

Spatial and trophic overlap of marked and unmarked Columbia River Basin spring Chinook salmon during early marine residence with implications for competition between hatchery and naturally produced fish

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Received: 2 August 2010 / Accepted: 12 May 2011 / Published online: 4 June 2011
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Abstract Ecological interactions between natural and hatchery juvenile salmon during their early marine residence, a time of high mortality, have received little attention. These interactions may negatively influence survival and hamper the ability of natural populations to recover. We examined the spatial distributions and size differences of both marked (hatchery) and unmarked (a high proportion of which are natural) juvenile Chinook salmon in the coastal waters of Oregon and Washington from May to June 1999–2009. We also explored potential trophic interactions and growth differences

between unmarked and marked salmon. Overlap in spatial distribution between these groups was high, although catches of unmarked fish were low compared to those of marked hatchery salmon. Peak catches of hatchery fish occurred in May, while a prolonged migration of small unmarked salmon entered our study area toward the end of June. Hatchery salmon were consistently longer than unmarked Chinook salmon especially by June, but unmarked salmon had significantly greater body condition (based on length-weight residuals) for over half of the May sampling efforts. Both unmarked and marked fish ate similar types and amounts of prey for small (station) and large (month, year) scale comparisons, and feeding intensity and growth were not significantly different between the two groups. There were synchronous interannual fluctuations in catch, length, body condition, feeding intensity, and growth between unmarked and hatchery fish, suggesting that both groups were responding similarly to ocean conditions.

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Keywords Columbia River Basin · Marine · Juvenile Chinook salmon · Spatial · Trophic · Competition · Hatchery · Wild

Introduction

Pacific salmon (*Oncorhynchus* spp.) have long been important to the economy, society, and culture of the

Pacific Northwest region of the United States. However, throughout this region, many populations of Pacific salmon have declined to critically low levels of abundance (Nehlsen et al. 1991). In particular, the abundance of fish spawning in the Columbia River Basin, which was once the source of some of the largest salmon runs in the Pacific Northwest (Chapman 1986), has declined to a fraction of their historical levels. Each year millions of hatchery spring (the designation “spring” is based on timing of the adult return) Chinook salmon (*O. tshawytscha*) are released into the Columbia River Basin. Yet, significant declines in the abundance of natural spring Chinook salmon have led to the listing of four reproductively isolated groups, or evolutionarily significant units (ESUs) in the Columbia River Basin as “endangered” or “threatened” under the US Endangered Species Act (NMFS 2009). Overharvest, habitat degradation, dams, and hatchery production have been considered the primary factors responsible for steep declines in naturally spawning populations (Ruckelshaus et al. 2002).

Managers have utilized hatchery produced fish in order to help mitigate for habitats losses and overfishing, to provide a consistent supply of fish for recreational and commercial uses, and to help restore and enhance salmon populations (Lichatowich 2001; Levin and Williams 2002; Naish et al. 2007). The use of hatchery produced fish has been controversial however, as there is evidence that suggests that hatchery fish have had detrimental effects on wild populations (Fresh 1997; Quinn 2005; Naish et al. 2007; Kostow 2009). Major concerns with the supplementation of hatchery fish include loss of genetic integrity, overharvest, disease transmittal, and ecological interactions such as competition and predation (National Research Council 1996). Much of the focus of ecological interactions between hatchery and wild salmon has been in freshwater (Fresh 1997; Naish et al. 2007) and considerably less is known about competition and predation between hatchery and wild fish during marine life (Fresh 1997). Marine life is now known to be an important period in the life history of Pacific salmon (Pearcy 1992; Beamish and Mahnken 2001; Quinn 2005). Most of the total marine mortality is thought to occur during the first summer following ocean entry of juvenile salmon (Pearcy 1992), and variable ocean conditions during this period can result in large variations in the number

and size of adult salmon returning each year (Pearcy 1992; Scheuerell and Williams 2005).

The purpose of our study was to assess spatial, temporal, and dietary overlap during early marine life between hatchery and naturally produced spring run Chinook salmon originating from the Columbia River Basin in order to assess the potential for competition between these two types of fish. We also examined the two groups of salmon for differences in fish size, condition, and growth. From this information we then considered implications for competition. Although not a formal test of competition, the challenges of working on the ocean necessitate this or some other type of indirect approach such as looking at scale patterns (Ruggerone et al. 2003, 2005). Our assumption was that high overlap would indicate an increased potential for resource competition, especially under variable or less productive ocean conditions, and this may be reflected in differences in the size, feeding intensity and/or growth between hatchery and unmarked fish. Specific objectives of our study were to ask the following questions: 1) What is the extent of spatial overlap in ocean distribution between unmarked and hatchery Chinook salmon juveniles? 2) Are the physical characteristics (fork length and a length-weight residual index), trophic habits and growth rates of unmarked and hatchery fish similar during their first several months at sea? 3) Are there shifts in relative abundance or biological characteristics of unmarked and hatchery fish on an interannual basis?

