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The Early Marine Biology of the Hatchery/Wild Juvenile Salmonid (*Oncorhynchus* sp.) Community in Barkley Sound, Canada

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Abstract: We conducted 11 purse seine/beachseine surveys over the summers of 2000 and 2001 to learn about the migration timing, distribution, and diet of hatchery chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*), and wild chinook, coho, sockeye (*O. nerka*) and chum (*O. keta*) juvenile salmon, in Barkley Sound, West Coast Vancouver Island. Juvenile salmon partitioned Barkley Sound by time and space, and by diet except for hatchery and wild coho. The analysis of migration timing included historic data for 1987-89, and results showed that timing differed between species and was consistent over years. Sockeye and chum dominated the juvenile salmon community until mid-June and hatchery and wild chinook dominated subsequently. Fish tended to be dispersed contagiously. Results of correlation analyses of catch suggested that fish of different origins and species did not co-occur. The euphausiid *Thysanoessa spinifera* was an important prey item but different fish species selected different sizes of *T. spinifera* at different times. The diet overlap between hatchery and wild coho did not affect return. Migration timing for sockeye and wild coho seems to reflect a strategy to enter the ocean when the biomass of the size fraction of *T. spinifera* that each species selects is likely to be maximal. Descriptions of migration timing, fish interactions, and diet provide information which appears to be useful for learning about the biological basis of salmon return variability.

Keywords: Distribution, feeding, hatchery/wild fish interactions, juvenile salmon, migration, prey selectivity.

INTRODUCTION

There have been many studies of the early marine biology of salmon. The implicit or explicit goal has been to contribute to learning about the biological basis of return variability. Initially, investigators (e.g. [1]) assumed that ocean conditions were constant and concluded that return variability must be generated during the freshwater life history. However, results of investigations by Vernon (1958) and Wickett (1958, both cited in [2]) for pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon respectively, and for Oregon Production Index (OPI) area coho (*O. kisutch*) [3 and others], began revealing that ocean conditions during the early marine life history determined variation in salmon returns. Subsequent reports [4, 5] defined more precisely when return variability was determined by concluding that mortality was highest in the first few weeks after sea entry. Results of recent research [6] found that return variability for sockeye (*O. nerka*) from the West Coast of Vancouver Island was explained by variations in prey (the euphausiid *Thysanoessa spinifera*) biomass during the first month at sea. Most recently, it has been reported [7] that winter larval fish biomasses measured off Newport, Oregon predicted returns of OPI coho and Columbia River hatchery chinook salmon, and that the winter larval fish community composition was more closely reflected in the diets of juvenile salmon collected in May than in June.

Most studies of the biology of juvenile salmon have focused on times after the first few weeks at sea, at a distance from the shore (> 3 km), and have not considered that juvenile salmon occur as a community with the inherent implications of potential competition for space and prey. Sampling later in the first year of marine life, and at a distance from the shore, may largely be a function of the decision to sample juvenile salmon using larger purse seines or mid-water trawls. This is perplexing because the only direct examination of the early marine survival [4], before Tanasichuk and Routledge [6] and now Daly *et al.* [7], showed that most of the marine mortality occurred within the first 45 days of marine life and near shore and those results were published 45 years ago. Juvenile salmon concentrate near shore during their early marine life history [8-10] which suggests that intra- and inter-specific interactions would be maximal then.

The consensus is that food availability during the early marine life history is the basis for return variability, and that the effect is not direct via energetics (i.e. starvation), but indirect by influencing growth and susceptibility to predation. It has been noted [11] that earlier studies reported that fish generally selected relatively large and heavily pigmented

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prey. Most studies of feeding periodicity (e.g. [11-13]) reported that juvenile salmon fed crepuscularly. These observations collectively suggest that diel vertical migrants (e.g. euphausiids, calanoid copepods) should be significant prey, which they appear to be. However, sampling for prey generally occurs during the day when the prey community is very different from that experienced by juvenile salmon while feeding at low light levels. There are important components to consider with any measure of prey selection [14]. These are: 1) obtaining an unbiased sample from the habitat which accurately represents the relative abundances of prey as they are encountered by the predator, and 2) obtaining an unbiased sample which accurately represents the relative abundances of the prey species as they are consumed.

Interactions, more specifically, competition for food during the early marine life history, have been studied infrequently. Results of previous studies suggest that competition may vary among locations, time periods, and species of fish. For example, Healey [15] and Landingham *et al.* [16] reported that there were times when the proportion of a given prey item varied among species, but times when diet overlap was apparent. Peterson *et al.* [17] and Brodeur *et al.* [18] found that diets were similar among juvenile salmon off Oregon, although, and interestingly, Peterson *et al.* [17] reported that different size ranges of chinook and coho had more similar diets.

The least investigated interaction is the one between hatchery and wild juvenile salmon ([19], [20]). Typically only a few hatchery fish are marked. This makes it impossible to describe the origin (hatchery, wild) of most fish. Also, it is difficult to show that responses in wild populations are attributed solely to the presence of hatchery fish. Boldt and Haldorson [21] compared energy densities of wild and hatchery pink salmon and concluded that, because energy contents were similar, neither group had a competitive advantage. Sweeting *et al.* [22] described instances where it appears that hatchery coho production in the Strait of Georgia had a negative effect on wild return although they suggested this was actually because of changes in marine survival and exploitation instead of an interaction between wild and hatchery fish. Nickelson [23] showed that wild production of Oregon coho declined as the number of hatchery smolts into freshwater basins increased, and suggested that the mechanism was increased predation because predators were attracted to larger aggregations of hatchery and wild fish in estuaries. However, this could be a result of young salmon becoming more conspicuous and having nothing to due with hatchery fish *per se*. Fisher and Pearcy [24] found that although the diets of wild fall-run and hatchery spring-run chinook overlapped there was no indication of competition based observations of higher stomach fullness in wild fish, no reduction in their stomach fullness when hatchery fish were present, and finally, the groups contained similar proportions of high energy prey. These authors pointed out that dietary overlap can simply indicate times when food is abundant. Cooney and Brodeur [25] developed a model to explore the effect of hatchery production on wild pink salmon in the North Pacific. They concluded that the high level of wild and hatchery production taxed the coastal and oceanic feeding domains and reduced growth with negative effects on the progeny.

The goal of this study was to learn about the early marine biology of the juvenile salmonid community (hatchery chinook (*O. tshawytscha*) and coho, and wild chinook, coho, sockeye and chum salmon), in Barkley Sound, West Coast Vancouver Island. We wanted to test null hypotheses that there were no interactions among species, and between hatchery and wild fish, with respect to distribution and diet. We sampled, using purse- and beachseines, bi-weekly over the summers of 2000 and 2001. All hatchery fish were marked so we could investigate hatchery/wild fish interactions. We took advantage of a zooplankton/euphausiid monitoring programme [26], where all sampling was at night in the Sound, to investigate prey selectivity using a realistic description of the prey community.

