/05	Chk	196	0.002	0.067	0.000	0.078	0.236	0.406	0.084	0.000	0.004	0.018	0.021	0.000	0.058	0.017	0.011
9/05	Coh	35	0.000	0.000	0.000	0.030	0.157	0.693	0.079	0.000	0.026	0.000	0.000	0.000	0.000	0.016	0.000
9/05	Chu	112	0.000	0.000	0.444	0.006	0.091	0.004	0.054	0.007	0.000	0.000	0.000	0.000	0.004	0.090	0.301
7/06	Chk	169	0.001	0.016	0.000	0.313	0.155	0.020	0.042	0.000	0.004	0.033	0.003	0.116	0.242	0.044	0.012
7/06	Coh	83	0.000	0.002	0.000	0.581	0.105	0.067	0.001	0.000	0.007	0.000	0.012	0.071	0.144	0.000	0.008
7/06	Chu	107	0.000	0.090	0.182	0.018	0.226	0.001	0.047	0.065	0.014	0.002	0.004	0.011	0.000	0.099	0.241
7/06	Pink	103	0.000	0.095	0.000	0.141	0.203	0.035	0.119	0.083	0.112	0.003	0.001	0.124	0.007	0.061	0.016
9/06	Chk	120	0.000	0.009	0.000	0.258	0.028	0.181	0.099	0.000	0.025	0.003	0.033	0.005	0.315	0.036	0.008
9/06	Coh	38	0.000	0.000	0.000	0.105	0.039	0.674	0.034	0.000	0.000	0.000	0.000	0.000	0.147	0.000	0.000
9/06	Chu	55	0.000	0.000	0.514	0.098	0.000	0.000	0.075	0.000	0.000	0.000	0.007	0.000	0.000	0.034	0.273
9/06	Pink	84	0.000	0.084	0.013	0.349	0.019	0.139	0.125	0.006	0.077	0.004	0.058	0.002	0.002	0.098	0.025
7/07	Chk	183	0.000	0.036	0.000	0.578	0.010	0.005	0.289	0.000	0.004	0.022	0.010	0.005	0.009	0.030	0.004
7/07	Coh	172	0.000	0.004	0.000	0.717	0.026	0.030	0.172	0.000	0.042	0.005	0.000	0.002	0.001	0.002	0.000
7/07	Chu	98	0.000	0.028	0.030	0.026	0.013	0.001	0.402	0.000	0.002	0.000	0.001	0.000	0.000	0.094	0.404
9/07	Chk	189	0.002	0.035	0.000	0.095	0.074	0.272	0.384	0.000	0.009	0.062	0.005	0.003	0.022	0.034	0.003
9/07	Coh	34	0.000	0.026	0.000	0.037	0.062	0.510	0.341	0.000	0.021	0.003	0.000	0.000	0.000	0.000	0.000
9/07	Chu	133	0.003	0.019	0.047	0.188	0.017	0.032	0.573	0.003	0.017	0.000	0.030	0.000	0.000	0.063	0.008
7/08	Chk	178	0.000	0.044	0.000	0.197	0.434	0.012	0.103	0.000	0.000	0.031	0.004	0.000	0.132	0.043	0.000
7/08	Coh	99	0.000	0.000	0.000	0.450	0.464	0.020	0.040	0.000	0.002	0.005	0.000	0.000	0.008	0.010	0.000
7/08	Chu	120	0.000	0.001	0.241	0.000	0.149	0.000	0.010	0.016	0.000	0.000	0.025	0.000	0.005	0.334	0.219
7/08	Pink	90	0.000	0.116	0.000	0.033	0.236	0.000	0.027	0.048	0.033	0.002	0.217	0.000	0.000	0.277	0.012
7/08	Herr	20	0.000	0.103	0.000	0.473	0.272	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.053
9/08	Chk	168	0.004	0.031	0.000	0.194	0.108	0.154	0.143	0.000	0.078	0.084	0.010	0.038	0.089	0.061	0.005
9/08	Coh	35	0.000	0.000	0.000	0.076	0.049	0.514	0.007	0.000	0.069	0.000	0.000	0.003	0.283	0.000	0.000
9/08	Chu	116	0.000	0.001	0.628	0.005	0.047	0.006	0.011	0.000	0.006	0.004	0.001	0.000	0.000	0.041	0.250
9/08	Pink	52	0.000	0.153	0.000	0.216	0.037	0.263	0.053	0.000	0.212	0.000	0.005	0.010	0.000	0.053	0.000

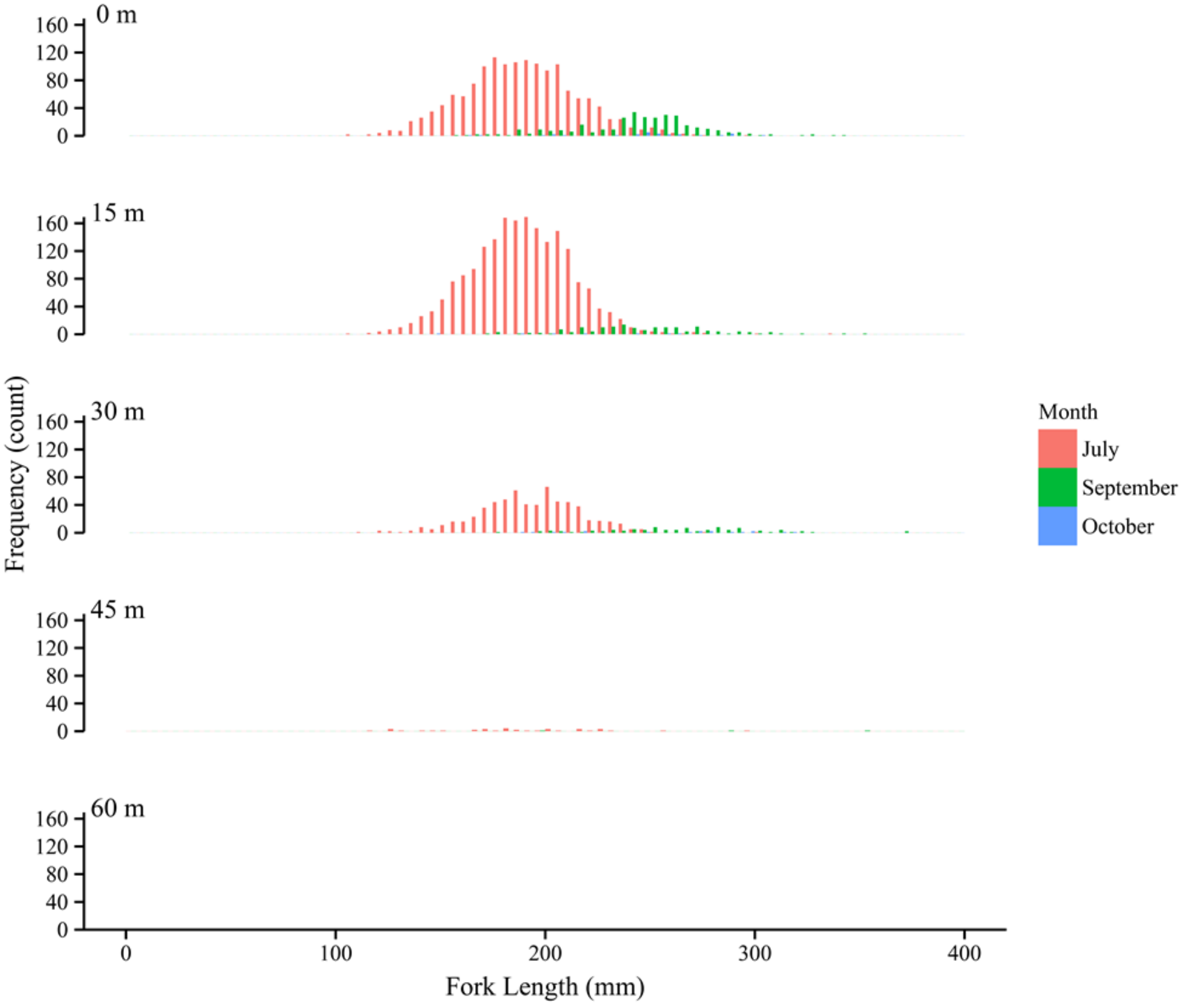
9/08	Herr	10	0.000	0.081	0.003	0.003	0.007	0.043	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.815
7/09	Chk	170	0.000	0.016	0.000	0.694	0.023	0.000	0.061	0.000	0.043	0.043	0.007	0.041	0.026	0.021	0.024
7/09	Coh	149	0.000	0.000	0.000	0.874	0.037	0.000	0.019	0.000	0.058	0.000	0.002	0.004	0.000	0.005	0.000
7/09	Chu	48	0.000	0.011	0.006	0.038	0.021	0.000	0.411	0.092	0.040	0.000	0.023	0.000	0.000	0.348	0.010
7/09	Herr	9	0.000	0.065	0.000	0.224	0.001	0.002	0.491	0.000	0.075	0.000	0.000	0.000	0.000	0.034	0.107
9/09	Chk	131	0.034	0.008	0.000	0.034	0.032	0.090	0.254	0.000	0.174	0.084	0.018	0.095	0.133	0.023	0.021
9/09	Coh	22	0.000	0.000	0.000	0.000	0.000	0.486	0.275	0.000	0.014	0.000	0.000	0.000	0.225	0.000	0.000
9/09	Chu	60	0.000	0.000	0.119	0.003	0.010	0.001	0.748	0.000	0.059	0.000	0.023	0.000	0.000	0.025	0.012
9/09	Herr	8	0.000	0.330	0.000	0.072	0.266	0.000	0.129	0.000	0.040	0.000	0.000	0.000	0.000	0.011	0.152
7/11	Chk	89	0.000	0.054	0.000	0.433	0.020	0.009	0.191	0.000	0.026	0.058	0.044	0.001	0.022	0.025	0.116
7/11	Coh	86	0.008	0.015	0.000	0.609	0.059	0.034	0.136	0.000	0.049	0.000	0.008	0.000	0.011	0.028	0.043
7/11	Chu	35	0.000	0.184	0.011	0.017	0.000	0.000	0.000	0.656	0.000	0.000	0.006	0.000	0.000	0.119	0.007
7/11	Herr	72	0.009	0.054	0.000	0.019	0.023	0.013	0.014	0.001	0.006	0.021	0.003	0.000	0.000	0.015	0.822
9/11	Chk	184	0.007	0.002	0.000	0.050	0.079	0.180	0.226	0.000	0.001	0.041	0.034	0.029	0.293	0.027	0.033
9/11	Coh	30	0.000	0.000	0.000	0.000	0.015	0.562	0.102	0.000	0.000	0.017	0.040	0.000	0.245	0.000	0.020
9/11	Chu	104	0.000	0.018	0.180	0.007	0.013	0.004	0.569	0.003	0.003	0.001	0.018	0.005	0.000	0.044	0.135
9/11	Herr	24	0.001	0.042	0.000	0.048	0.045	0.006	0.368	0.000	0.003	0.014	0.000	0.000	0.000	0.003	0.471

