Contents lists available at ScienceDirect

Fisheries Research

Catching the prey: Sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence

Richard D. Brodeur [a,*], Elizabeth A. Daly [b], Cassandra E. Benkwitt [c], Cheryl A. Morgan [b], Robert L. Emmett [a]

[a] National Marine Fisheries Service, Northwest Fisheries Science Center, Hatfield Marine Science Center, Newport, OR 97365, USA
[b] Cooperative Institute for Marine Resources Studies, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, USA
[c] Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

ARTICLE INFO

ABSTRACT

Marine diets of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) in the northern California Current are made up primarily of micronekton prey including juvenile fish, adult euphausiids, and large crab megalopae. However, these animals are seldom caught in the conventional plankton gears used to define juvenile salmon prey fields in ocean salmon programs. Four types of sampling gears with various mouth openings and configurations were examined for the ability to catch known juvenile salmon prey. Samples were examined for differences in species composition, relative biomass, length distribution, and taxonomic overlap with prey in the diets of salmon sampled concurrently. The herring, Marinovich, and Methot trawl nets generally caught juvenile prey fish such as hexagrammids, rockfish, cottids, and osmerids. These prey were in the 15–95 mm fork-length range, consistent with the type and size eaten by juvenile salmon. The bongo net sampled smaller invertebrate prey, which are rarely eaten by juvenile salmon, but instead are common prey of the juvenile fish that salmon consume. Overlap between prey fields and salmon diets was moderate for samples from the larger gear types but low for those from bongo nets towed in the same area. The fact that no gear matched exactly with coho and Chinook salmon diets was related to differences in catchability of the prey in different gears but may also in part be probably due to the high mobility of juvenile salmon, which enables these fish to consume food in locations distant from where they are sampled, and also to selectively feed in areas of high prey concentration. Based on our analysis, we recommend the use of micronekton gears with larger mouth openings and mesh sizes for better filtration rather than standard plankton gears (i.e., bongo nets) for direct estimates of available prey resources for juvenile coho or Chinook salmon. Sampling the abundance, size, and distribution of prey fields for juvenile salmon during their first summer in the ocean, a period of high natural mortality, may help us to better understand the mechanisms of bottom-up forcing on interannual changes in salmon mortality.

Published by Elsevier B.V.

1. Introduction

Understanding the relationship between juvenile salmon (*Oncorhynchus* spp.) and the environment in which they forage can provide insight into the high interannual variability in ultimate survival of these fish (Logerwell et al., 2003; Weitkamp and Sturdevant, 2008; Daly et al., 2009). All species of salmon experience a dramatic change in forage base as they traverse from freshwater to estuarine and then coastal marine habitats (Keeley and Grant, 2001; Daly et al., 2009, 2010), and this change is accompanied by a period of high mortality extending throughout the first summer of ocean residence (Pearcy, 1992).

Most sampling programs targeting the juvenile salmon marine life history stage employ fine-mesh zooplankton nets with relatively small-openings to estimate prey availability. This practice has successfully sampled the prey fields of species such as juvenile chum (*Oncorhynchus keta*), pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon, which are primarily planktivorous, and generally consume small prey relative to their body size (DeRobertis et al., 2005; Brodeur et al., 2007; Bollens et al., 2010). However, juvenile coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon are primarily piscivorous, feeding mostly on larval and young-of-the-year juvenile fish (e.g., Brodeur and Pearcy, 1990; Brodeur et al., 2007; Daly et al., 2009; Weitkamp and Sturdevant, 2008), with the remainder of their diet consisting of larger invertebrates capable of evading conventional plankton sampling gears (Schabetsberger et al., 2003). Most organisms that make up the diets of these two species may be classified as

micronekton (Brodeur et al., 2005), an intermediate-sized grouping that is generally not caught in either plankton gear or large-mesh trawls.

Our research has focused on examining prey selectivity of and possible food limitation for juvenile salmon in coastal waters of the northern California Current ecosystem. A sampling protocol that targets the entire range of potential prey in the environment is clearly a requisite for robust estimation of the amount of food available to juvenile salmon. Such estimates are also a requisite for models that examine whether salmon are growing at an optimum rate (Reser, 2009) or whether sufficient food resources exist to sustain natural and hatchery juvenile salmon populations (Brodeur et al., 1992). In studies from other regions, the available micronektonic food base has been obtained indirectly by applying a feeding electivity model to the known dietary composition of salmon (Zavolokin, 2009). However, this methodology requires many assumptions that make its usefulness uncertain. Thus there remains a need to directly measure abundance, biomass, and spatial distribution of prey fields used by juvenile Chinook and coho salmon. At the present time we do not have a good understanding of which sampling gears can most effectively target the full breadth of the salmon prey field.

The objective of this study was to compare the species and size composition of potential salmon prey organisms caught in a range of plankton/micronekton sampling gears with those found in juvenile coho and Chinook salmon stomachs collected concurrently in the same locations in coastal marine waters. This comparison was done during two periods: the first shortly after yearling Chinook and coho salmon entered the ocean in May and the second after a period of marine residence in June, after salmon had adapted to feeding on marine organisms (Daly et al., 2010) with a goal of evaluating factors related to prey estimation using different gears.

2. Methods

2.1. Field sampling

Sampling occurred off the northern coast of Oregon and the southern coast of Washington at 11 stations in May 2008 and 10 stations in June 2008. Concurrent sampling took place from two vessels, as part of an ongoing study by the Northwest Fisheries Science Center of NOAA Fisheries of juvenile salmonids during their early ocean life. In May, the NOAA ship RV *Miller Freeman* deployed three nets in randomized order. The first was a modified herring trawl, similar to that used by Abookire and Piatt (2005) with a mouth opening of 37.2 m^2 and variable mesh ranging from 5 cm in the wings of the trawl to 1 cm in the codend. The second net used was a Marinovich trawl with a mouth opening of 27 m^2, and graded mesh going from 3.2 cm in the wings to 0.6 cm in the codend. Both these nets had a 3 mm liner extending well into the throat of the trawl. Two 3-m foam-filled Lite doors (Net Systems, Inc.) were used to keep the mouth open during the tows. The herring and Marinovich trawls were fished near the surface in the upper 10 m of the water column. Finally, a 5-m^2 Methot frame trawl with a body of 3-mm × 2-mm oval mesh and a cod-end of 1-mm mesh (Methot, 1986) was fished obliquely to a depth of 20 m. All tow speeds were 5.6 km h^{-1}, and nets were towed for 20 min.