MATERIALS AND METHODOLOGY

Sample Collection and Analysis

We conducted purse seine/beachseine surveys in Alberni Inlet/Barkley Sound, located on the southwest coast of Vancouver Island (WCVI), during the summers of 2000 and 2001. There were 14 sampling locations in the Inlet and Sound (Fig. **1**). Table **1** shows survey dates, and the number of purse- and beachseine sets made in the Inlet, and the easternmost (Trevor), middle (Imperial Eagle), and westernmost (Loudon) channels of the Sound. The purse seine was 179 m long and 16 m deep. It consisted of 133 m of 3.2 cm mesh netting and a 46 m bunt of 1.9 cm mesh netting. Purse seine sets were round hauls at specific locations, without any consideration of showings of fish at the surface or on the electronic sounder. We calculated that the purse seine sampled a 40,812 m^3 cylinder of water. The beachseine was 30 m long and 3 m deep. It consisted of three 10 m panels; the two outside panels were 13 mm mesh, and the middle panel was 3 mm mesh. The beachseine was assumed to fish as a half-cylinder, cut diagonally from the offshore top to the inshore bottom of the beach seine, and sample 108 m^3 of water.

We counted and identified all fish to species when catches were smaller than about 500 fish. The catch was subsampled when we caught more fish. In these instances, dipnets were used to empty the seine net. The number of fish of each species caught (N_j) was estimated as:

$$N_j = t \bullet (k \bullet d_j^{-1}) \qquad (1)$$

where N is the number of fish, j is species, t is the number of dipnet samples required to remove the catch, k is number of fish per species in the dipnet subsamples retained, and d is aggregate number of dipnet subsamples retained. A subsample of up to 25 juvenile salmon per species from each set was preserved for laboratory analysis. Fish were stored in 85% ethanol. Chinook hatcheries occur in the study area and all hatchery fish had thermally marked otoliths. We stored all fish in ethanol to preserve otolith integrity for chinook and to avoid bias associated with preservation effects on size between species. In the laboratory, fish were blotted dry, fork length was measured to the nearest mm, and total mass was measured to the nearest 0.01 g. There are coho hatcheries in the study area as well where all smolts had clipped adipose fins. Therefore, we examined all coho juveniles for fin clips.

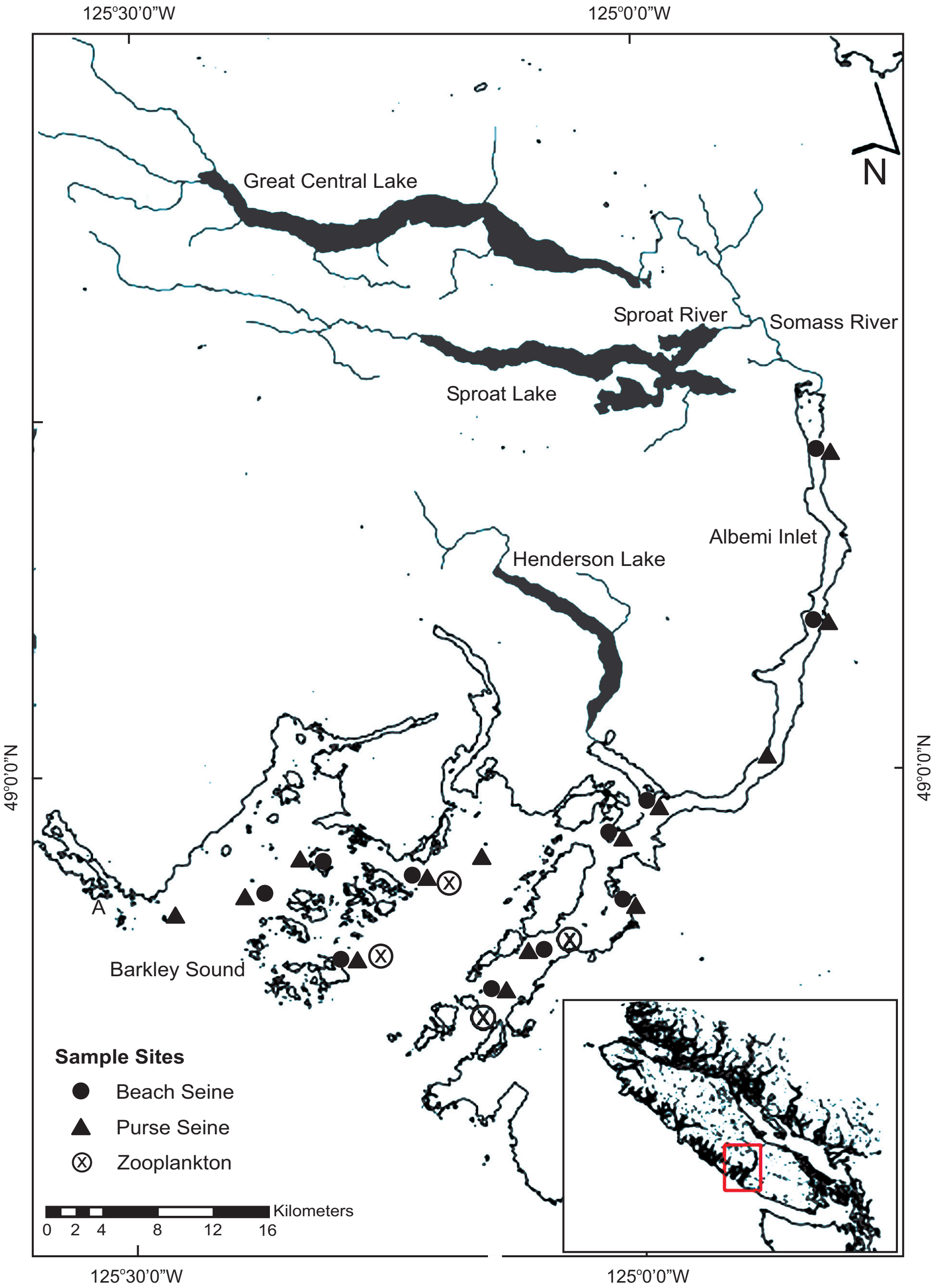

Fig (1). Study area.