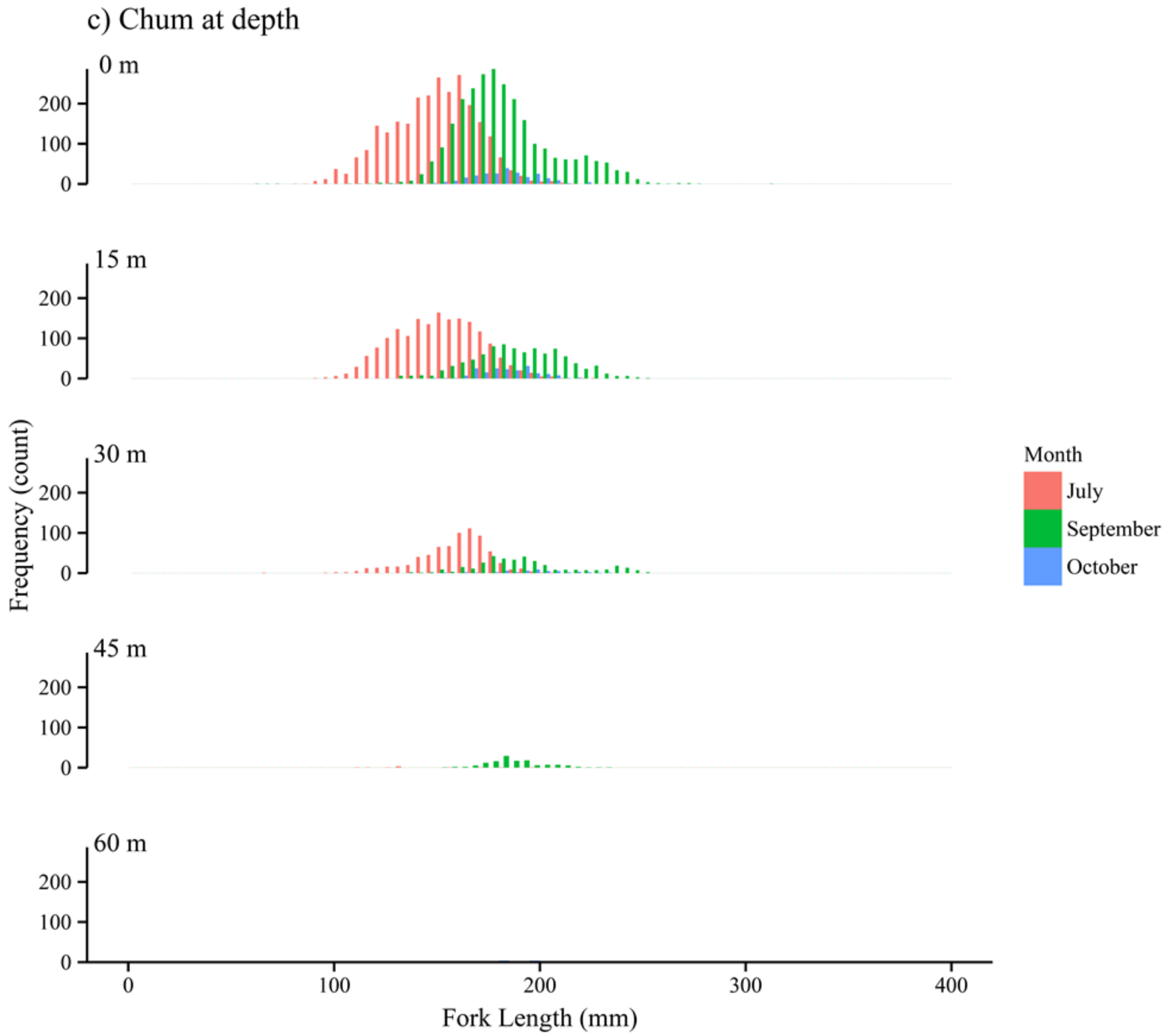
Table A4. Bioenergetics model inputs and results for Main Basin.

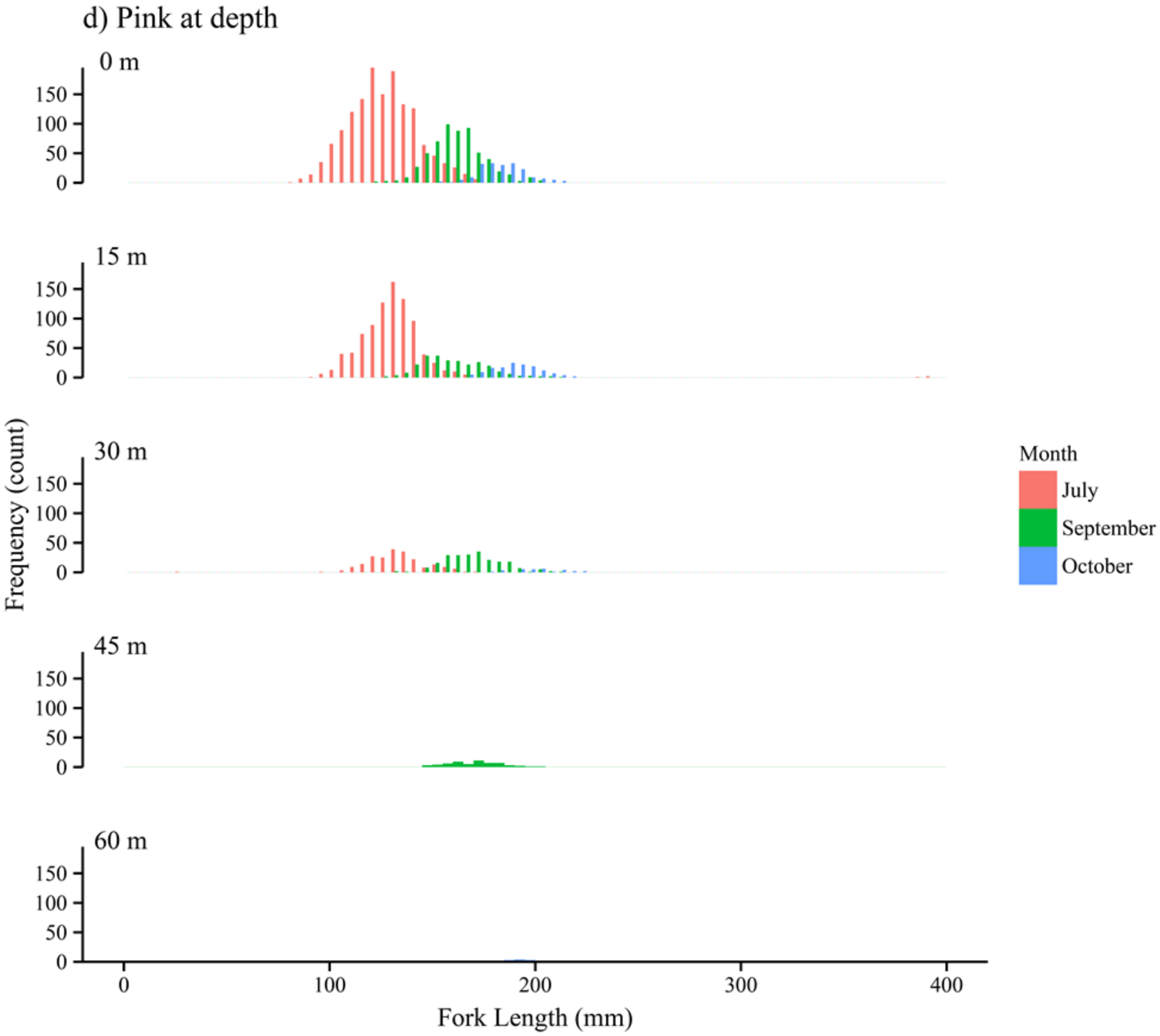
Start Date	End Date	Species	Start Weight (g)	Total Growth (g)	Mean Daily Growth (%bw/d)	% Cmax	Total Consumption (g)
7/16/2001	9/14/2001	Chinook	22.1	32.4	1.5	90.1	205.4
		Chum	30.3	25.5	1.0	83.8	214.5
		Coho	97.2	74.3	0.9	77.7	455.8
		Herring	32.0	23.7	0.9	29.3	181.3
7/13/2002	9/29/2002	Chinook	18.4	37.5	1.4	79.6	228.6
		Chum	20.9	21.5	0.9	82.7	224.0
		Coho	67.0	89.1	1.1	69.5	445.8
		Pink	14.4	25.0	1.2	71.8	176.7
7/14/2004	10/15/2004	Chinook	27.2	67.0	1.3	94.8	455.3
		Chum	41.1	21.0	0.4	50.7	227.7
		Coho	71.9	136.4	1.1	79.4	704.9
		Herring	30.7	19.9	0.5	26.6	237.6
		Pink	22.5	23.3	1.2	77.3	294.8
7/22/2005	9/22/2005	Chinook	32.9	41.0	1.3	79.9	240.4
		Chum	44.9	85.3	1.7	166.5	714.3
		Coho	97.6	126.6	1.3	92.0	607.6
7/21/2006	9/22/2006	Chinook	43.0	44.1	1.1	75.6	279.5
		Chum	47.5	23.0	0.6	82.4	286.5
		Coho	108.1	170.2	1.5	95.9	753.4
		Pink	26.4	13.7	0.9	56.7	133.7
7/25/2007	9/29/2007	Chinook	28.1	22.1	0.9	72.7	187.2
		Chum	34.8	44.1	1.2	93.8	306.2
		Coho	101.4	50.9	0.6	65.1	395.5
7/8/2008	9/26/2008	Chinook	31.2	18.2	0.6	49.9	163.8
		Chum	42.9	19.3	0.5	73.0	291.3
		Coho	104.3	125.5	1.0	69.0	612.0
		Herring	39.3	21.8	0.5	23.9	219.7
		Pink	17.3	50.6	1.0	54.6	133.8
7/8/2009	9/26/2009	Chinook	17.4	26.5	1.2	79.9	207.6
		Chum	17.8	39.8	1.5	102.7	302.0
		Coho	80.7	58.4	0.7	62.5	413.8
		Herring	23.7	70.6	1.7	42.5	391.9
7/8/2011	9/29/2011	Chinook	23.6	44.3	1.3	83.0	283.9
		Chum	28.0	25.0	0.8	63.8	211.4
		Coho	63.6	113.5	1.2	79.9	547.9
		Herring	29.1	27.8	0.8	28.9	239.5