Methods

Juvenile Chinook salmon were collected during NOAA Fisheries pelagic trawl surveys for juvenile salmonids off Washington and Oregon from 1999 through 2009. These surveys typically occurred over a 3–10 day period during both late May and late June each year. The survey area consists of 3–9 transects that extend from inshore to near the coastal shelf break, each with 5–7 predetermined sampling stations. Surveys during May of 2000 through 2005 included only three transects: one just off the Columbia River and one north and south of the river (Fig. 1). All other May and June sampling effort included 8 to 9 transects north and south of the Columbia River.

Juvenile salmon were collected using a Nordic 264 pelagic rope trawl, which has a mouth opening 30 m wide by 20 m deep, fitted with a 0.8-cm cod-end liner. The rope trawl was towed at the surface during daylight for 30 min at approximately 6 km·h⁻¹ (Brodeur et al. 2005). All captured salmon were identified to species, measured (fork length to the

nearest 1 mm), checked for adipose fin clips, individually labeled, and immediately frozen. Juvenile Chinook salmon (maximum 25 individuals per haul) were bled at sea to determine insulin like growth factor 1 (IGF-1) levels, an indicator of instantaneous growth rates which has been validated as a growth index for juvenile salmon (Beckman et al. 2004a, b).

(a)

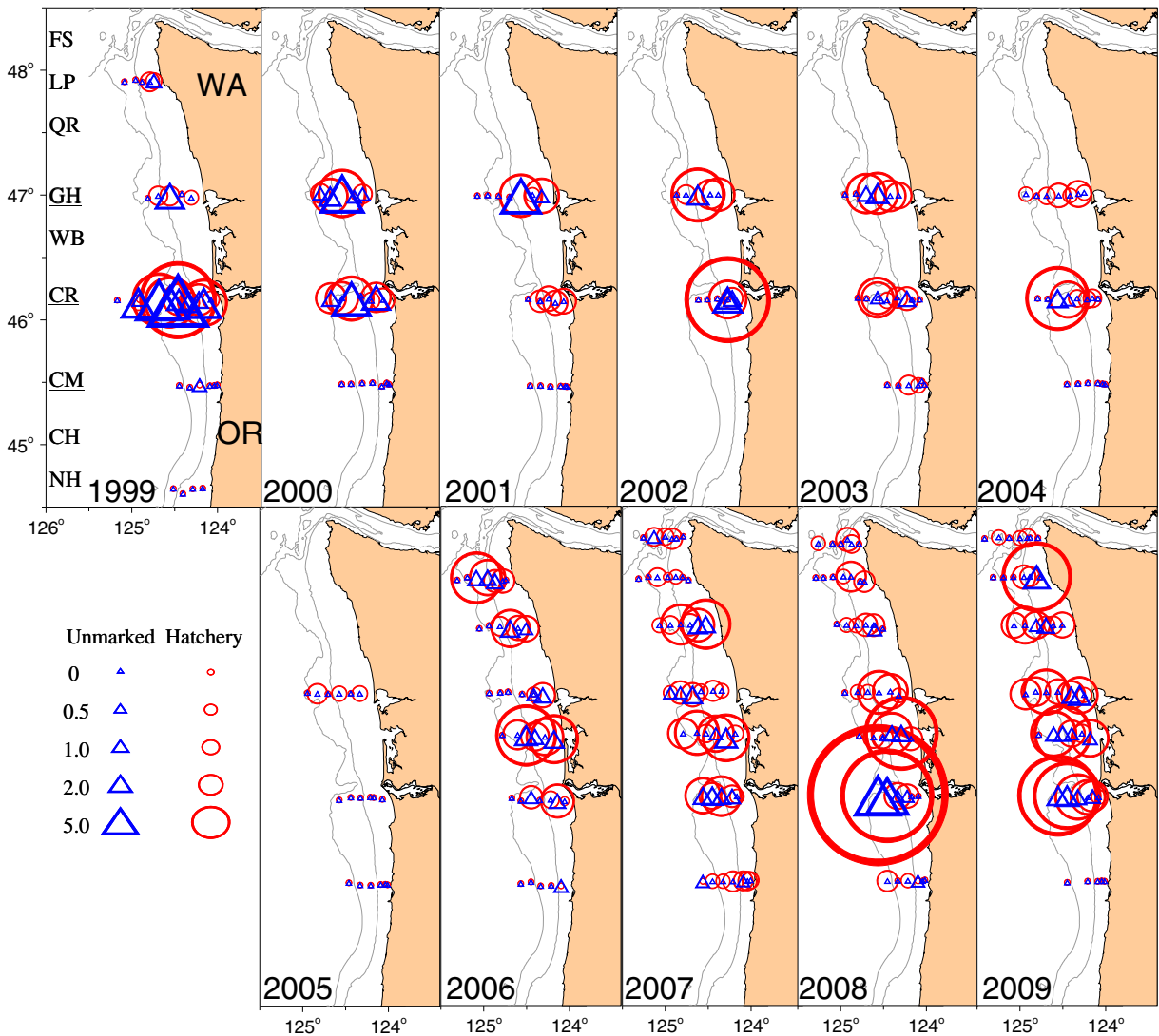


Fig. 1 Sampled station catch per unit effort (CPUE) in number per km towed of unmarked (*triangles*) and hatchery (*circles*) juvenile Columbia River basin spring Chinook salmon caught in May (a) and June (b). Area of the symbols vary continuously and are directly proportional to CPUE with minimum catches of zero to maximum catches of 10.9 unmarked fish per km towed (May 1999), and 60.2 hatchery fish per km towed (May

2008). Transect names are abbreviated and are defined as follows: FS=Father and Son; LP=LaPush; QR=Queets River; GH=Grays Harbor; WB=Willapa Bay; CR=Columbia River; CM=Cape Meares; CH=Cascade Head; and NH=Newport hydrographic line. Underlined transects in leftmost panels represent the most consistently sampled areas

(b)