Diet Description and Estimation of Selectivity and Diet Overlap

Diet was described in detail for up to 5 fish, by species and source (hatchery, wild) category, from each set; sample sizes are presented in Table **2**. Full and then emptied stomachs were weighed to the nearest 0.001 g. Stomach contents were pooled by species, source, sampling gear and survey. Each prey item was identified to the lowest possible taxon and prosome or total length was measured to the nearest 0.01 mm. Individual prey mass was estimated using survey- and species-specific length-mass relationships based on samples collected during zooplankton/euphausiid monitoring programme in Barkley Sound (see [26]). The length-mass relationships for euphausiids were estimated using observed length and mass data from the zooplankton monitoring programme (R. Tanasichuk *In prep*). The relationships for other prey were calculated after estimating species-specific prosome- or total length-specific volume relationships using samples from the monitoring programme. Volume was estimated using prosome- or total length-specific length-width and length-depth relationships developed for each species (Tanasichuk *unpubl. res.*). Zooplankter volume was converted to mass using the equation presented in Tanasichuk *et al.* [27] where:

Table 1. Number of beach (BS) - and purse seine (PS) sets made during the study of the early marine biology of juvenile salmon in Barkley Sound. Regions within the study are Alberni Inlet (AI), Trevor (T), Imperial Eagle (IE) and Loudon (L) channels.

Date	Region								Sum
	AI		T		IE		L		
	BS	PS	BS	PS	BS	PS	BS	PS	
	2000								
May 15-16	3	4	3	3	1	3	1	3	21
May 29-30	4	5	3	3	1	3	2	3	24
June 13-14	4	5	3	3	1	3	2	3	24
July 5-6	4	5	3	3	1	3	2	3	24
July 26-27	4	5	4	4	1	3	2	3	26
Sum	19	24	16	16	5	15	9	15	119
	2001								
May 14-15	4	5	3	3	0	3	0	3	21
May 29-30	4	5	3	3	1	3	2	3	24
June 12-13	4	5	3	3	1	3	1	3	23
June 29	4	5	3	3	0	3	2	3	23
June 24-25	4	5	3	3	1	3	1	3	23
August 28-29	4	5	3	3	1	3	2	3	24
Sum	24	30	18	18	4	18	8	18	138

Table 2. Sample sizes for diet analysis for juvenile salmon from Barkley Sound. BS – beachseine; PS – purse seine.

Date	Species										Sum
	Coho				Chinook				Chum	Sockeye	
	Wild		Hatchery		Wild		Hatchery		Wild	Wild	
	BS	PS	BS	PS	BS	PS	BS	PS	PS	PS	
	2000										
May 15-16	0	0	0	0	0	0	0	0	70	69	139
May 29-30	5	37	0	33	5	0	0	0	20	47	137
Jun 13-14	0	10	0	7	0	14	1	48	30	40	149
Jul 5-6	0	0	0	0	5	41	0	70	0	0	111
Jul 26-27	0	0	0	0	0	54	0	100	0	0	154
Sum	5	47	0	40	10	109	1	218	120	156	690
	2001										
May 14-15	0	0	0	0	0	0	0	0	25	40	65
May 29-30	1	32	1	26	0	1	0	9	22	41	131
Jun 12-13	0	12	0	18	0	5	0	36	42	50	163
Jun 29	0	5	0	5	0	6	0	37	0	0	53
Jul 24-25	0	0	0	0	0	25	0	41	0	0	66
Aug 28-29	0	0	0	0	0	0	0	0	0	0	0
Sum	1	49	1	49	0	37	0	123	89	131	478

$$m = 1.08 \bullet v \quad (2)$$

where m is mass (g) and v is volume (mL). Stomach contents were expressed as potential diet energy (PDE (kJ • % predator mass • h^{-1}), where h is hour) where:

$$PDE = m_j \bullet G_j \bullet r \quad (3)$$

and m_j is mass of prey, G_j is gross prey energy density and r is an evacuation rate of 0.12% predator mass • h^{-1} for euphausiids [27]. The gross energy density estimates (kJ • g wet mass^{-1}) were based on the values provided by Foy and Norcross [28] and are presented in Tanasichuk and Routledge [6]. We used the PDE index because it described the amount of energy that a prey item can provide. The term "potential" was included because there is apparently very little information on assimilation efficiency in fish in the wild, and the fate of ingested matter with respect to biotransformation. The evacuation rate was assumed to be the same for all prey because they are invertebrates with thin exoskeletons.

The energy available to juvenile salmon in the water column was estimated using Foy and Norcross' gross energy estimates and estimates of zooplankter biomass from the euphausiid/zooplankton monitoring programme. Prosome or total lengths of zooplankters were rounded up to the nearest mm and length-specific biomass was estimated using the equations for prey volume and then mass described above. Length-specific biomass for each taxon was then multiplied by the gross energy density estimates to calculate taxon- and length-specific energy in the water column.

Selectivity was quantified using Strauss' [14] linear food selection index (L) where:

$$L_i = r_i - p_i \quad (4)$$

and i is taxon-specific length interval, and r_i and p_i are the proportion of consumed and available energy in the water column respectively.

Statistical Analysis

We designed the sampling program to test the effects of source, area (Inlet and each of the three channels in Barkley Sound), distance from shore (beach- versus purse seine), and time on species-specific distribution. The sampling locations were a subset of those established for Hargreaves *et al.* [29]. These sampling sites monitored the various habitats in the Inlet/Sound comprehensively, and allowed us to use Hargreaves *et al.*'s data to develop a discontinuous time series for describing migration timing variability over 14 years (1987-89, 2000-01). Budgetary and logistical considerations limited replicate sampling sites. We endeavoured to select purse-seining sites where bathymetry allowed for beachseining onshore while trying to replicate the Hargreaves *et al.* [29] survey. This resulted in 4 replicates for purse seining in Alberni Inlet, and 3 replicates in each of the 3 channels of Barkley Sound. For beachseining, there were 4 replicates in Alberni Inlet, 3 replicates in Trevor Channel, 2 replicates in Loudon Channel, and 1 site in Imperial Eagle Channel.

We used Poisson regression to evaluate the effects of time, species, source, area and distance from shore (sampling gear) on catch so that we could explore fish community composition variability. We decided to consider juvenile salmon as part of a community, because that is how they occur in nature, rather than evaluating the effect of time and location of species- and source-specific catch. Poisson regression was used because catches of fish are relatively rare. *Ln* volume was used as an offset to account for the different volumes of water sampled by beach- and purse seines. We did not test for interactions which included a gear effect because there were inadequate numbers of beachseine sites in Imperial Eagle and Loudon channels. Results of preliminary analyses showed evidence of over-dispersion for all sampling trips. Analyses were repeated using the adjustment of over-disperison to correct the standard errors and test statistics.