Alongside the RV *Miller Freeman*, the FV *Frosti* obliquely towed a 0.60-m diameter bongo net fitted with 335-μm mesh. The net was fished by letting out 60 m of cable and retrieving it immediately at 30 m min^{-1} while the vessel was underway at 4 km h^{-1}. The angle of the wire was maintained so that it fished to a maximum depth of 20–30 m. A calibrated flow meter (General Oceanics, Inc.) located inside the mouth of the net was used to estimate the amount of water filtered in each sample. After each bongo tow, the FV *Frosti*

towed a large Nordic trawl (336-m^2 mouth opening) at the surface to collect juvenile salmon for stomach content analysis (Emmett et al., 2004). In June, the FV *Frosti* was used again for bongo and Nordic trawl sampling, and the FV *Piky* simultaneously towed only the herring trawl at the surface.

The herring, Marinovich, and Methot trawl samples were roughly sorted at sea, with all gelatinous specimens (mainly large jellyfish, ctenophores and salps) removed, and were then bagged and frozen (−20 °C). Plankton caught in the bongo net was sieved (335 μm) to remove gelatinous zooplankton, which were measured and quantified but not preserved, and the remaining sample was preserved in 5% buffered formalin. Juvenile salmon caught within the Nordic trawl were identified, measured, and individually frozen at sea. Stomachs were excised in the laboratory and preserved initially in 10% buffered formalin and then transferred to ethanol for storage.

2.2. Laboratory processing

In the laboratory, samples from the herring, Marinovich, and Methot net were thawed and specimens were identified and enumerated. Up to 30 individuals per taxon and station were measured (nearest 0.1 mm) and weighed (nearest 0.001 g). We calculated the biomass as wet weight (g/1000 m^3) for each net per station using the following trophic groupings: Cottidae, "fish" (comprised Cyclopteridae, Agonidae and Cryptacanthodidae), Pleuronectiformes, *Microgadus proximus*, *Anoplopoma fimbria*, Hexagrammidae, Osmeridae, *Sebastes* spp., *Ronquilus jordani*, *Ammodytes hexapterus*, Amphipoda (almost entirely *Atylus tridens* but with some other gammarid and caprellid amphipods), *Cancer* spp. megalopae, *Cancer* spp. zoea, non-*Cancer* spp. megalopae, non-*Cancer* spp. zoea, large copepods, Cirripedia cyprids, Euphausiidae, Hyperiidae, Insecta, Mysidae, Pteropoda, and Pandalidae.

To calculate the volume of water sampled by the herring and Marinovich trawl nets, we used distance traveled (geographic distance between the beginning and ending positions) during the tow multiplied by the mouth area of the net. Volumes of water filtered in the Methot and bongo fixed-frame nets were calculated by multiplying flow through the mouth (estimated using a calibrated flow meter mounted in the center of the net) by area of the mouth for each net.

Bongo samples were counted for all organisms over 2.5 mm. In addition to these larger organisms, all developmental stages of pteropods, amphipods, euphausiids, crabs, and fish were enumerated. These taxa were selected to correspond with known prey organisms of juvenile Chinook and coho salmon in this area (Brodeur and Pearcy, 1990; Schabetsberger et al., 2003; Daly et al., 2009), and all are effectively retained by 335-μm mesh. First, the sample was rinsed and the entire sample was scanned for large and rare organisms, which were removed using a light table. The sample was then split using a Folsom splitter, and the more common mid-size organisms were removed using a light table. Finally, a subsample of the split was taken using a Hensen stempel pipette (5–20 ml) to count the smallest and the most common organisms. A dissecting microscope was used to identify all organisms to the lowest possible taxonomic level and developmental stage from each of the above steps.

After extrapolating catch sizes from subsample counts, the plankton biomass was calculated for each station using the same trophic groupings listed for the herring, Marinovich, and Methot nets. Data were then normalized using sampling volume to produce density estimates in number of organisms m^{-3}. Biomass of a given species/trophic grouping was calculated by multiplying the number of organisms m^{-3} by the carbon weight of individuals of a given developmental stage and then converting the product to

wet weight. Estimates of zooplankton carbon content and conversion factors to wet weight were derived from the literature values (Morgan et al., 2005) or from our own estimates of dry weight. The following organisms caught in bongo nets but rarely eaten by juvenile coho and Chinook salmon were not included in our analysis: fish eggs, crab zoea < stage 4, chaetognaths, jellyfish, copepods < stage 5, and euphausiids < stage 4 furcillia.

Stomach contents of juvenile coho and Chinook salmon were identified to the lowest possible taxonomic order under a dissecting scope. The mean size of Chinook salmon examined in May (182.9 ± 30.9 mm (s.d.)) was slightly larger than that of coho salmon (151.0 ± 20.6). The mean sizes of Chinook (211.0 ± 36.6 mm) and coho (185.4 ± 26.9 mm) both increased by similar amounts by June, but these size differences were relatively minor based on a previous size variation study (Daly et al. 2009). All fish we examined were classified as yearling fish having spent one winter in freshwater prior to entering the ocean. Prey were enumerated and weighed (nearest 0.001 g), and up to 6 prey per taxon per stomach were measured (nearest mm). For each taxon, we also recorded a condition code based on apparent state of digestion that ranged from 0 to 4, with 0 being fully digested and 4 being recently eaten or fresh. Total lengths of fish prey and the longest dimensions of invertebrate prey were measured to the nearest mm using an ocular or stage micrometer.

2.3. Analytical methods

For comparison of salmon diets with composition of net samples, we used only prey that appeared to be freshly eaten (condition code 3 or 4). Percent gravimetric composition of prey was calculated for each salmon and then averaged for stations where three or more salmon had been caught and had eaten fresh food. Trophic groupings used to compare salmon diets with gear samples consisted of any prey grouping that represented ≥2% of the salmon diets in either May or June. These trophic groupings consisted of Cottidae, Hexagrammidae, *A. hexapterus*, *Sebastes* spp., *A. fimbria*, Amphipoda, *Cancer* spp. megalope, Euphausiidae, and Pandalidae.

For each sample period, we used non-metric multidimensional scaling (NMDS) to evaluate multivariate species-level differences in taxonomic composition among samples from the different gear types and from coho and Chinook salmon prey taxa. As an ordination technique that projects the ranked dissimilarities of samples in a reduced ordinate space, NMDS minimizes a function that relates the difference between original ranked dissimilarities and distance between objects in a two-dimensional ordinate space. The NMDS ordinations are displayed as plots where samples (trawls, stomachs) that are most similar in species composition are close together and samples that are dissimilar in species composition are far apart. When the underlying community gradients are nonlinear or unknown, NMDS is generally considered the preferred ordination technique (McCune and Grace, 2002).