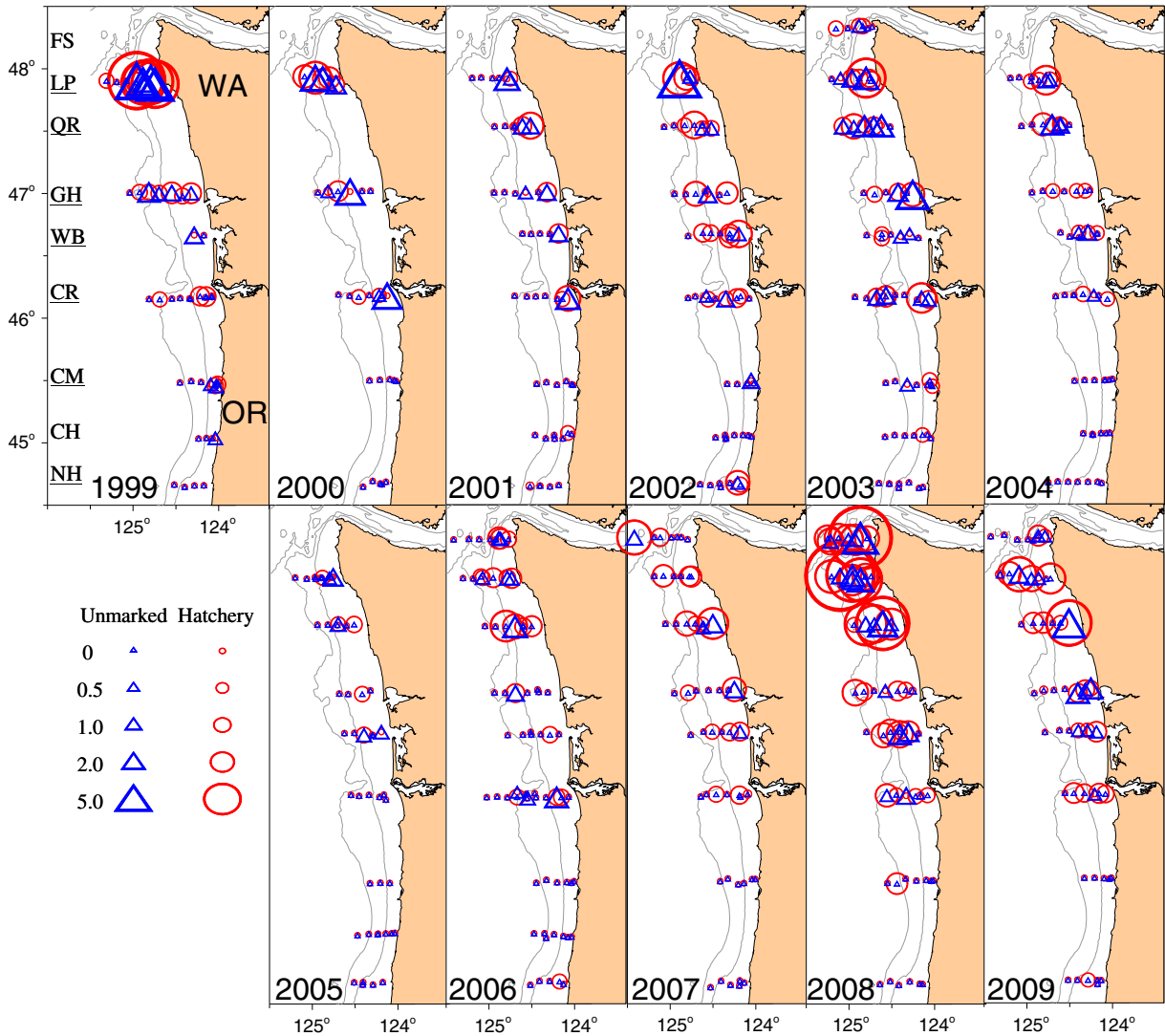


Fig. 1 (continued)

Blood was drawn from dead fish with a heparinized syringe within 45 min of the trawl coming on board; samples were kept on ice (up to 4 h) and then centrifuged at $3000\times G$. Plasma was removed from the centrifuged samples and frozen on board the ship (at -30°C), then transferred on dry ice to the NOAA NWFS laboratory in Seattle. Samples were then stored in a -80°C freezer until they were assayed by radioimmuno assay according to the methods of Shimizu et al. (2000).

In the laboratory, field identifications of salmon were verified, and each salmon was remeasured and

weighed, and checked for various markings (clipped adipose fin, coded-wire (CWT), passive integrated transponder (PIT), and/or latex tag). Salmon were considered unmarked if they were free from any of the previously listed markings and were considered of hatchery origin if any marks were present. In addition, samples of fin tissue were taken for genetic analysis and stored in 100% ethanol. Finally, stomachs were removed and placed in a 10% formaldehyde solution for approximately 2 weeks, then rinsed with fresh water for 24 h before being transferred into 70% ethanol.

Chinook salmon collected during our marine surveys were from numerous stock groups, and for our analysis, we first needed to identify spring-run fish originating from the Columbia River Basin. This was accomplished by genotyping the sampled fish. Specifically, Chinook salmon were genotyped for 13 microsatellite loci that have been recently standardized among several Northeast Pacific genetics laboratories (Seeb et al. 2007). A total of 4596 fin clip samples were genotyped using the protocols described by Teel et al. (2009). The relative probability of stock origin was estimated for each sample using the likelihood model of Rannala and Mountain (1997), as implemented in the genetic stock identification software ONCOR (Kalinowski et al. 2007).