We used Taylor's power law method to describe the distribution of fish in the study area by year, sampling period, species and source. Analysis was restricted to purse seine sets because very few fish were caught in beachseines (Table **3**). Elliott [30] recommended Taylor's dispersion index for a series of samples. Taylor's index is independent of n (sample size), the mean observation, and the sum of the observations, which implicitly allows for comparison among sampling strata. We estimated regressions of species-source-year-survey- specific *ln* catch variance on *ln* mean catch using variance and mean estimated for each area. The slope of the regression line is the index of dispersion and we used a *t*-test to determine if the slope (β) showed that the animals were randomly (β=1), regularly (β=0.7), or contagiously (β> 2) distributed. We also followed Elliott's advice when we could not distinguish between regular and random distributions, and accepted the null hypothesis, which is that fish were distributed randomly.

We used correlation analysis to determine if the distributions of species and/or source groups overlapped. Kendall's τ statistic was used to described co-variation in catch. We tested the significance of the correlations using Bonferroni-adjusted probabilities, as recommended by Wilkinson *et al.* [31], to minimise the possibility of committing a Type I experimental error. The adjusted probabilities (p_{adj}) were estimated as:

$$p_{adj} = 0.05 \bullet q^{-1} \quad (5)$$

where q is the number of correlations tested.

RESULTS

Migration Timing

Migration timing differed between species but was consistent within species during 1987-89, 2000-01 (Fig. **2**). Coho were first captured in early May and about 90% of the catch for the year had taken place by mid-June. Hatchery coho appeared later than wild ones in 2000 and showed the same trend in catch over time as wild coho did. Sockeye and chum migrated earlier (May) and moved more rapidly through the Inlet and Sound. A comparison of trends in catch between the 1987-89 and 2000-01 periods suggested that sockeye at least were moving through the study area before the 2000-01 surveys began. Chinook were absent until early June. The results for 2001, when sampling continued until

Table 3. Catches of juvenile salmon during the juvenile salmon study in Barkley Sound by sampling period, species, source, and gear.

	Coho				Chinook				Chum		Sockeye	
Sampling	**Wild**	**Hatchery**	**Wild**	**Hatchery**	**Wild**	**Hatchery**	**Wild**	**Hatchery**	**Wild**		**Wild**	
Period	**Beachseine**		**Purse seine**		**Beachseine**		**Purse seine**		**Beachseine**	**Purse seine**	**Beachseine**	**Purse seine**
	2000											
May 15-16	23	0	76	0	116	0	24	0	13	2927	0	3524
May 29-30	13	0	111	196	63	2	8	25	0	2306	2	1463
Jun 13-14	4	0	58	27	23	12	279	3386	0	1572	4	1221
July 5-6	0	0	8	3	11	4	526	1905	0	12	1	325
July 26-27	0	0	7	2	1	0	253	723	0	76	0	117
	2001											
May 14-15	4	0	52	0	1	0	1	0	23	10999	4	2087
May 29-30	8	2	584	1529	2	1	6	27	7	7187	0	3101
Jun 12-13	4	0	89	166	4	8	79	1659	0	2493	0	2047
29-Jun	0	0	21	27	1	0	66	1216	0	5	0	133
July 24-25	0	0	3	1	1	2	94	412	0	14	0	159
August 28-29	0	0	0	0	1	0	48	36	0	0	0	1

late August, showed that chinook occurred until at least August, and that hatchery fish moved more rapidly through the study area.

Community Composition Variability

Community composition varied as a result of migration of fish through Barkley Sound. Catches by species, sampling gear and survey are presented in Table **3** and the results of the Poisson regression analyses are summarized in Table **4**. The statistically significant effects of species/source was a consequence of high sockeye and chum abundance in mid-May and early June, and the subsequent progressive increase in relative abundance of hatchery and wild chinook juveniles. There were three instances of a significant interaction effect of species/source and area. The first was in mid-June 2000 and was due to higher catches of sockeye and hatchery chinook in Alberni Inlet. The second took place in mid-May 2001 and the third occurred in mid-June 2001 but the Chi-square probabilities did not disclose the reason for the significant effect.

Correlations with Respect to Species, Source, Location and Time and Dispersal

Results of Kendall correlation analyses showed significant correlations for catch in three of 128 tests; these were for hatchery and wild coho during the May 29-30, 2001 survey, hatchery chinook and wild coho for the June 12-13, 2001 survey, and for hatchery and wild chinook during the July 24-25, 2001 survey.

We found that, in most instances, dispersal patterns based on purse seine catches were contagious (Table **5**). The non-contagious, ie. random, disperals occurred mostly when fish were entering the ocean.

Diet

Preferred prey differed among species and occurrences of overlap were infrequent (Table **6**). *T. spinifera* contributed the most energy to the wild and hatchery coho diets, and both groups selected that euphausiid. Chinook diet was more varied and there was no prey item that accounted consistently for a considerable amount of ingested energy. *Calanus marshallae* appeared to be the most important prey for juvenile chum. Sockeye juveniles selected *T. spinifera* strongly in mid-May and these prey accounted for about 0.75 of the ingested energy then. *C. marshallae* were selected strongly in late May when this prey accounted for about 0.50 of the ingested energy.

There were 10 instances of diet overlap which we considered to be biologically significant, that is, where the prey item accounted for at least 0.25 of the ingested energy for each predator. Five instances of overlap were for wild and hatchery coho consuming *T. spinifera* or gammarid amphipods, 4 instances were for wild and hatchery chinook consuming *T. spinifera*, juvenile calanoids, mysids or porcellanid crabs, and one instance of overlap were between chum and sockeye feeding on *C. marshallae*. Wild and hatchery coho ate the same size of *T. spinifera* (>19 mm). Wild and hatchery chinook fed on the same size of *T. spinifera*