Relative biomass data from the four nets were fourth-root transformed to downweight the importance of abundant species, and a similarity matrix based on the Bray–Curtis coefficient of similarity was calculated (Clarke and Warwick, 2001). We considered ordination solutions with a stress value of less than 0.20 as acceptable for interpretation (stress value is a measure of faithfulness between the ordination solution and the original similarity matrix).

In addition to the NMDS analysis, we also tested for differences in catch composition between nets for each sampling period using analysis of similarities (ANOSIM), a non-parametric multivariate analogue to ANOVA that tests the null hypothesis that there is no difference in assemblage structure between two or more a priori groups. Using station means, the ANOSIM tested for differences between net samples and diet composition for each month and salmon species. This method consisted of calculating the test statistic *R*, which relates between-group differences in sample similarities to within-group differences. If within-group differences in similarity are larger than between-group differences, *R* approaches 0; if the opposite is true, *R* approaches 1. Significance was determined by permuting the underlying data matrix 5000 times to generate a null distribution of test statistics for comparison with the real *R*. Where significant differences were found, a SIMPER (similarity percentages) test was employed to identify species that contributed most to between-gear differences. Multivariate statistics were done using PRIMER v.6 (Clarke and Gorley, 2005).

Lastly, we tested for size differences between fish caught in the sampling gears and fish eaten by juvenile coho and Chinook salmon. As the length frequencies were not normally distributed following transformations, we used a non-parametric Mann–Whitney rank sums test, with $p < 0.05$ denoting a significant difference.

3. Results

### 3.1. Comparison of gear types

The plankton and micronekton sampling nets collected a total of 35 fish taxa and 31 invertebrate taxa, which encompassed 27 prey taxa commonly eaten by juvenile salmon. Juvenile *M. proximus* (Pacific tomcod) and larval osmerids were the fish taxa caught most consistently by all sampling gears except the bongo (Fig. 1 and Table 2) and *M. proximus* comprised the highest biomass of any fish caught overall (May Methot – 1.33 g/1000 m³). Osmerids were found in over 90% of the herring trawls in both May and June. Hexagrammids made up a large proportion of the herring trawl biomass in May (17.8%; Table 2) and June (32.9%: Table 2) but were rarely caught in the other nets. Flatfish were caught at almost every station in herring and Marinovich nets during May. The only fish taxa consistently collected in June were hexagrammids and osmerids by the herring trawl. There was an increase in *Sebastes* spp. biomass caught between May and June (Fig. 1). In May, cottids were collected in moderate amounts in the bongo, Marinovich, and herring trawls (Fig. 1). The nets with the highest proportion of fish biomass were the herring trawl in May (86.4%) and June (95.1%), and the Methot trawl in May (77.1%: Fig. 1).

The largest mean biomass of any taxa collected was that of the copepods caught in the May bongo net (51.7 g/1000 m³; Fig. 1), which also consistently sampled pteropods and Pandalidae larvae. *Cancer* spp. megalopae were sampled by all nets in both months. The Marinovich collected a substantial concentration of adult euphausiids at one station in May (3.2 g/1000 m³).

The standardized biomass composition of taxa collected by bongo net in May and June was significantly different from that collected by all the other sampling gears (ANOSIM, $p = 0.001$; Table 3). No significant differences were found in total biomass of taxa collected in May by the herring, Marinovich, and Methot nets (Table 3). Net biomass differences were clearly demonstrated in the NMDS ordination plot, which showed a distinct separation between the bongo net and the larger trawls (Fig. 2). SIMPER analysis showed that the mean dissimilarity in the biomass of taxa collected by the bongo net compared with the other nets was 99.5%. This dissimilarity was primarily due to the higher biomass of copepods, *Cancer* spp. megalopae and pteropods sampled in the bongo net, which were rarely caught in the other gears. The higher biomass of fish such as osmerids and *M. proximus* in the larger nets further separated them from both the May and June bongo samples (Fig. 2).

3.2. Comparison to diets of juvenile salmon

Juvenile Chinook and coho salmon principally ate juvenile fish such as *A. hexapterus*, *Sebastes* spp. and hexagrammids, and inver-
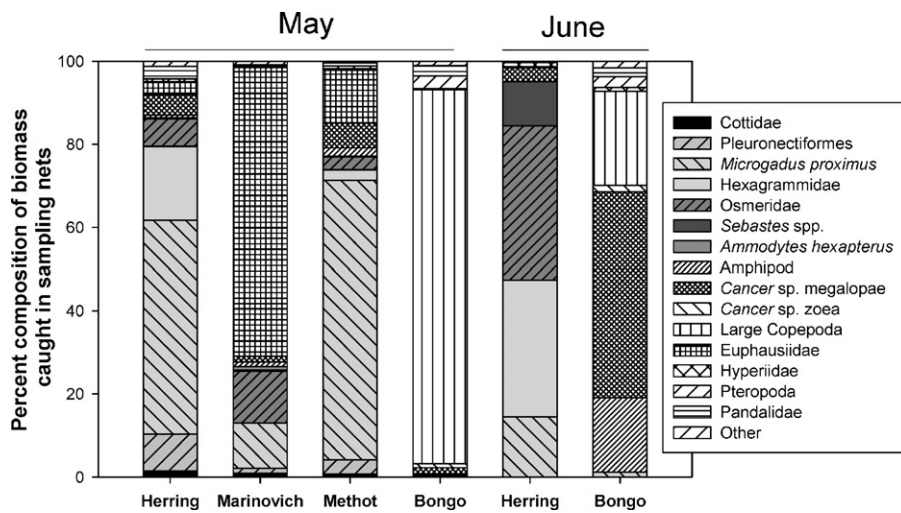
Fig. 1. Percent composition of mean biomass of taxa collected in May and June for each gear type. Rare taxa were grouped in the category "other" and was made up of Bathymasteridae, Agonidae, Stichaeidae, Cryptacanthodidae, Liparidae, non-*Cancer* sp. crab megalopae and zoea, Cirripedia cyprids, and Mysidacea.