a) Chinook at depth
0 m
15 m
30 m
45 m
60 m
500
400
300
200
100
0
Frequency (count)
0
100
200
300
400
Fork Length (mm)
Month
July
September
October

b) Coho at depth




c) Chum at depth
0 m
15 m
30 m
45 m
60 m
200
100
0
Frequency (count)
0
100
200
300
400
Fork Length (mm)
Month
July
September
October


d) Pink at depth
0 m
15 m
30 m
45 m
60 m
150
100
50
0
Frequency (count)
0
100
200
300
400
Fork Length (mm)
Month
July
September
October

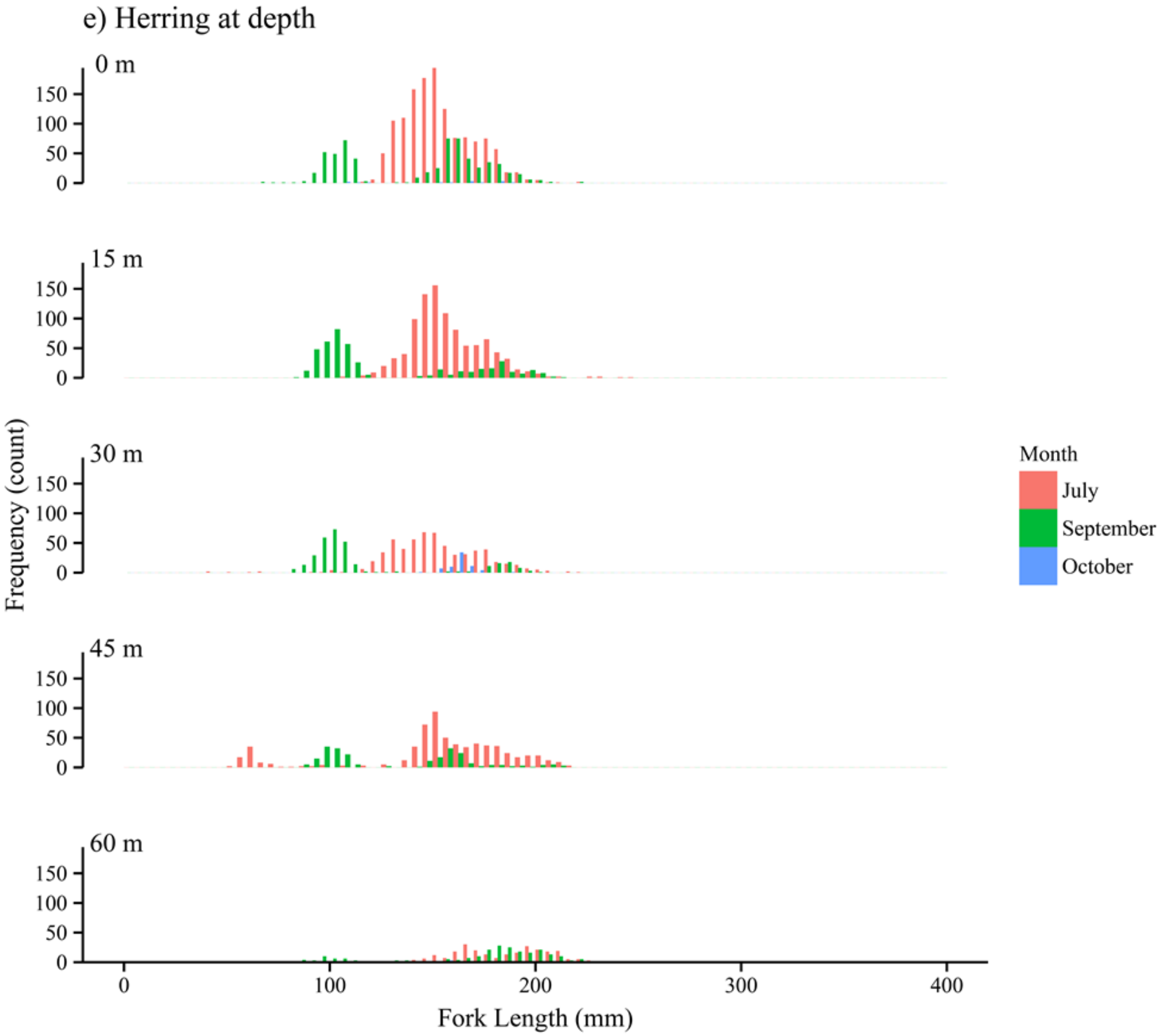
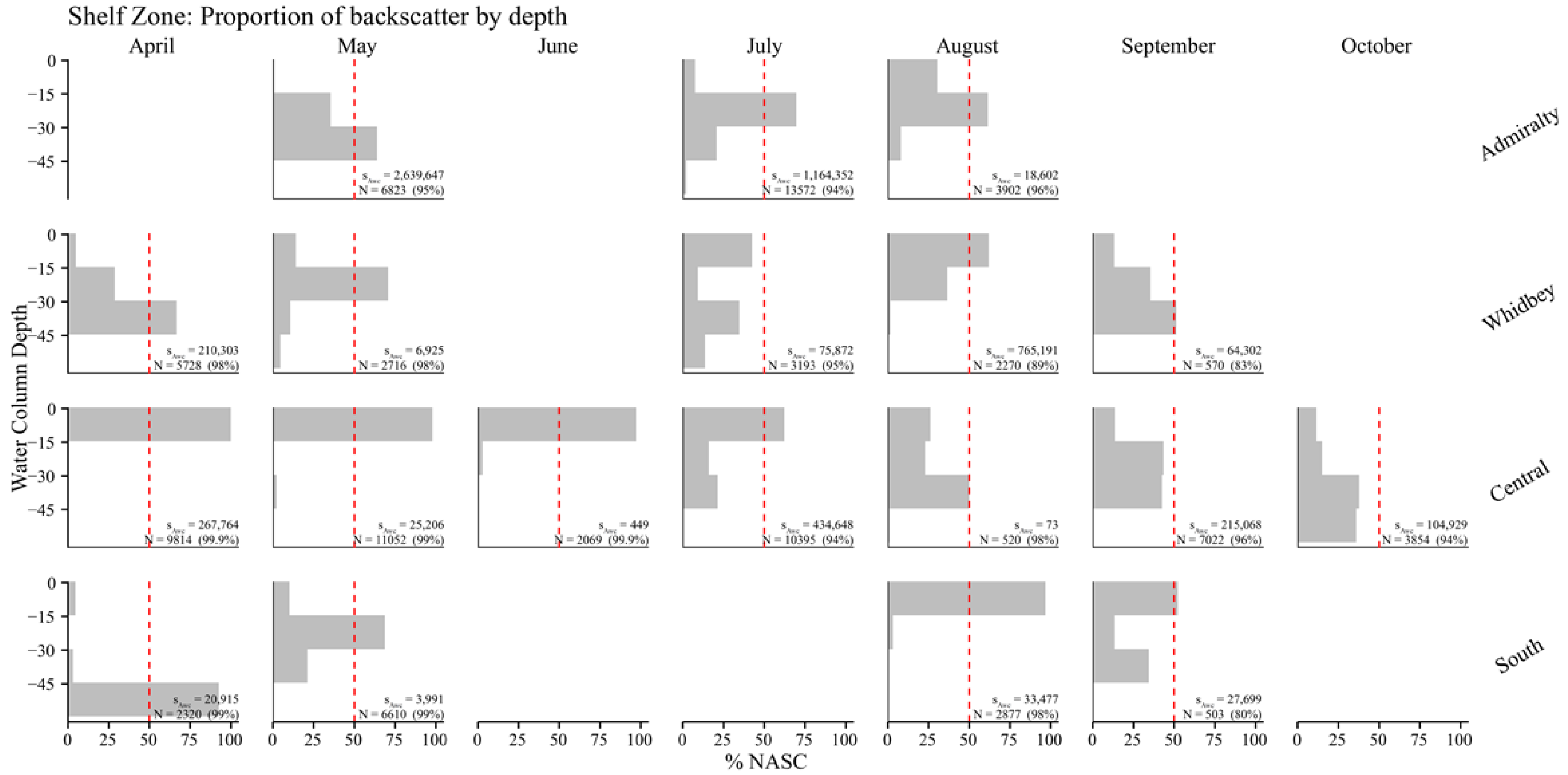
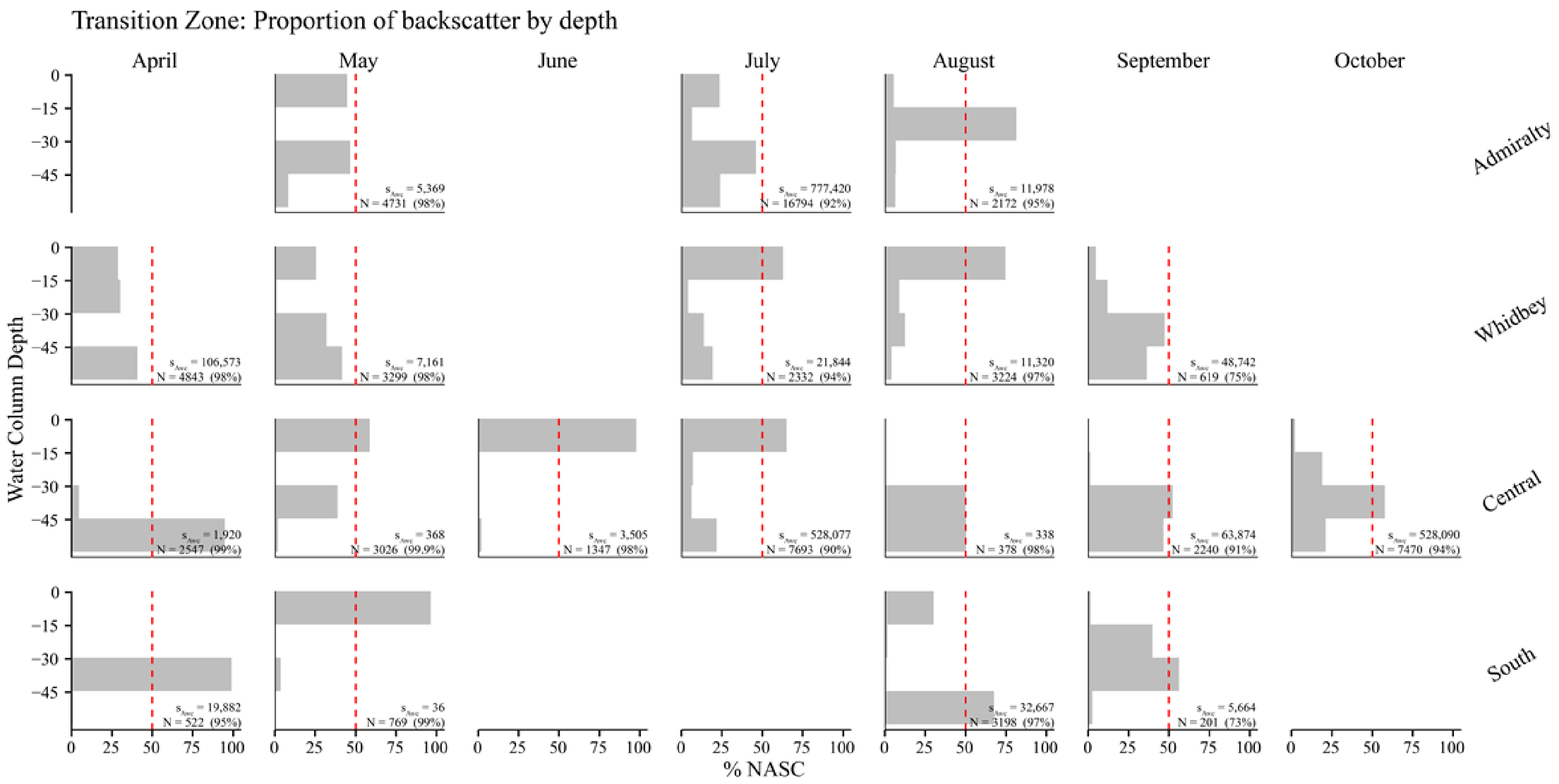