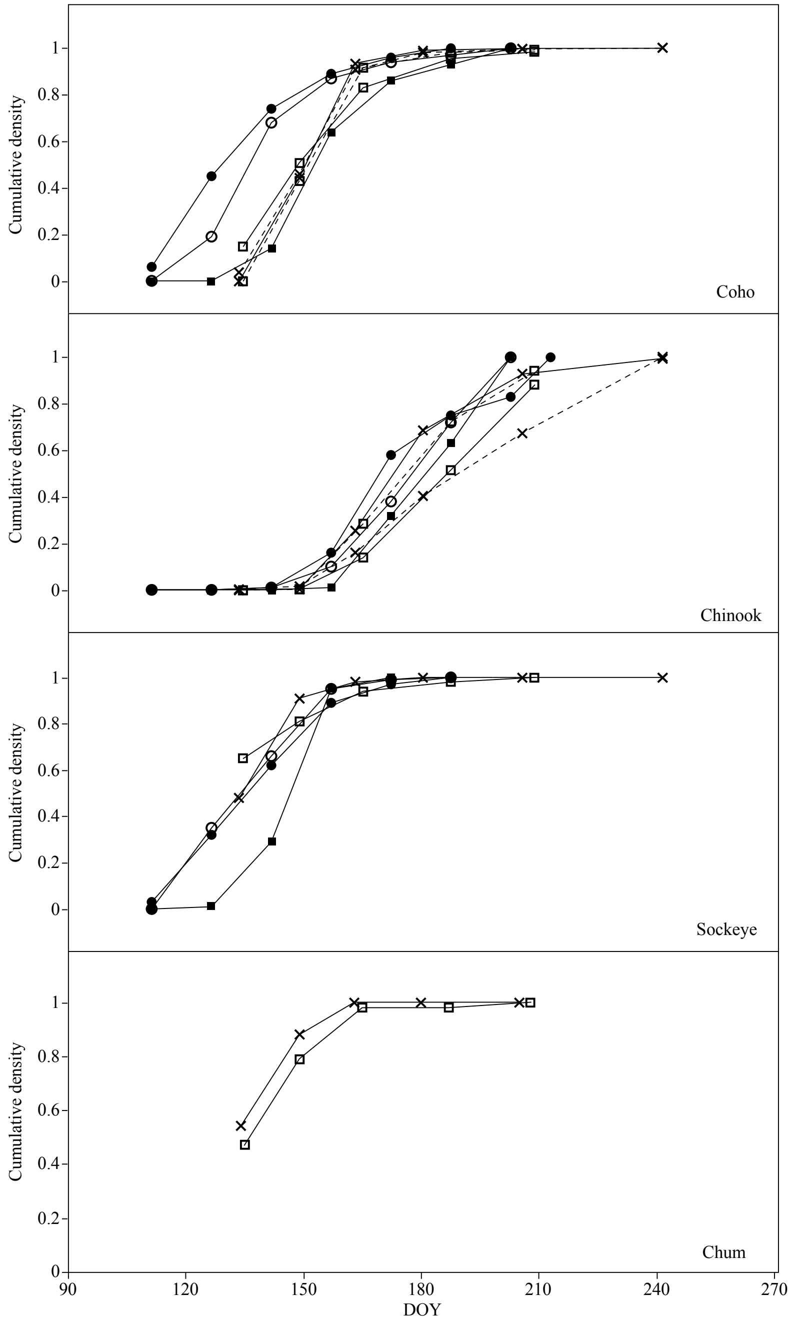

Fig (2). Cumulative probability of juvenile salmon catch. Closed circle, solid line – 1987; open circle, solid line – 1988; closed square, solid line – 1989; open square, solid line – wild, 2000; open square, dashed line – hatchery, 2000; x, solid line – wild, 2001; x, dashed line – hatchery, 2001. DOY – day of the year.

(>23 mm), juvenile calanoids (~3 mm), mysids (2-14 mm) and porcellanid crabs (2-5 mm). Chum fed on smaller *C. marshallae* (2-4 mm) than sockeye did (3-5 mm). Wild and hatchery coho, and sockeye and chum all consumed *T. spinifera* in mid-June 2001; however chum and sockeye ate much smaller euphausiids than coho did.

DISCUSSION

Our results showed that juvenile salmon partition Barkley Sound with respect to space (null hypothesis accepted) and time (null hypothesis accepted) and diet (null hypothesis rejected for coho). We rejected the null hypothesis for wild and hatchery coho because *T. spinifera* persisted as an important prey item. In contrast, we accepted the null hypothesis for wild and hatchery chinook because they did not select specific prey items consistently even though those prey were available most of the time. It is interesting to speculate why partitioning should occur. With respect to space, Tanasichuk [26] found that there was no effect of sampling location in Barkley Sound on the size-specific abundance of *T. spinifera* adults (>9 mm) and this implies that there should be no effect of location on the availability of prey, at least euphausiids, for juvenile sockeye and coho. There appears to be no

Table 4. ***p*-values for Poisson regressions calculated to test for the effects of species, source and sampling gear on the catches of juvenile salmon in Barkley Sound.**

	p				
Sampling period	**Model fit**	**Area**	**Gear**	**Species/Source**	**Area*Source**
	2000				
May 15-16	4.4 e-19	1.00	0.13	2.0 e-5	1.00
May 29-30	6.1 e-12	0.92	0.12	5.9 e-7	0.66
June 13-14	1.8 e-36	0.54	0.20	9.5 e-13	1.8 e-4
July 5-6	3.9 e-59	0.89	0.32	1.2 e-40	0.14
July 26-27	6.3 e-44	1.00	0.94	2.2 e-25	0.30
	2001				
May 14-15	6.2 e-41	1.00	0.82	3.1 e-3	0.03
May 29-30	1.1 e-22	0.98	0.82	4.5 e-8	0.23
June 12-13	1.4 e-22	0.06	0.98	1.3 e-5	0.04
June 29	8.3 e-51	0.95	0.70	1.1 e-15	0.46
July 24-25	6.9 e-31	1.00	0.59	4.7 e-15	0.24
August 28-29	2.1 e-31	1.00	0.17	2.5 e-10	0.18

Table 5. **Conclusions of regressions calculated to test Taylor indices of dispersal for juvenile salmon purse seined in Barkley Sound. . – no fish caught; ns – not statistically significant.**

Sampling	**Wild**				**Hatchery**	
period	**Coho**	**Chinook**	**Chum**	**Sockeye**	**Coho**	**Chinook**
	2000					
May 15-16	ns	Contagious	.	Random	.	.
May 29-30	ns	Contagious	Random	ns	ns	ns
June 13-14	ns	Contagious	Contagious	Contagious	Contagious	ns
July 5-6	ns	ns	Random	ns	Contagious	Contagious
July 26-27	ns	Contagious	Contagious	ns	Random	Contagious
	2001					
May 14-15	ns	ns	Contagious	Random	.	.
May 29-30	Contagious	Contagious	Contagious	Contagious	Contagious	Contagious
Jun 12-13	Contagious	Contagious	Contagious	Contagious	Contagious	Contagious
June 29	Contagious	Contagious	ns	ns	Contagious	Contagious
July 24-25	ns	ns	Contagious	Contagious	ns	ns
August 28-29	.	Contagious	.	ns	.	Contagious

strategy in place to avoid predators by occupying nearshore habitat because there was no effect of gear on catch. With respect to time, migration timing does appear to be related to the seasonality of *T. spinifera* productivity because peak migration of sockeye and coho occurs when it is most likely that the size range of euphausiid they prefer (see below) dominates the euphausiid community. Therefore, partitioning the early marine environment with respect to time is coincidental. With respect to diet, Tanasichuk [26] presents a series of length-frequency histograms which show that adult abundance of *T. spinifera* is determined at the size of sexual maturity which does not coincide with the length of