Table 1

Comparison of gear specifications and towing methods for the four gear types used in the prey capture comparison study.

|	Herring	Marinovich	Methot	Bongo
Mouth opening area (m²)	37.2	27.0	5.2	0.3
Mesh size of filter cone (mm)	3	3	3[a]	0.3
Tow method	Surface	Surface	Double oblique	Double oblique
Tow speed (knots)	3	3	3	2
Av. volume filtered (m³) (SD)	86,128 (18,938)	70,022 (6531)	13,931 (1464)	74.4 (10.2)
Water volume indicator	Distance trawled	Distance trawled	Flow meter	Flow meter

[a] Cod end mesh size 1 mm.

tebrates such as *Cancer* spp. megalopae, adult euphausiids, and amphipods. We observed differences in prey type between months as well as between salmon species. In May, Chinook and coho salmon ate adult euphausiids and juvenile *A. hexapterus* (Fig. 3). Chinook salmon in May also consumed cottids and the gammarid amphipod, *A. tridens*, while coho salmon also ate hexagrammids (Fig. 3). In June, both juvenile salmon ate primarily juvenile *Sebastes* spp. and hexagrammids, and in addition coho salmon also consumed *Cancer* spp. megalopae (Fig. 3).

We found the highest degree of similarity between salmon diets and the larger trawl nets, but there were monthly differences (Table 4). The NMDS ordination of salmon diets (averaged by sampling station) and monthly net composition demonstrated monthly changes in diet and net composition, with the salmon diets clustering around the composition of the sampling gears (Fig. 4). For May, the diets of juvenile salmon and the catch compositions from her-

ring, Marinovich, and Methot nets were not significantly different from each other (Table 4). However for June, biomass composition of the herring trawl catch was significantly different from that of Chinook salmon diets (ANOSIM; $p = 0.003$), but was not different from that of coho salmon diets ($p > 0.05$).

The prey taxon most responsible for significant compositional differences between the herring trawl and Chinook salmon diets in June was hexagrammids based on the SIMPER analysis. Even though the overall mean diet composition of Chinook salmon in June (Fig. 3) showed a high degree of predation upon hexagrammids, this was principally at one station, whereas the herring trawl consistently caught hexagrammids (7 of 10 stations). A second notable difference was that although cottids were a part of Chinook salmon diets in June, they were not collected at all in the herring trawl in June,
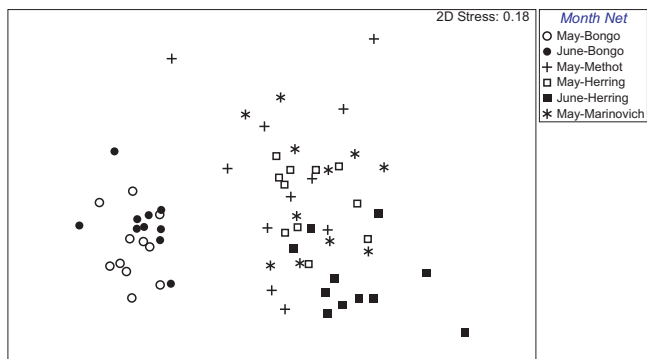
Fig. 2. Nonmetric multidimensional scaling (NMDS) plot of biomass composition of different gear types for May and June 2008 cruises. Each data point represents a different station–gear combination.
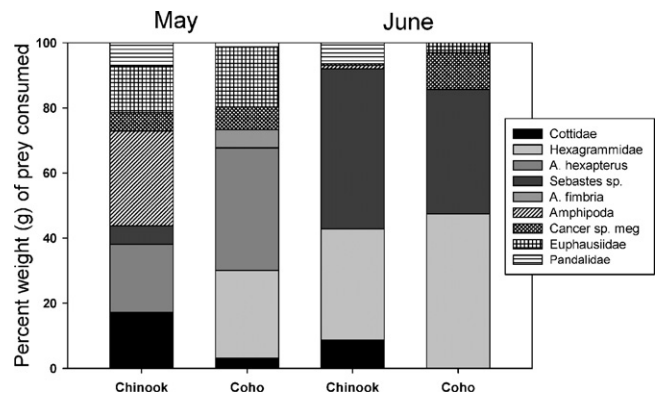
Fig. 3. Diets of juvenile Chinook and coho salmon in May and June by percent weight of prey consumed. Sample sizes of May and June Chinook salmon with fresh prey were 45 and 38, respectively. May and June coho salmon stomach sample sizes were 62 and 64, respectively.

Table 2

Mean biomass (ww/1000 m^3) and mean length of taxa collected in May and June for each gear type.

Prey Categories	May Herring		May Marinovich		May Methot		May Bongo		June Herring		June Bongo	
	Mean (ww/1000 m^3)	Mean length	Mean (ww/1000 m^3)	Mean length	Mean (ww/1000 m^3)	Mean length	Mean (ww/1000 m^3)	Mean length	Mean (ww/1000 m^3)	Mean length	Mean (ww/1000 m^3)	Mean length
Pteropoda	0.001	7.1	<0.001	5.6	0.009	4.9	1.734	3.5			0.170	0.4
Large Copepoda			<0.001	6.5			51.706	3.1			1.489	2.7
Cirripedia cyprids							0.026	1.5			<0.001	1.8
Hyperiidae	0.002	13.3	0.001	14.7	0.008	9.0	0.163	2.9	0.005	14.0	0.062	2.0
Amphipoda (mostly Gammaridae)	0.002	21.4	0.005	17.7	0.079	22.0	0.147	7.4			1.175	4.7
Euphausiidae	0.011	25.9	0.291	27.0	0.254	28.1	0.004	10.4	0.001	20.2		
Mysidae							0.442	10.5			0.051	3.3
Cancer sp. megalopae	0.017	c	0.006	c	0.059	c	0.851	b	0.014	b	3.251	c
Cancer sp. zoea			<0.001	c			0.578	c	<0.001	b	0.099	c
Non-*Cancer* sp. megalopae							0.025	1.7			0.003	b
Non-*Cancer* sp. zoea							0.131	3.0			0.054	2.3
Pandalidae	0.010	25.9	0.001	24.9	0.014	23.7	1.432	6.9	<0.001	b	0.138	5.4
Osmeridae	0.023	31.7	0.052	37.1	0.060	34.3	0.001	7.9	0.155	41.1		
Microgadus proximus	0.183	31.3	0.045	31.8	1.331	33.8			0.060	39.9	0.074	b
Sebastes spp.	0.001	18.8	0.001	b	0.015	b	0.004	5.4	0.044	53.6	0.004	4.0
Hexagrammidae	0.063	62.5			0.203	b			0.138	85.3		
Cottidae	0.005	21.5	0.004	18.5	0.018	23.3	0.107	9.3			0.001	4.7
Ronquilus jordani	<0.001	26.0	<0.001	b					0.001	34.3		
Ammodytes hexapterus	<0.001	b	0.004	51.1			0.168	b				
Pleuronectiformes	0.032	21.6	0.005	20.2	0.055	24.0	0.005	5.9	<0.001	b	<0.001	3.0
Other fish[a]	0.004	20.0	0.004	19.4	0.011	25.0						

[a] Includes Agonidae, Stichaeidae, Cryptacanthodidae, and Liparidae.