Figure A1. Length frequencies by 15-m depth increments in the water column over all years for Chinook salmon (a), coho salmon (b), chum salmon (c), pink salmon (d), and herring (e).


Shelf Zone: Proportion of backscatter by depth
April
May
June
July
August
September
October
Admiralty
Whidbey
Central
South
Water Column Depth
0
−15
−30
−45
% NASC
0
25
50
75
100
s_{Awc} = 2,639,647
N = 6823 (95%)
s_{Awc} = 1,164,352
N = 13572 (94%)
s_{Awc} = 18,602
N = 3902 (96%)
s_{Awc} = 210,303
N = 5728 (98%)
s_{Awc} = 6,925
N = 2716 (98%)
s_{Awc} = 75,872
N = 3193 (95%)
s_{Awc} = 765,191
N = 2270 (89%)
s_{Awc} = 64,302
N = 570 (83%)
s_{Awc} = 267,764
N = 9814 (99.9%)
s_{Awc} = 25,206
N = 11052 (99%)
s_{Awc} = 449
N = 2069 (99.9%)
s_{Awc} = 434,648
N = 10395 (94%)
s_{Awc} = 73
N = 520 (98%)
s_{Awc} = 215,068
N = 7022 (96%)
s_{Awc} = 104,929
N = 3854 (94%)
s_{Awc} = 20,915
N = 2320 (99%)
s_{Awc} = 3,991
N = 6610 (99%)
s_{Awc} = 33,477
N = 2877 (98%)
s_{Awc} = 27,699
N = 503 (80%)