Table 6. **Diet and selectivity of juvenile salmon collected in Barkley Sound. Data are for dominant prey for which the summation meets or just exceeded 0.90 of the total PDE. PDE – prop. total diet energy accounted for by a prey item. L – linear food selection index.**

Prey item	Coho				Chinook				Chum		Sockeye	
	Wild		Hatchery		Wild		Hatchery		Wild		Wild	
	PDE	L	PDE	L	PDE	L	PDE	L	PDE	L	PDE	L
	May 15-16, 2000											
Calanus marshallae									0.59	0.59	0.10	-0.08
Thysanoessa spinifera									0.19	0.01	0.72	0.71
Oikopleura									0.11	0.11	0.05	0.05
Centropages abdominalis									0.03	0.03	0.07	0.07
	May 29-30, 2000											
Gammarid amphipods	0.37	0.37	0.25	0.37								
Thysanoessa spinifera	0.33	0.31	0.46	0.33								
Hyperid amphipods	0.18	0.18	0.07	0.18					0.03	0.03		
Parathemisto	0.04	0.04										
Euphausia pacifica			0.19	0.02								
Pinnotherid crabs			0.02	0.01								
Calanus marshallae									0.54	0.49	0.55	0.50
Calanus pacificus									0.14	0.14	0.23	0.23
Decapod larvae									0.10	0.10	0.06	0.06
Centropages abdominalis									0.07	0.07	0.04	0.04
Eucalanus bungii											0.03	0.02
	June 13-14, 2000											
Thysanoessa spinifera	0.42	0.42	0.91	0.90								
Pinnotherid crabs	0.37	0.37										
Porcellanid crabs	0.17	0.17			0.22	0.22	0.42	0.42	0.09	0.09	0.05	0.05
Calanus marshallae					0.41	0.38	0.23	0.20	0.16	0.13	0.07	0.04
Calanoid juveniles					0.14	0.10						
Epilabidocera longipedata					0.08	0.08						
Euphausia pacifica							0.15	0.06				
Parathemisto							0.14	0.14				
Barnacle									0.20	0.20	0.37	0.37
Oikopleura									0.16	0.16	0.08	0.08
Podon									0.16	0.13	0.17	0.17
Calanus pacificus					0.05	0.05			0.11	0.11		
Eucalanus bungii									0.07	0.07		
Evadne											0.17	0.17
	July 5-6, 2000											
Thysanoessa spinifera					0.60	0.42	0.83	0.66				
Hyperid amphipods					0.20	0.20						

(Table 6) contd….

Prey item	Coho				Chinook				Chum		Sockeye	
	Wild		Hatchery		Wild		Hatchery		Wild		Wild	
	PDE	L	PDE	L	PDE	L	PDE	L	PDE	L	PDE	L
Porcellanid crabs					0.12	0.12	0.10	0.10				
	July 26-27, 2000											
Calanoid juveniles					0.59	0.57	0.28	0.26				
Porcellanid crabs					0.16	0.16	0.43	0.43				
Epilabidocera longipedata					0.11	0.11	0.12	0.12				
Calanus marshallae					0.08	0.07	0.05	0.05				
Hyperid							0.06	0.06				
	May 14-15, 2001											
Calanus marshallae									0.43	0.42	0.17	0.26
Evadne									0.22	0.22		
Podon									0.04	0.04		
Hyperid amphipods									0.04	0.04		
Gammarid amphipods									0.03	0.02		
Porcellanid crabs									0.03	0.02		
Barnacle									0.01	0.01		
Centropages abdominalis									0.00	0.00		
Oikopleura									0.00	0.00		
Mysid									0.00	0.00		
Thysanoessa spinifera											0.76	0.46
	May 29-30, 2001											
Thysanoessa spinifera	0.75	0.52	0.88	0.65					0.37	0.14		
Euphausia pacifica	0.25	-0.08	0.11	-0.22					0.26	-0.07		
Oikopleura									0.11	0.10	0.05	0.05
Calanus marshallae									0.09	0.09	0.43	0.43
Evadne									0.09	0.08	0.24	0.23
Metridia pacifica											0.10	0.10
Barnacle											0.05	0.04
Calanus pacificus											0.05	0.05
	June 12-13, 2001											
Thysanoessa spinifera	0.89	0.56	0.94	0.56					0.44	0.11	0.38	0.05
Euphausia pacifica	0.09	0.06							0.10	0.07	0.03	0.00
Mysid					0.94	0.94	0.67	0.67				
Pinnotherid crabs							0.13	0.13				
Calanus marshallae							0.09	0.08	0.17	0.16	0.30	0.30
Metridia pacifica									0.07	0.07	0.12	0.12
Barnacle									0.05	0.05	0.04	0.03
Hyperid amphipods											0.05	0.05

(Table 6) contd….

Prey item	Coho				Chinook				Chum		Sockeye	
	Wild		Hatchery		Wild		Hatchery		Wild		Wild	
	PDE	L	PDE	L	PDE	L	PDE	L	PDE	L	PDE	L
Oikopleura									0.04	0.04		
Centropages abdominalis									0.03	0.02		
Calanus pacificus							0.02	0.02				
	June 29, 2001											
Euphausia pacifica	0.85	0.36	0.35	-0.14								
Thysanoessa spinifera	0.15	0.13	0.29	0.26			0.34	0.32				
Hyperid amphipods			0.26	0.26	0.70	0.70	0.07	0.07				
Mysid			0.11	0.11			0.24	0.24				
Calanus marshallae					0.19	0.19	0.16	0.16				
Calanus pacificus						0.05	0.05					
Porcellanid crabs							0.13	0.13				
	July 24-25, 2001											
Porcellanid crabs					0.83	0.83	0.49	0.49				
Gammarid amphipods					0.16	0.16	0.28	0.28				
Mysid							0.21	0.21				

euphausiid consumed by fish species for which euphausiid prey size has been measured (Tanasichuk [32], Tanasichuk [33], Tanasichuk and Routledge [6]), and there is no detectable abrupt change in the length-frequency distribution of *T. spinifera* which would reflect top-down control of euphausiid production, and the possibility of competition among wild and hatchery coho. Therefore, *T. spinifera* prey availability appears to be determined by bottom-up effects so predator-specific size selectivity is irrelevant. There are no other instances in our data of consistent diet overlap which could explain partitioning as a consequence of prey availability. Studies describing diet overlap in juvenile salmon in coastal areas present results ranging from no overlap (e.g. Kaczynski *et al.* [34], Bollens *et al.* [35]) through overlap with the potential for effects on production (e.g. Brodeur and Pearcy [36]) to strong overlap (e.g. Healey [37]). Emmett *et al.* [38] noted that overlap may reflect food availability, and not signal competition. Pearcy *et al.* [39] and Welch and Parsons [40] found that food was partitioned among salmon feeding in oceanic areas. We offer no explanation for the partitioning of the early marine environment in Alberni Inlet/Barkley Sound.