[b] <3 measured.

[c] Not measured.

Table 3
Analysis of similarity (ANOSIM) test p values resulting from the comparison of standardized biomass (4th root transformed) of taxa collected in the various sampling gears for May and June.

	May				June	
	Bongo	Herring	Marinovich	Methot	Bongo	Herring
Bongo	–				–	0.001
Herring	0.001	–				–
Marinovich	0.001	0.600	–			
Methot	0.001	0.061	0.231	–		

Table 4
Analysis of similarity (ANOSIM) test p values resulting from the comparison of the taxa eaten by juvenile Chinook and coho salmon (calculated as a percent composition by weight of taxa eaten) and the percent biomass composition from the various sampling gears for May and June. Also shown is the intraspecific overlap in diet between Chinook and coho salmon in each month (in italics).

	May					June		
	Bongo	Herring	Marinovich	Methot	Coho	Bongo	Herring	Coho
Coho	0.002	0.126	0.104	0.136		0.002	0.087	–
Chinook	0.006	0.095	0.602	0.116	*0.132*	0.006	0.016	*0.048*

though they had been commonly captured by the herring trawl in May.

There were statistical differences between Chinook and coho salmon diets when compared to the bongo net for both months (ANOSIM all pairs; $p < 0.05$; Table 4). SIMPER analysis determined that May bongos consistently caught more pandalid shrimp and *Cancer* spp. megalopae than were eaten by either salmon species. Both species consumed more *A. hexapterus* than were caught in the bongo net. These three prey categories accounted for approximately 60% of the significant dissimilarity between May bongo net catch and salmon diets. Similarly for June, *Cancer* spp. megalopae in the bongo net, *Sebastes* spp. in coho salmon diets, and cottids in Chinook salmon diets accounted for almost 60% of the dissimilarity between gear types and stomach contents. Juvenile salmon ate primarily fish prey, but only 13 fish were caught in the 11 bongo tows during May and 11 in the 10 bongo tows during June.
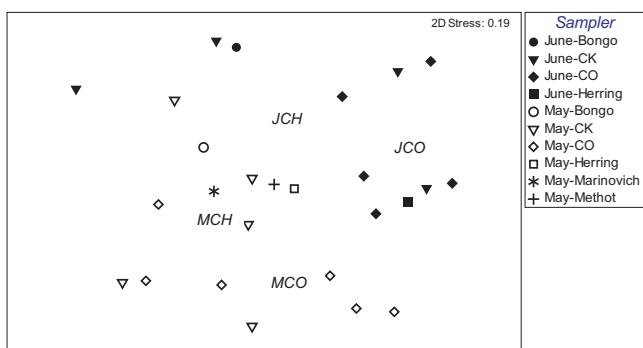
3.3. Prey length comparison

The length of the fish caught in the various sampling gears was compared to the length of fish eaten by juvenile salmon. In May, Chinook salmon ate fish that averaged 29.8 mm in total length, while coho salmon ate fish slightly longer, at 32.3 mm (Fig. 5). The sizes of fish prey eaten by Chinook and coho salmon in May were not significantly different from the lengths of fish caught in either the

Fig. 4. NMDS plot of juvenile Chinook and coho salmon diets averaged at each sampling station overlaid upon the overall monthly centroid of each sampling gear. Filled symbols represent June net or stomach composition. See Fig. 2 for individual station values for the different nets. The centroids of each salmon monthly diet composition is also given in italic labels (MCH, May Chinook; MCO, May Coho; JCH, June Chinook; JCO, June Coho) for easier comparison to the gear centroids.