Transition Zone: Proportion of backscatter by depth

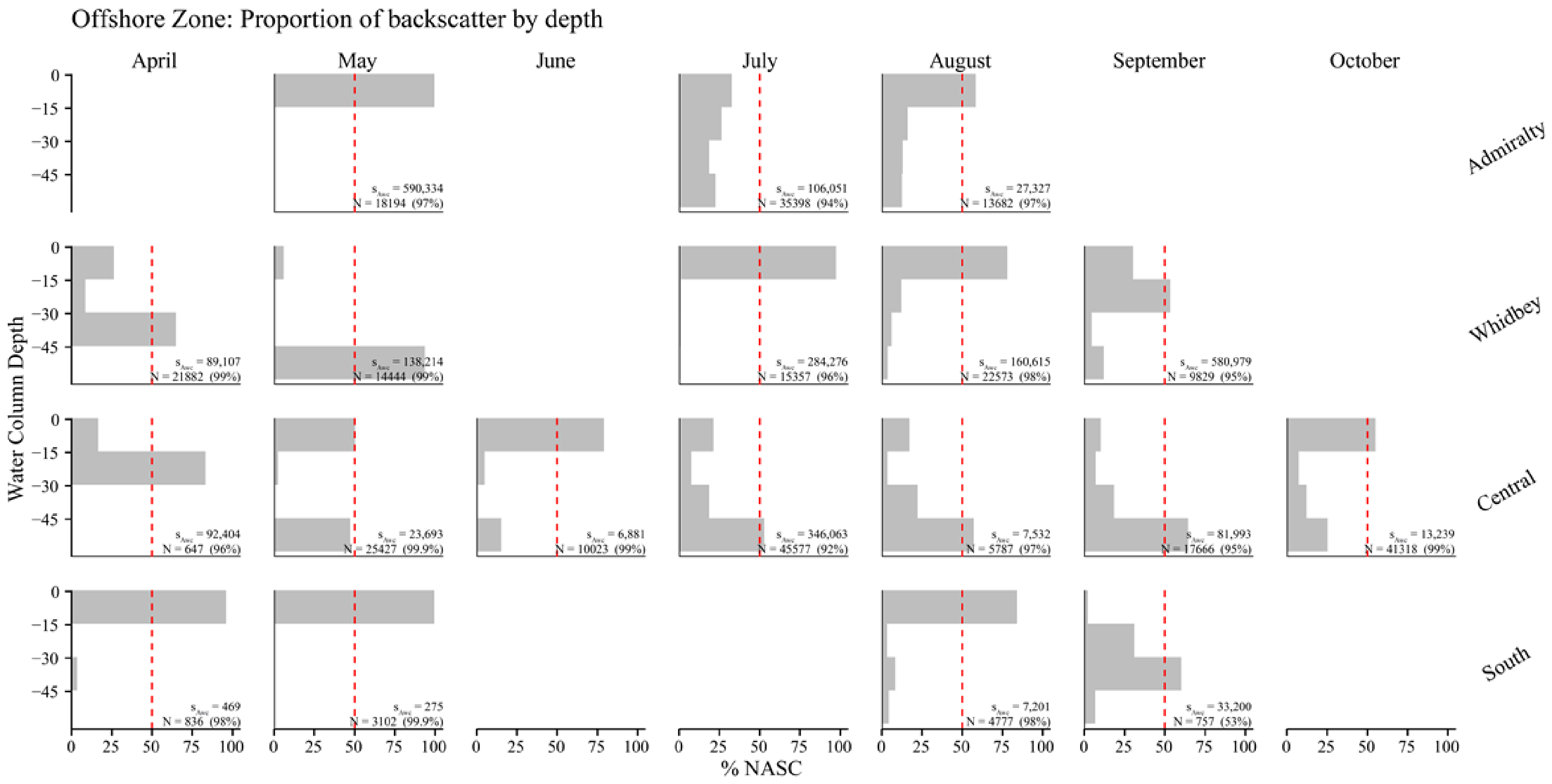
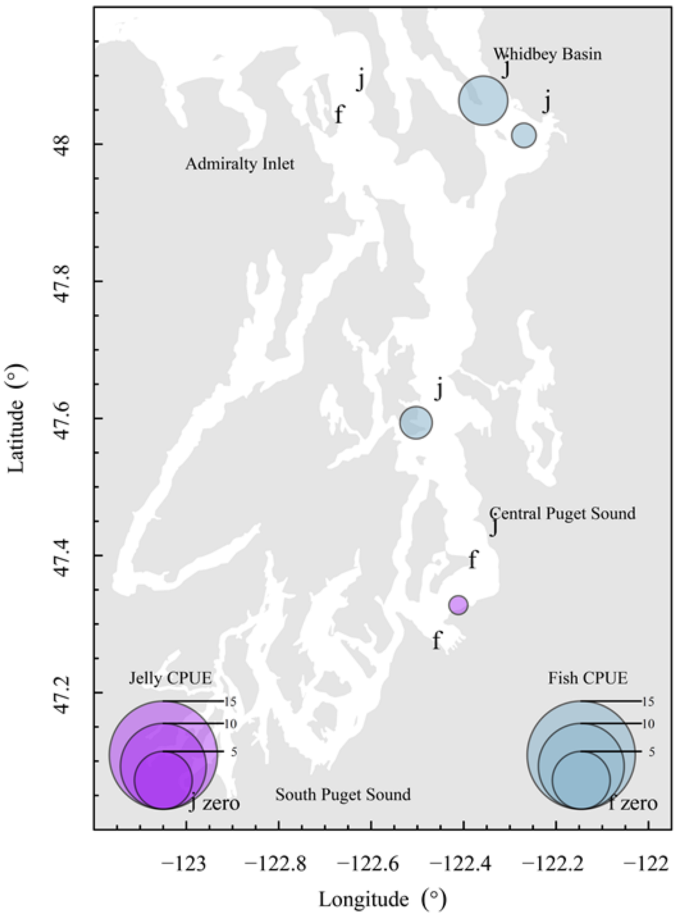
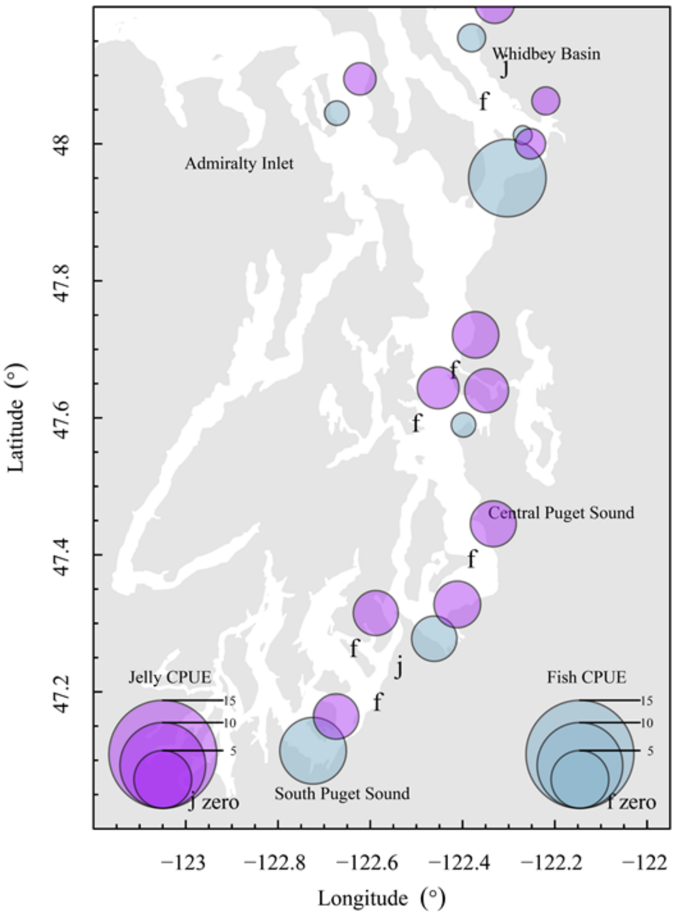


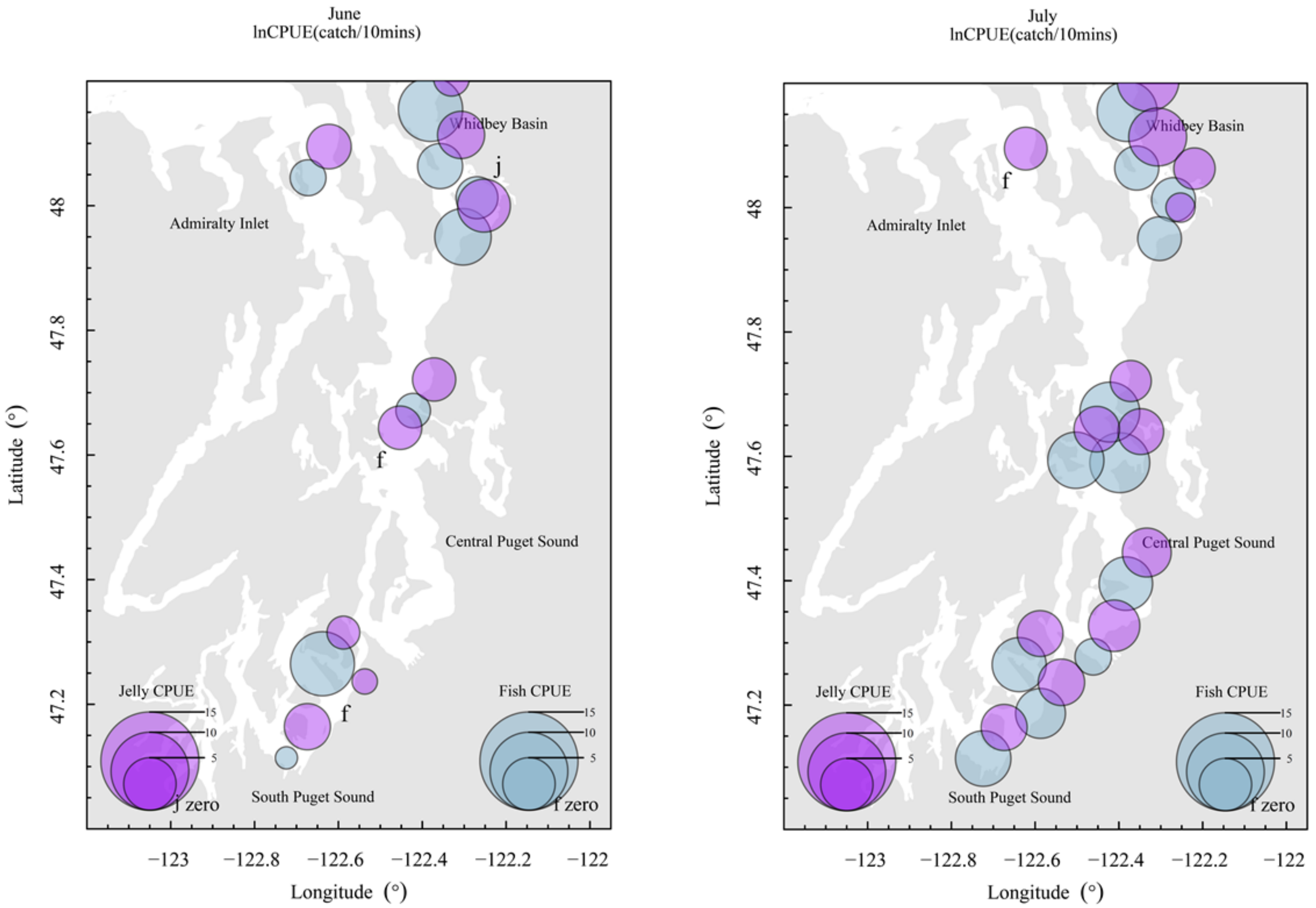
Figure A2. Proportional distribution of integrated backscatter (NASC) in the water column for shelf, transition, and offshore zones in four regions of Puget Sound. Note that axes are consistent for all plots. Results are presented as the proportion of total integrated backscatter observed within 15 m depth increments for each month and basin. The red dotted line indicates the 50% mark on each plot. Each column is a month (from April to October) and each row is a region of Puget Sound (from north to south). In the bottom right corner of each plot, total integrated backscatter (s_{Awc}), total number of samples (N), and percent of samples that had 0 backscatter (%) are listed.