Healey [41] suggested that juvenile salmon in the Strait of Georgia partition it in terms of feeding, location and time. Secondary prey items differed among species when dominant prey was the same, and these dominant prey were ingested in different proportions. For example, harpacticoid copepods and shrimp larvae were dominant food of chum throughout their estuarine residence while chinook fed on harpacticoids only for a few days after migrating downstream and then concentrated on amphipods, insect larvae and adults, and mysids. Healey stated that diet differences occurred while the young fish lived together, often in mixed schools and presumably presented with the same range of foods. He suggested that such differences are a mechanism to reduce competition. Kaczynski *et al.* [34] reported behavioural differences in prey selection between juvenile pink and chum that they thought could be an example of a strategy to minimise competition. Healey [41] describes differing migration timing for juvenile sockeye, chum, chinook, coho and pink salmon in the Strait of Georgia. Orsi *et al.*'s [42] data show a partitioning of early marine habitat among juvenile pink, chum, sockeye, coho and chinook in southeastern Alaska. These authors described how fish move between inshore, strait and coastal marine habitats in relationship to zooplankton settled volume (ZSV). Pink and chum appeared abruptly in strait habitat in June, when the ZSV is maximal in inshore and strait habitat, and essentially were absent as of August. Sockeye appear in June as well and occur in strait habitat over June and July, and also in the coastal marine habitat in July as ZSV in inshore and Strait habitats decline to the coastal marine habitat levels. Concentrations of coho persisted in inshore and strait habitats in June and July, and fish occur in all three habitats in August, and in strait and coastal marine habitats in September-October. Chinook were collected almost exclusively in nearshore habitats and, unlike the other species, catch was maximal in July. Dawley *et al.* [8] found that chinook and coho migrated through the Columbia River estuary at consistent times over years which differed between species; however, it is unknown how much of this can be attributed to natural migration timing and how much to the timing of release from the hatcheries.

The results of our study show that coho, chinook, sockeye and chum migrate throughout Alberni Inlet/Barkley

Sound at consistent species-specific times. We speculate that the differences in prey selectivity and migration timing are a consequence of fish maintaining their freshwater feeding strategy, with respect to prey size and behaviour, to minimise the physiological/energetic challenge of moving into the ocean. This would only be true for sockeye and coho which feed selectively, so the basis for migration timing for chinook and chum is a mystery. Sheridan (1962, cited in Orsi *et al.* [42]) suggested that migration timing of pink salmon is based on encountering optimal temperature, salinity and food availability in the ocean.

A review of the literature shows instances when juvenile salmon co-occur or segregate but these results have to be interpreted carefully. In general, there are three analytical weakness: 1) Bonferroni-adjusted probabilities, which would minimise the possibility of committing a Type I error, are not used, 2) the measure of central tendency commonly used is mean CPUE without testing if CPUE is normally, log-normally, or not normally distributed and, 3) parametric correlations are tested without considering data distribution. Healey [41] reported that chinook and coho in the Strait of Georgia segregated. Unfortunately, Healey did not test the statistical significance of his observations. Tanasichuk *et al.* [43] presented the results of purse seine surveys done in the Strait of Georgia in 1972-74. They used Bonferroni-adjusted probabilities and found that CPUE correlations varied over time and that the only significant correlation with respect to chinook and coho was a negative correlation in September-October between wild chinook and hatchery coho. Godfrey [44] provided catch information from purse seine sets made in bays and inlets in the Strait of Georgia during June 1965. Results of our correlation analyses of their data, using Bonferroni-adjusted probabilites, showed that juvenile chinook, coho and chum co-occurred in the southwest and northern Strait of Georgia but not in the vicinity of the Fraser River. We analysed the July-August purse seine catch data for juvenile chinook, coho, chum, sockeye and pink salmon provided in Beamish *et al.* [10] and found that only pink and chum salmon distributions were related ($\tau=0.57$, $p<0.0001$).

We found that the composition of the juvenile salmon community changed, and that these changes did not necessarily reflect migration timing because of relative abundances. Sockeye and chum dominated the community until mid-June, even though most of these fish had migrated through the study area by the end of May. Hatchery chinook dominated subsequently even though chinook migration peaked in July. However, these changes in composition are likely irrelevant to species-specific productivity because there are no interactions with respect to space and diet. Barraclough and Phillips [45] reported that the relative abundances of juvenile chinook and coho in the southern Strait of Georgia were always low, and it is highly likely that this was a consequence of different migration patterns among the different salmon species.

Juvenile salmon in Alberni Inlet/Barkley Sound aggregate, and dispersal patterns vary between loose (random distribution) and tight (contagious distribution); in most instances fish were dispersed contagiously. Jaenicke and Celewycz [46] used Morista's Index of Dispersion and found that juvenile pink, chum, coho and sockeye were highly aggregated in southeast Alaska and northern British Columbia. They contrasted their results with those of Hartt and Dell [47] who concluded that juvenile salmon were distributed evenly. Janeicke and Celewycz [46] attributed the difference in results to them using a smaller seine and their seining duration being considerably shorter which collectively provided more of a “point estimate”. In contrast, Pearcy and Fisher [48] reported that chinook and coho were evenly dispersed on the continental shelf off Oregon and Washington, and Miller *et al.* [49] reported similar results for the Oregon coast over the summer of 1980. Dawley *et al.* [8] found that subyearling chinook purse seined within 24 km of the mouth of the Columbia River were aggregated and occurred in waters less than 4 m deep. Moulton [50]'s observations of juvenile salmon distributions in Cook Inlet, Alaska, suggested that fish were dispersed randomly.