herring, Marinovich, or Methot nets, but were significantly longer than fish captured in the bongo net (Mann–Whitney; $p < 0.001$). However, in June, coho salmon consumed fish that were significantly longer than fish caught in either the herring trawl or the bongo net (Mann–Whitney; $p < 0.001$). The overall average size of fish prey eaten in June was 57.5 mm for coho salmon and 36.5 mm for Chinook salmon (Fig. 6). Chinook salmon ate fish prey that were significantly shorter than fish caught in the herring trawl and significantly longer than fish caught in the bongo net (Mann–Whitney; $p < 0.001$; Fig. 6). These observed differences were principally the result of the different species of fish eaten in June. During June, coho salmon consumed longer prey fish such as hexagrammids (mean size = 71.9 mm) and *Sebastes* spp. (54.2 mm), while Chinook salmon consumed the smaller cottids (19.1 mm), which may not have been retained by the herring trawl due to its larger mesh size.
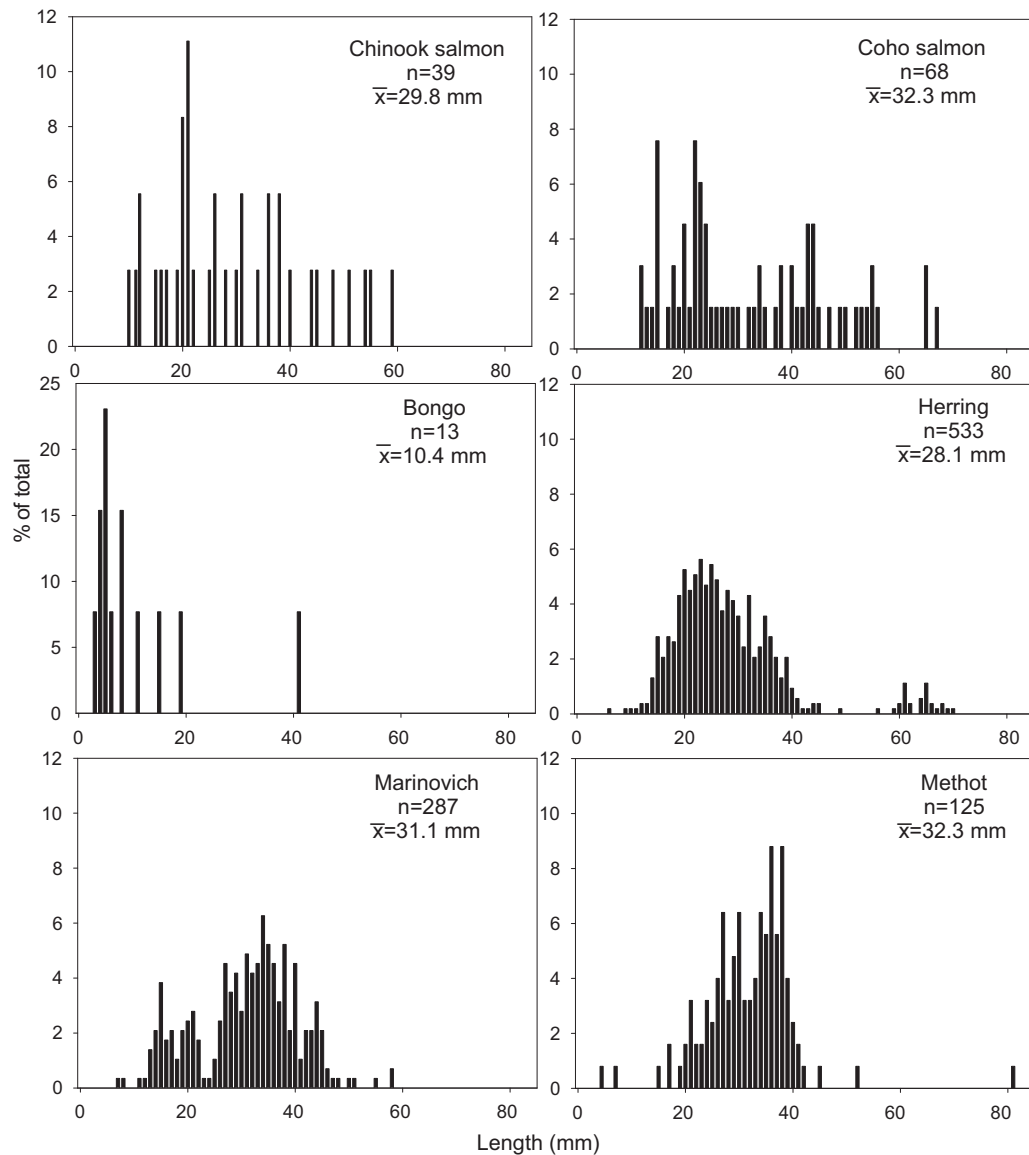
Similar size differences were noted for the invertebrate prey categories captured in the bongo versus the other gear types (see particularly Amphipoda, Euphausiidae, Pteropoda, and Pandalidae in Table 1), although the sample sizes were generally insufficient to make detailed statistical comparisons between these sampling gears.

4. Discussion

This study represents the first attempt to utilize a broad range of micronekton gears to sample available prey of predominantly piscivorous juvenile salmon in coastal waters. Catch from the micronekton gears we tested (herring, Methot, and Marinovich) did show some overlap with juvenile salmon diets, and all three of these gears showed more overlap with the diets than the bongo net in terms of species composition and size of prey consumed. It is not surprising that small plankton nets such as the bongo used in this study do not compare favorably with the diets of piscivorous predators such as juvenile coho and Chinook salmon. In our study, this mismatch remained even after smaller contents of the net were excluded from analysis. The effective sampling area of a 0.60-m bongo net is rather limited, and large, highly mobile prey, such as juvenile fish and euphausiids, can easily evade the path of the tow prior to the arrival of the net. Although these small plankton nets may be highly effective for catching copepods and the eggs and early life stages of most fish, they are not reliable as quantitative samplers for larger fish in the micronekton size range (Shima and Bailey, 1994; Jump et al., 2008). These small-opening nets provide only an index of the smaller food resources available in that they

Fig. 5. Comparison of size of fish collected in the bongo net and Marinovich, Methot, and herring trawls with the fish prey found in the diets of Chinook and coho salmon during May 2008. Sample size and overall mean is given for each plot. Note the different *y*-axis scale for the bongo net.
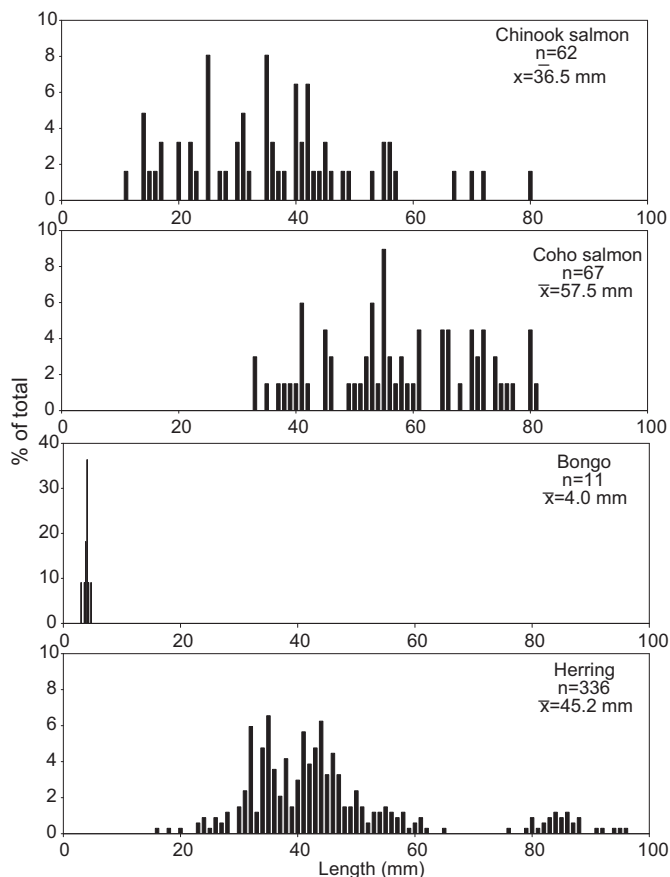
generally collect plankton (e.g., copepods, larvaceans, pteropods) in size categories encompassing the prey of larger juvenile fish ultimately eaten by salmon.