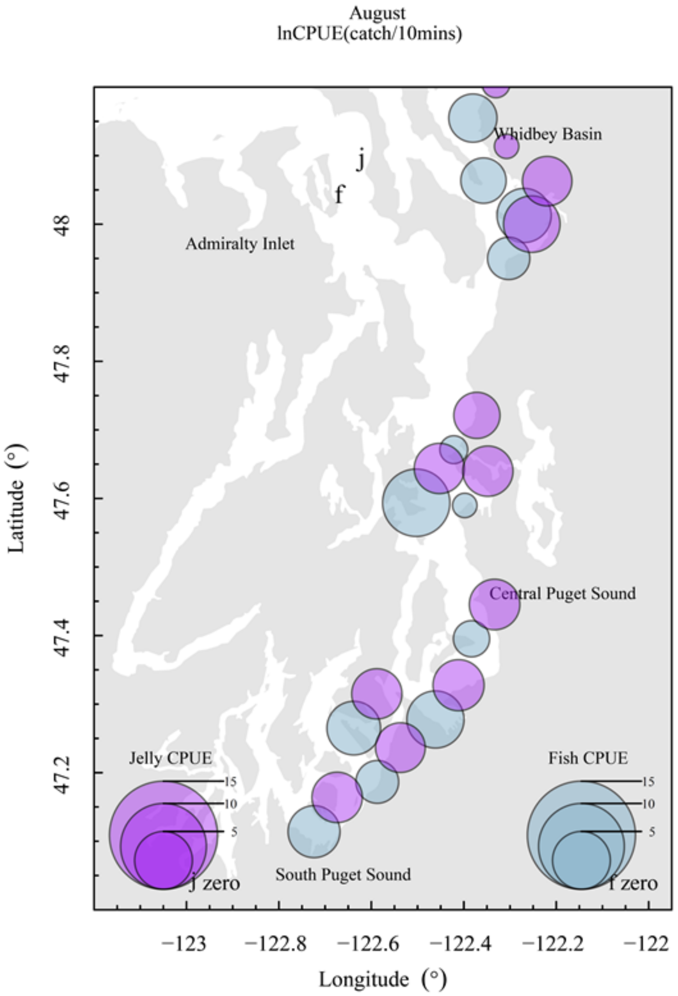


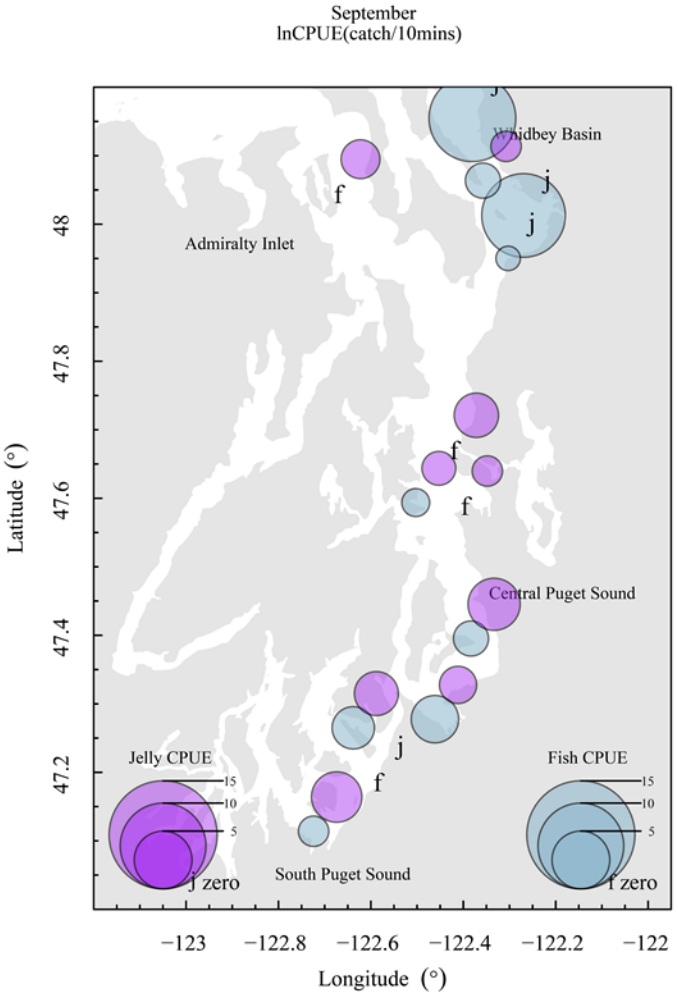
April
lnCPUE(catch/10mins)



May
lnCPUE(catch/10mins)


June
lnCPUE(catch/10mins)
July
lnCPUE(catch/10mins)
Whidbey Basin
Admiralty Inlet
Central Puget Sound
South Puget Sound
j
f
Jelly CPUE
Fish CPUE
15
10
5
j zero
f zero
Latitude (°)
Longitude (°)
48
47.8
47.6
47.4
47.2
−123
−122.8
−122.6
−122.4
−122.2
−122


August
lnCPUE(catch/10mins)
Whidbey Basin
j
f
Admiralty Inlet
Central Puget Sound
South Puget Sound
Jelly CPUE
15
10
5
j zero
Fish CPUE
15
10
5
f zero
48
47.8
47.6
47.4
47.2
Latitude (°)
−123
−122.8
−122.6
−122.4
−122.2
−122
Longitude (°)


September
lnCPUE(catch/10mins)
j
Whidbey Basin
j
j
f
Admiralty Inlet
f
f
Central Puget Sound
j
f
South Puget Sound
Jelly CPUE
15
10
5
j zero
Fish CPUE
15
10
5
f zero
48
47.8
47.6
47.4
47.2
Latitude (°)
−123
−122.8
−122.6
−122.4
−122.2
−122
Longitude (°)