We found that juvenile coho and sockeye fed selectively whereas chinook and chum did not. Thus, contrary to Brodeur and Pearcy [36], and in agreement with Schabetsberger *et al.* [11], coho and sockeye select a specific size range of a prey species. The observation of selective feeding suggests the possibility of match-mismatch scenario [51], as suggested by Peterson [52] and such appears to be the case for sockeye [6]. Brodeur and Pearcy [36] contemplated whether salmon would switch to alternate prey when preferred prey are scarce. Tanasichuk and Routledge's results [6] suggested that, for Barkley Sound sockeye at least, the predators did not switch to alternate prey when even another species of euphausiid (*Euphausia pacifica*) was readily available (R. Tanasichuk, *unpubl. res.*). The selective feeding by coho and sockeye also creates a partitioning of food resources in two ways, first between coho and sockeye because they feed on different sizes of *T. spinifera*, and second, among all species because coho and sockeye select prey that are not important for chinook and chum. It is especially interesting that the selectivity or lack of it is consistent with the results of analyses which have explored the biological basis of sockeye, coho, chinook, and chum return variability on the West Coast of Vancouver Island. Tanasichuk and Routledge [6] reported that return variability of sockeye was determined by prey (3-5 mm *T. spinifera*) availability when the fish are migrating through Barkley Sound. A preliminary analysis of return variability for wild coho from Carnation Creek, in Barkley Sound, indicates that spawning escapement, stream discharge when eggs are incubating, and the biomass of *T. spinifera* selected for, influence return. Preliminary analyses of hatchery chinook and chum returns indicate no effect of prey variability. Finally, the apparent feeding strategies that coho and sockeye use reflect optimal foraging [53] but there appear to be no selective feeding strategies employed by chinook and chum. Sockeye and coho return variability is affected by food, and the timing and nature of migration appear to reflect the availability of the size of *T. spinifera* preferred by each species. Table **7** gives the proportion of instances when the peak of the biomass of the sizes of *T. spinifera* that sockeye and coho selected for occurs in a given month. Sockeye migrate rapidly in May when there is the highest probability (0.41) that they will encounter the peak of 3-5 mm *T. spinifera*. In contrast, coho migration is more protracted and may reflect the probability that the peak of *T. spinifera* biomass that they prefer is likely to occur between May and August. By migrating earlier (May-June) coho maximise the likelihood of

Table 7. Month-specific probability of the occurrence of peak biomass of preferred euphausiid prey for juvenile sockey and coho in Barkley Sound, 1991-2012.

Species	Prop. of Occurrences of Peak *T. spinifera* Biomass							
	March	April	May	June	July	August	September	October
Sockeye	0.00	0.00	0.41	0.29	0.12	0.12	0.06	0.00
Coho	0.06	0.12	0.18	0.18	0.18	0.18	0.12	0.06

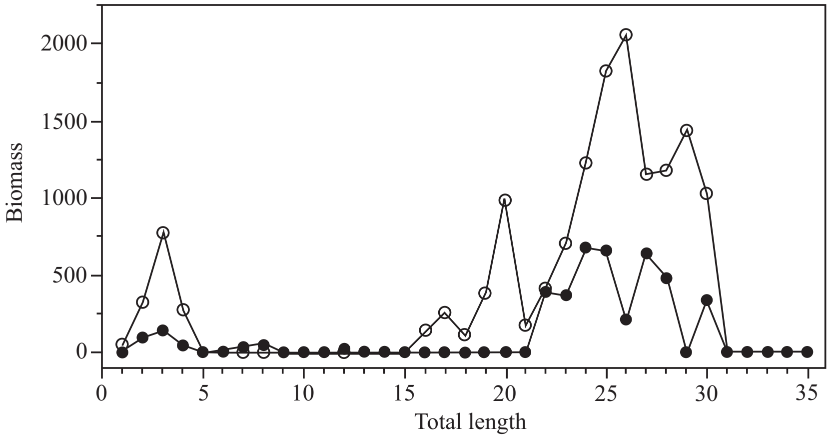

Fig (3). Distribution of *T. spinifera* biomass by length for May 2000 (open circles) and 2001 (filled circles).

encountering the peak. Chinook and chum migrate consistently at specific times. We cannot suggest that this is related to prey availability. These species do not feed as selectively as coho and sockeye do so there is no apparent reason to time migration with respect to prey availability.

The selection of specific sizes of *T. spinifera* by juvenile sockeye and coho in the ocean reflects the concentration of size-specific biomass in the prey population but not the size of prey predicted by Keeley and Grant [54]. Fig. (**3**) shows length-specific biomass (mg dry mass•m^{-2}) from the Barkley Sound euphausiid/zooplankton monitoring programme for May 2000 and 2001; biomass peaks coincided with the size range of *T. spinifera* selected by sockeye and coho respectively. Keeley and Grant [54] found the that size of invertebrates eaten by salmonids in lakes and the ocean could be described by a common regression equation, log10 prey length (mm)=0.35•log10 fork length (cm)-0.12. The mean length of sockeye in May was 8.9 cm which corresponds to a predicted prey length of 1.6 mm. The equation Keely and Grant provide for stream fish feeding on invertebrates, which should apply to migrant coho, is: log10 prey length (mm)=0.85•log10 predator length (cm) – 0.23•log10 predator length^2 (cm)+0.033. The mean length of coho was 11.5 cm which predicts a prey length of 4.7 mm. We note that none of the references used to estimate the relationship between prey and predator sizes for sockeye and coho described prey and predator size during the earlier marine life history. Another explanation for the discrepancy between preferred prey lengths and the prey lengths that Keeley and Grant would have predicted for Barkley Sound sockeye and coho is that Keeley and Grant's analysis did not consider selectivity. We developed length-frequency distributions of prey in sockeye and coho in mid-May. Prey length was lognormally distributed and the back-transformed geometric mean prey length was 1.4 and 6.0 mm for sockeye and coho, which is similar to what Keeley and Grant's equations predicted. However, our results show that sockeye and coho are highly selective for prey (*T. spinifera*) which has the highest energy density (see Foy and Norcross [28]) and occur in biomass peaks of recruiting euphausiids from the current year's production in the case of sockeye, and biomass peaks of adult euphausiids from the previous year's production, as in the case of coho. Therefore, we are concerned that Keeley and Grant's analysis may not be describing salmonid prey selection realistically. Finally, it is possible that the length-specific distribution of prey biomass explains Feller and Kaczynski's observation [55] that juvenile chum selected smaller harpacticoid copepods in Puget Sound.

We found that there were no hatchery/wild fish interactions with respect to distribution, and that hatchery and wild coho selected the same prey, but with no apparent consequences for wild fish production. The numbers of smolts released from the Robertson Creek Hatchery, or migrating out from Carnation Creek, in 2000 and 2001 averaged 1,000,000 and 3,000 respectively. The preliminary analysis of Carnation Creek coho return variability showed that there was no effect of hatchery smolt production on return. Analyses of impacts of hatchery production on wild fish generally focus on situations where hatchery fish are introduced into streams (eg. [23]), and it is unclear if consequences are a function of the origin of the introduced fish, or simply the carrying capacity of the recipient watercourses [56].

CONCLUSIONS

Our results showed that hatchery and wild juvenile salmon partition the early marine habitat in Barkley Sound.

Outmigration timing is species-specific and conservative. The migration timing of coho and sockeye, for which marine prey influences return, coincides with the peaks in biomass of the fraction of euphausiid production that these fish select. There appears to be no biological consequence of diet overlap between hatchery and wild coho with respect to wild coho return variability. Finally, information on the early nearshore marine biology of juvenile salmon in Alberni Inlet/Barkley Sound has contributed to learning about the biological basis of salmon return variability there.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflicts of interest.

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