Nevertheless, no single net collected organisms that provided complete overlap with coho and Chinook salmon diets for several possible reasons. First, a direct comparison between the diet of a marine predator and its potential prey resources presupposes that collections from both sources are spatially and temporally compatible. There are several sources of error that may account for differences in these two measurements. We attempted to sample prey resources from the same geographic location where salmon were caught, and at approximately the same time. However, due to the patchy nature of most prey in the plankton, as well as the mobility of juvenile salmon, it is likely that our gear did not sample the same volume of water that predators encountered. Prey patches may aggregate in frontal regions (Franks, 1992; Morgan et al., 2005) or in distinct layers in the water column (Peterson and Peterson, 2008). These patches may be sampled only briefly by most towed sampling gears, but may be foraged intensely over an extended period by predators capable of maintaining position within the patch. Previous studies have shown that juvenile salmon

early in the summer are found predominantly in the upper part of the water column (Emmett et al., 2004). Although the upper water column was also sampled with our gear types, some individuals could have made brief or perhaps even extended excursions into deeper layers to feed.

Time of day when sampling is conducted can have a major effect on catch, with catches generally larger at night due to both decreased light-aided avoidance of the gear and enhanced surface abundance of prey due to diel vertical migration. We chose to sample during the day based on previous studies in this geographic area (Brodeur and Pearcy, 1987; Schabetsberger et al., 2003; Benkwitt et al., 2009), which indicated that both juvenile coho and Chinook salmon feed primarily during daylight or crepuscular periods.

Despite our inclusion of only stomachs containing relatively fresh or undigested food (digestion code 3 or 4), the digestion period of juvenile salmon is sufficiently long (~24 h; Brodeur and Pearcy, 1987; Benkwitt et al., 2009), and the temperatures we observed sufficiently low (9–12 °C), to allow for the possibility that the stomach contents we observed were actually consumed some distance away. Ocean migration rates of up to 8 km d^{-1} have been reported for juvenile Columbia River salmon (Fisher and Pearcy,

Fig. 6. Comparison of size of fish collected in the bongo net and herring trawl with the prey fish found in the diets of Chinook and coho salmon during June 2008. Note different *y*-axis scale for bongo net.

atively large mesh sizes in the forward part of the herring and Marinovich trawls. However, prior studies have suggested that there would likely be some herding of many of the fish into the center of the net (Ramm and Xiao, 1995) where they would eventually encounter the finer mesh liner, and that this effect would be more pronounced with the larger prey fish and invertebrates we examined (Lee et al., 1996) and during daylight sampling (Ryer and Olla, 2000). Therefore we used the full mouth area in the calculations of the biomass but used relative percentages of the taxa caught in the nets in statistical comparisons to the stomach contents of the salmon, although size-related variation within a taxon may still exist (Lee et al., 1996). Moreover, radiated noise from trawling vessels, including the vessel we used during May sampling (DeRobertis and Wilson, 2006), has been shown to affect the behaviour of fish in the water column and this would particularly be relevant to the near surface sampling we conducted in this study. Thus, although the relative catches may be useful in determining what prey may be available to salmon foraging in surface waters, we caution that these may be minimum estimates and will probably be adjusted higher once the true sampling volumes and selectivities of each net are determined.

Among the three micronekton trawls we examined, none showed significant differences in proportional composition from stomach contents according to ANOSIM results. Each micronekton trawl caught unique taxa not found in the other two nets, which again may be related to the patchiness of prey fields. Unfortunately, the larger prey eaten by juvenile Chinook and coho salmon are generally not abundant enough to be assessed by independent methods (e.g., acoustics, video plankton recorders) to determine the true catchability of these micronekton gears (see also Pakhomov and Yamamura, 2010). Of the three trawls, the herring net, which had the largest effective mouth area, caught the highest diversity of prey and would be most likely to catch prey that salmon rarely encounter.

5. Conclusions

The catches of several new micronekton gears and the bongo net presently in use were tested and compared to the stomach contents of juvenile salmon. No single gear was able to catch samples that completely overlapped with prey found in juvenile coho and Chinook stomachs. However, samples from the bongo had the least overlap with the prey of these salmonids in terms of both type and size of animals caught. Conversely, the other gears (Methot, herring, and Marinovich trawls) caught a more diverse set of potential prey and overlapped to some degree with the stomach contents of both species. When analyzed only for prey taxa typically eaten by juvenile salmon, none of the three micronekton gear types caught samples that were significantly different from either coho or Chinook diets. The size ranges of fish captured were also fairly similar to those found in the diets, especially for the herring net. We therefore do not recommend the use of standard plankton gears (i.e., bongo nets) for direct estimates of available prey resources for juvenile coho or Chinook salmon. Rather, we suggest the use of micronekton gear with larger mouth openings and mesh sizes for better filtration. Using these larger nets will enable better estimation of salmon prey resources which can be used in modeling and predicting salmon carrying capacity.

Acknowledgements

1995; Morris et al., 2007). In addition, the prey themselves may be moving in a different direction than the salmon due to currents, so the temporal/spatial mismatch between the two can be quite substantial. Moreover, differential digestion rates of hard versus soft prey (e.g., Arai et al., 2003) may give a biased representation of actual consumption from stomach content analysis. However, these temporal mismatches between location of feeding and prey sampling were likely minimized in our study, since we included only those stomachs with fresh contents that had most likely eaten only a few hours before capture.

Finally, salmon foraging behaviour is another source of potential disparity we need to consider. One would generally expect that a predator would not forage in the same manner as a simple net towed unidirectionally through the water. Predators that forage selectively on individual prey may use visual or tactile cues to detect prey some distance outside the circumference of the mouth area of any net, and thus may alter their course to attack or pursue these prey. Optimal foragers are also capable of remaining within a patch of prey for an extended period in order to capitalize on one or several highly aggregated prey taxa (Eggers, 1977; Lazzaro, 1987). Schabetsberger et al. (2003) have shown that juvenile salmon appear to select the more heavily pigmented prey within the normal prey size range available in the plankton, and the prey types found in our analysis were consistent with this finding. Other factors involved with prey selection, such as the ability of salmon to perceived the relative quality of prey or the presence of predators, can also affect the food consumption of a predator that would not be reflected in the sampling gear (Link and Keen, 1999).

We acknowledge that the biomass estimates of many of the smaller prey may be under-estimated due to loss through the rel-

References

Abookire, A.A., Piatt, J.F., 2005. Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. Mar. Ecol. Prog. Ser. 287, 229–240.

Arai, M.N., Welch, D.W., Dunsmuir, A.L., Jacobs, M.C., Ladouceur, A.R., 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. Can. J. Fish. Aquat. Sci. 60, 825–829.

Benkwitt, C.E., Brodeur, R.D., Hurst, T.M., Daly, E.A., 2009. Diel feeding chronology, gastric evacuation and daily food consumption of juvenile Chinook salmon in coastal waters. Trans. Am. Fish. Soc. 138, 111–120.