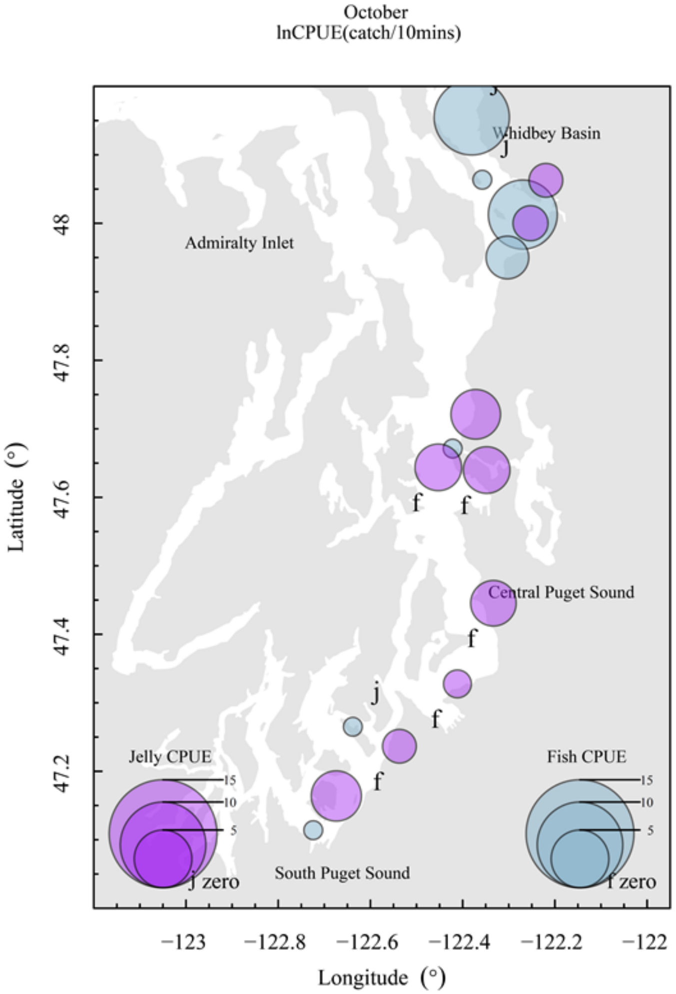
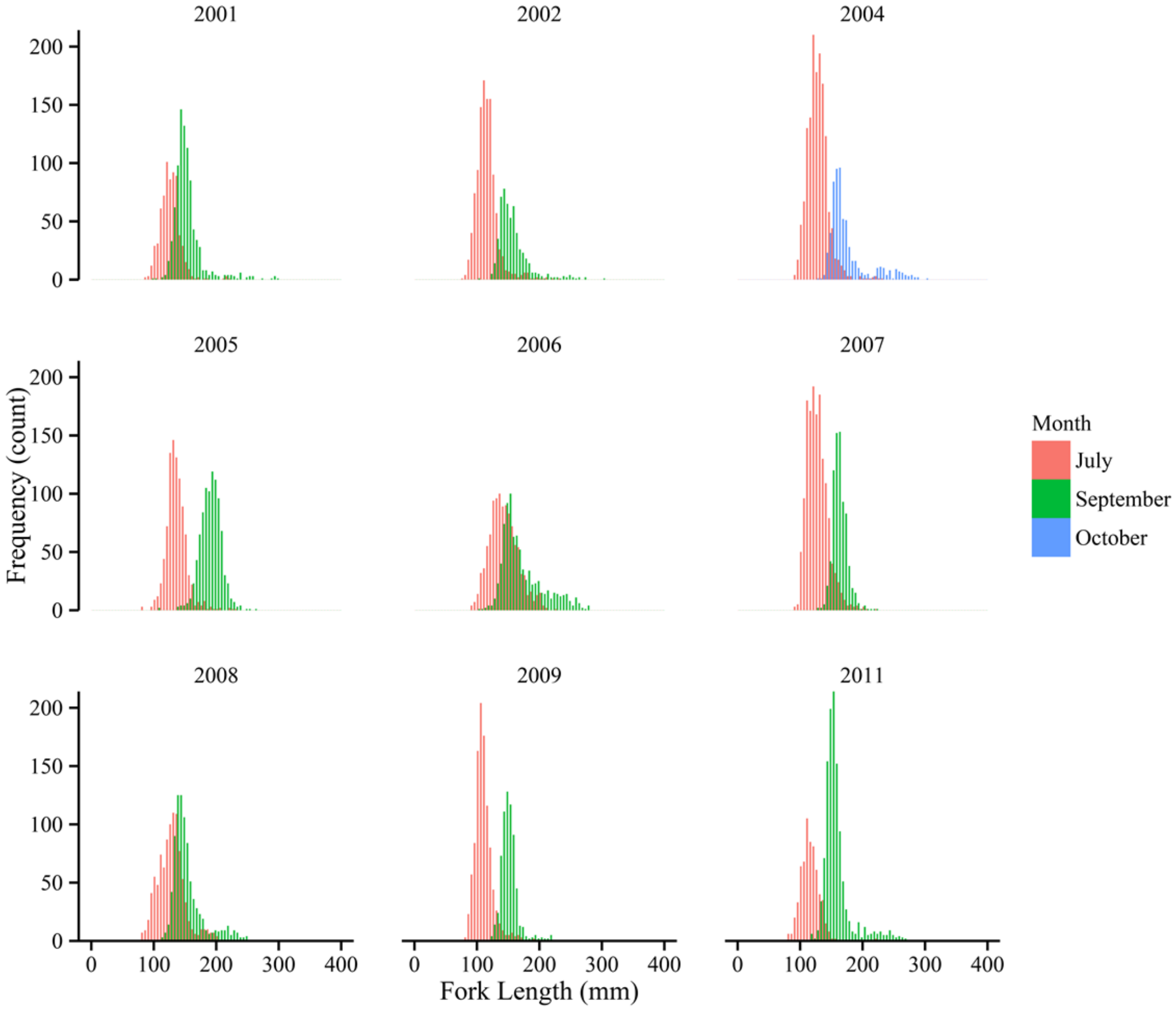
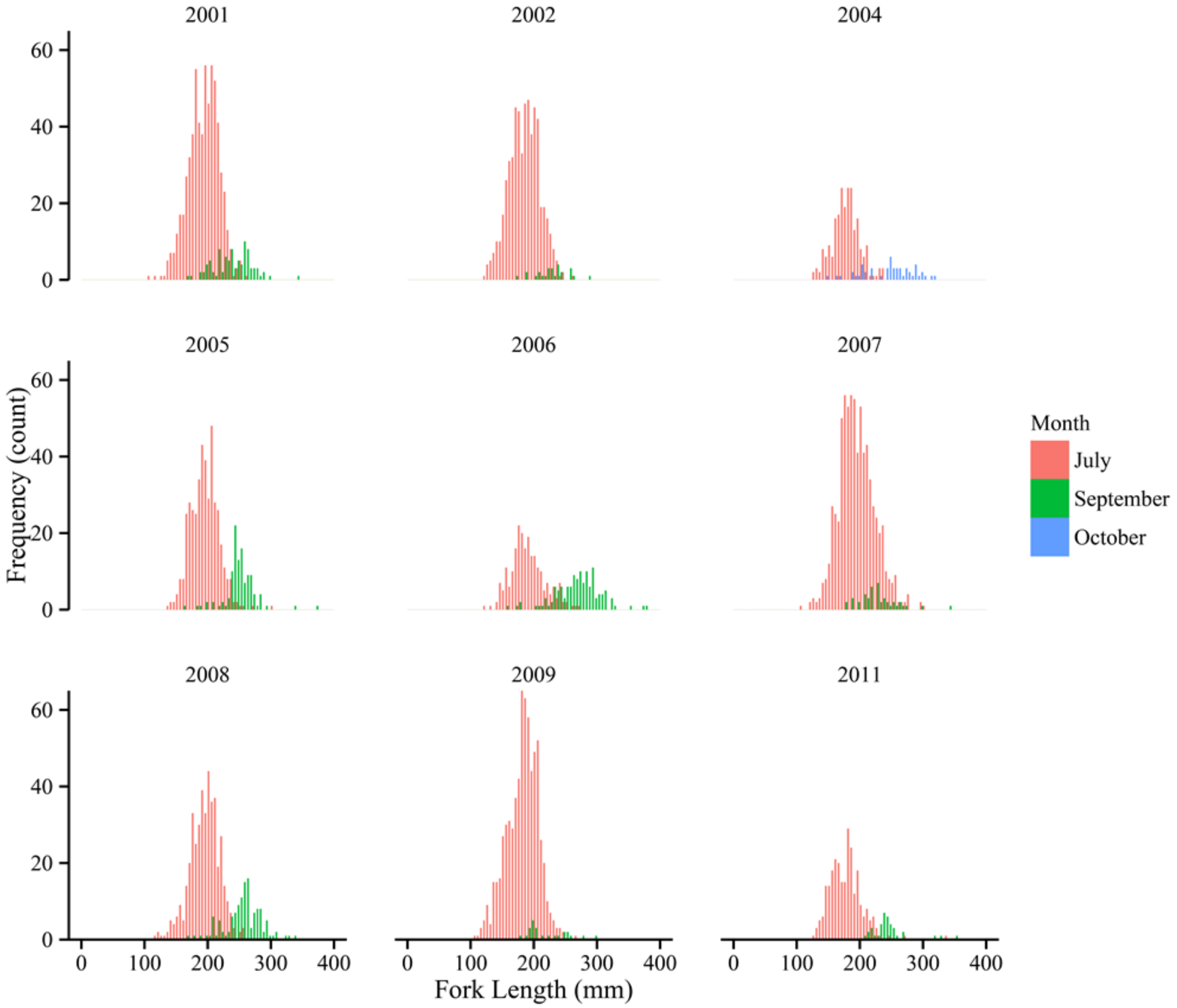


Figure A3. Log-scaled CPUE of fishes (blue) and jellyfish (purple) in surface townets from April to October 2011. “j” represents zero jellyfish catch and “f” represents zero fish catch.

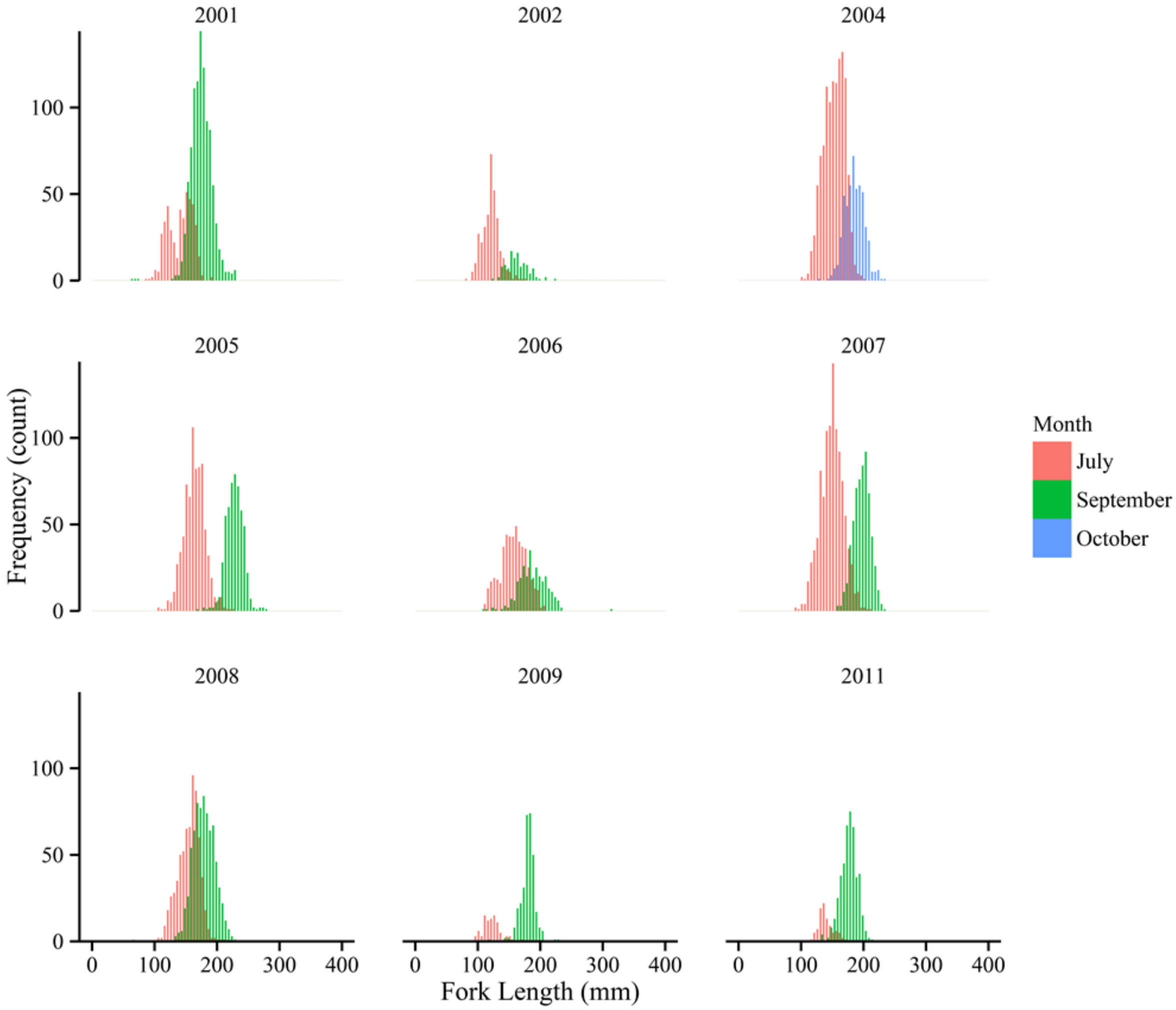
a) Chinook

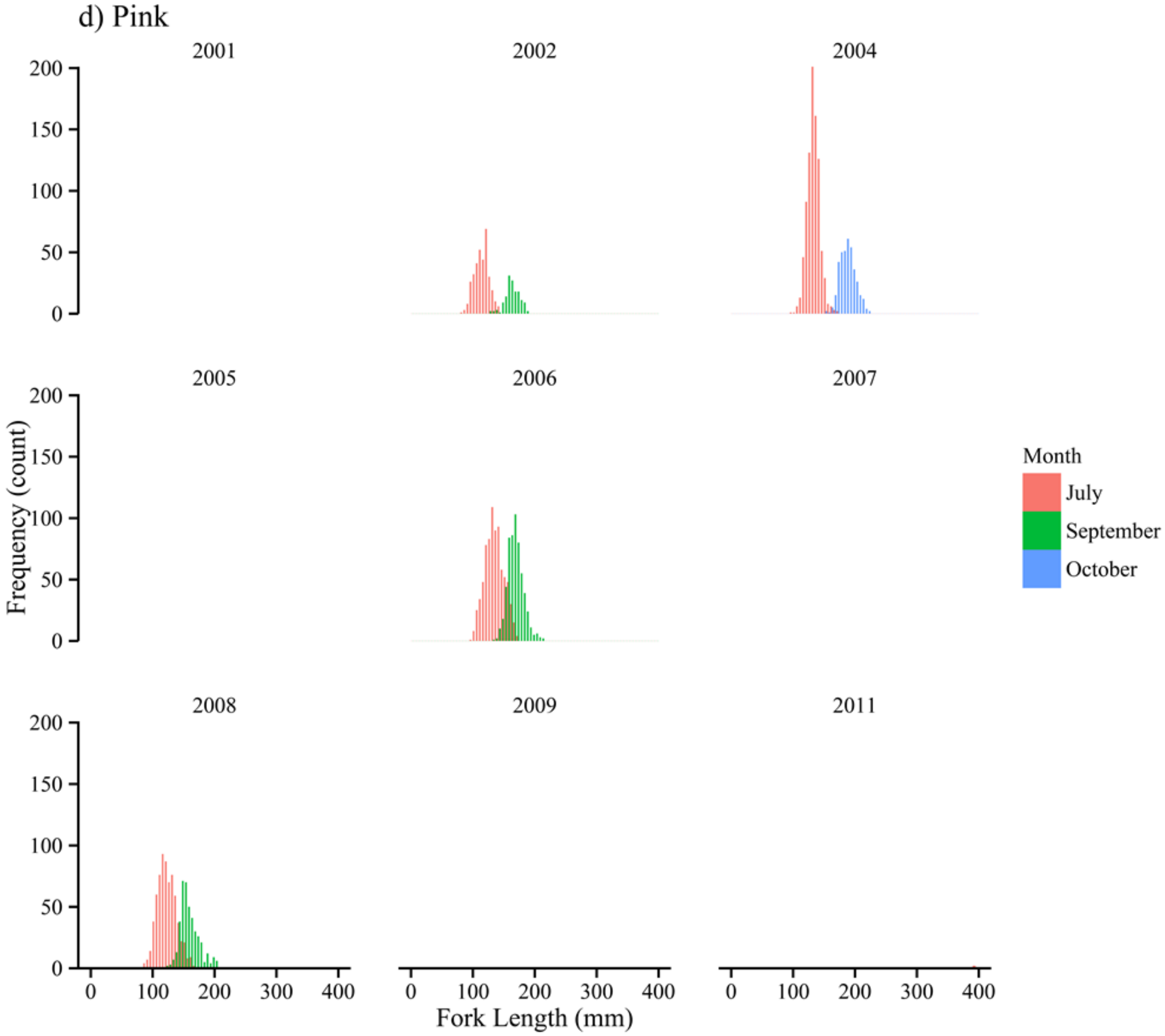

2001
2002
2004
2005
2006
2007
2008
2009
2011
Frequency (count)
0
50
100
150
200
Fork Length (mm)
0
100
200
300
400
Month
July
September
October

b) Coho


2001
2002
2004
2005
2006
2007
2008
2009
2011
60
40
20
0
Frequency (count)
0
100
200
300
400
Fork Length (mm)
Month
July
September
October

c) Chum


2001
2002
2004
2005
2006
2007
2008
2009
2011
Frequency (count)
0
50
100
0
100
200
300
400
Fork Length (mm)
Month
July
September
October


d) Pink
2001
2002
2004
2005
2006
2007
2008
2009
2011
Frequency (count)
0
50
100
150
200
Fork Length (mm)
0
100
200
300
400
Month
July
September
October

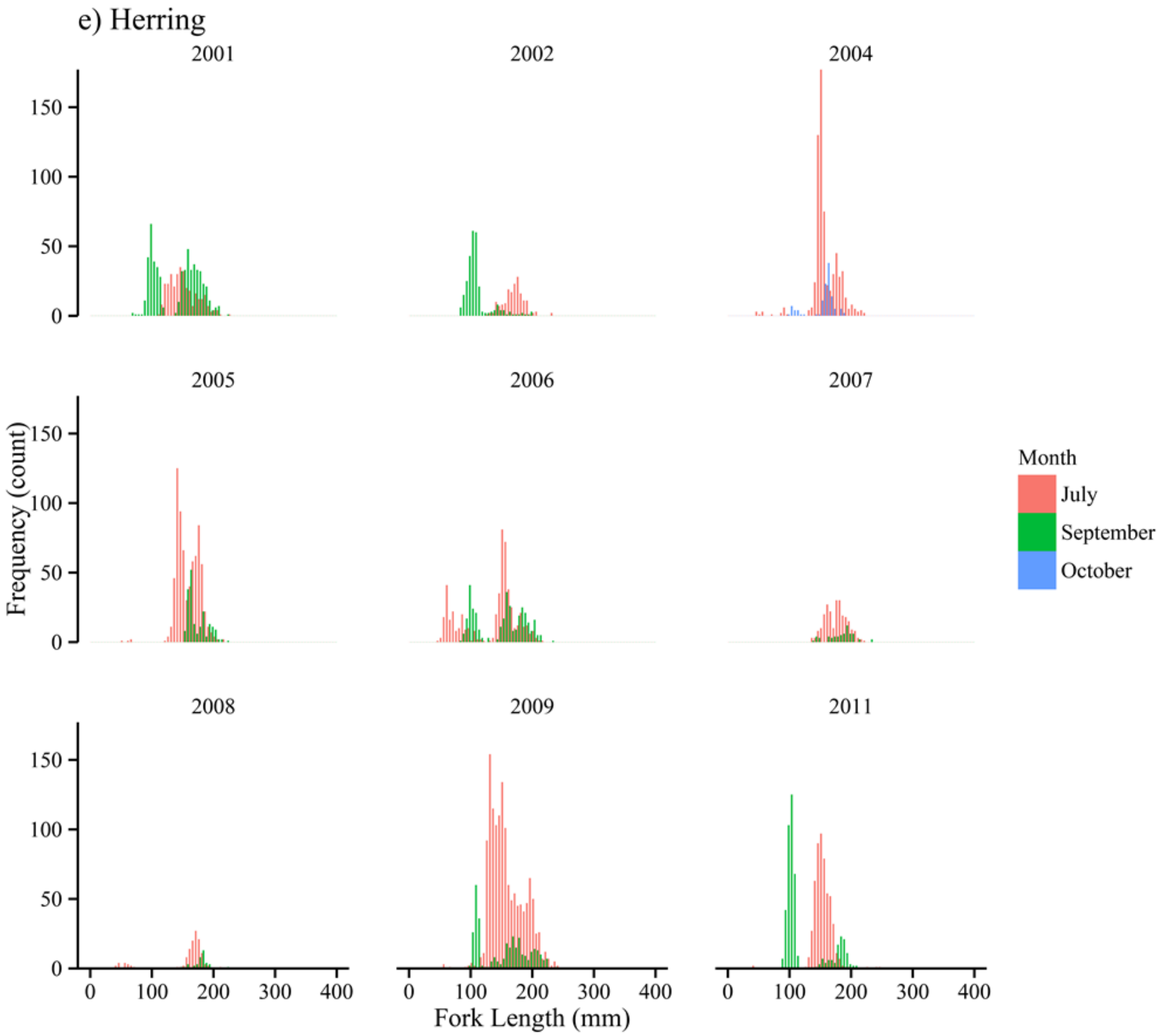


Figure A4. Length frequencies by year for Chinook salmon (a), coho salmon (b), chum salmon (c), pink salmon (d), and herring (e).