Bollens, S.M., Hooff, R., Butler, M., Cordell, J.R., Frost, B.W., 2010. Feeding ecology of juvenile Pacific salmon (*Oncorhynchus* spp.) in a northeast Pacific fjord: diet, selectivity for prey, and potential competition for prey resources. Fish. Bull. 108, 393–407.

Brodeur, R.D., Pearcy, W.G., 1987. Diel feeding chronology, gastric evacuation and estimated daily ration of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), in the coastal marine environment. J. Fish Biol. 31, 465–477.

Brodeur, R.D., Pearcy, W.G., 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. Fish. Bull. 88, 617–636.

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

Brodeur, R.D., Seki, M.P., Pakhomov, E.A., Suntsov, A.V., 2005. Micronekton – what are they and why are they important? PICES Press 13, 7–11.

Brodeur, R.D., Daly, E.A., Sturdevant, M.V., Miller, T.W., Moss, J.H., Thiess, M., Trudel, M., Weitkamp, L.A., Armstrong, J., Norton, E.C., 2007. Regional comparisons of juvenile salmon (*Oncorhynchus* spp.) feeding in coastal marine waters off the West Coast of North America. Am. Fish. Soc. Symp. 57, 183–203.

Clarke, K.R., Gorley, R.N., 2005. PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd ed. PRIMER-E Ltd., Plymouth.

Daly, E.A., Brodeur, R.D., Weitkamp, L.A., 2009. Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? Trans. Am. Fish. Soc. 138, 1420–1438.

Daly, E.A., Benkwitt, C.E., Brodeur, R.D., Litz, M.N.C., Copeman, L., 2010. Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar. Biol. 157, 1975–1987.

DeRobertis, A., Wilson, C.D., 2006. Walleye pollock respond to trawling vessels. ICES J. Mar. Sci. 63, 514–522.

DeRobertis, A., Morgan, C.A., Schabetsberger, R.A., Zabel, R.W., Brodeur, R.D., Emmett, R.L., Knight, C.M., Krutzikowsky, G.K., Casillas, E., 2005. Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. Mar. Ecol. Prog. Ser. 299, 33–44.

Eggers, D.M., 1977. The nature of prey selection by planktivorous fish. Ecology 58, 46–59.

Emmett, R.L., Brodeur, R.D., Orton, P.M., 2004. The vertical distribution of juvenile salmon (*Oncorhynchus* spp.) and associated species in the Columbia River plume. Fish. Oceanogr. 13, 392–402.

Fisher, J.P., Pearcy, W.G., 1995. Distribution, migration, and growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, off Oregon and Washington. Fish. Bull. 93, 274–289.

Franks, P.J.S., 1992. Sink or swim: accumulation of biomass at fronts. Mar. Ecol. Prog. Ser. 82, 1–12.

Jump, C.M., Duffy-Anderson, J.T., Mier, K.L., 2008. Comparison of the Sameoto, Manta, and MARMAP neustonic ichthyoplankton samplers in the Gulf of Alaska. Fish. Res. 89, 222–229.

Keeley, E.R., Grant, J.W.A., 2001. Prey size of salmonids fishes in streams, lakes, and oceans. Can. J. Fish. Aquat. Sci. 58, 1122–1132.

Lazzaro, X., 1987. A review of planktivorous fishes: their evolution, feeding behaviors, selectivities, and impacts. Hydrobiologia 146, 97–167.

Lee, K.-T., Lee, M.-A., Wang, J.-P., 1996. Behavioural responses of larval anchovy schools herded within large-mesh wings of trawl net. Fish. Res. 28, 57–69.

Link, J.S., Keen, R.E., 1999. A model of salmonids planktivory: field test of a mechanistic approach to size-selection. Ecol. Model. 117, 269–283.

Logerwell, E.A., Mantua, N., Lawson, P.W., Francis, R.C., Agostini, V.N., 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish. Oceanogr. 12, 554–568.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. Software Design, Gleneden Beach.

Methot, R.D., 1986. A frame trawl for sampling juvenile fish. CalCOFI Rep. 27, 267–278.

Morgan, C.A., De Robertis, A., Zabel, R.W., 2005. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. Mar. Ecol. Prog. Ser. 299, 19–31.

Morris, J.F.T., Trudel, M., Thiess, M.E., Sweeting, R.M., Fisher, J., Hinton, S.A., Fergusson, E.A., Orsi, J.A., Farley Jr., E.V., Welch, D.W., 2007. Stock-specific migrations of juvenile coho salmon derived from coded-wire tag recoveries on the continental shelf of western North America. Am. Fish. Soc. Symp. 57, 81–104.

Pakhomov, E., Yamamura, O., 2010. Report of the advisory panel on micronekton sampling inter-calibration experiment. PICES Sci. Rep. 38, 1–108.

Pearcy, W.G., 1992. Ocean Ecology of North Pacific Salmonids. University of Washington Press, Seattle, WA.

Peterson, J.O., Peterson, W.T., 2008. Influence of the Columbia River plume (USA) on the vertical and horizontal distribution of mesozooplankton over the Washington and Oregon shelf. ICES J. Mar. Sci. 65, 477–483.

Ramm, D.C., Xiao, Y., 1995. Herding in groundfish and effective pathwidth of trawls. Fish. Res. 24, 243–259.

Reser, B.A., 2009. Bioenergetics individual based model explorations of juvenile coho salmon growth during their first summer on the Oregon shelf. M.S. Thesis, Oregon State University. Available from: http://ir.library.oregonstate.edu/xmlui/handle/1957/13956.

Ryer, C.H., Olla, B.L., 2000. Avoidance of an approaching net by juvenile walleye pollock *Theragra chalcogramma* in the laboratory: the influence of light intensity. Fish. Res. 45, 195–199.

Schabetsberger, R., Morgan, C.A., Brodeur, R.D., Potts, C.L., Peterson, W.T., Emmett, R.L., 2003. Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish. Oceanogr. 12, 523–540.

Shima, M., Bailey, K.M., 1994. Comparative analysis of ichthyoplankton sampling gear for early life stages of walleye pollock (*Theragra chalcogramma*). Fish. Oceanogr. 3, 50–59.

Weitkamp, L.A., Sturdevant, M.V., 2008. Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish. Oceanogr. 17, 380–395.

Zavolokin, A.V., 2009. Forage base of Pacific salmon in the western Bering Sea and adjacent Pacific waters in 2002–2006. N. Pac. Anadr. Fish Comm. Bull. 5, 165–172.