Population baseline data were from the multi-laboratory standardized Chinook salmon database described by Seeb et al. (2007). The baseline contained data for populations of Chinook salmon ranging from California to southern British Columbia. We used the Columbia River Basin baseline dataset described by Teel et al. (2009), which includes all of the major genetic stock groups in the basin. Allocations to individual baseline populations were summed to estimate the probability for each individual of belonging to a Columbia River Basin spring run stock group. Fish included for analysis were only those estimated to be Columbia River Basin spring run with a probability of at least 80% relative to membership in a different stock group. The five stock groups used in our analysis were Upper, Middle, and Lower Columbia River spring Chinook, Snake River spring Chinook, and Upper Willamette River spring Chinook.

Overall approximately 85% of our juvenile Chinook salmon catches over 11 years were genotyped. However, the percentage of catch that was genotyped varied among surveys and ranged from 45% in May 2008, the survey with our largest juvenile Chinook salmon catch ($n=650$) to 97% in June 2006. We therefore estimated the total number of Columbia River Basin spring run fish in each catch by multiplying the proportion of Columbia River Basin spring Chinook in the genetic sample by the total number of juvenile Chinook caught. These numbers were estimated separately for each sampling station and for unmarked and marked fish.

Catch per unit effort (CPUE) for marked and unmarked fish was calculated by dividing the esti-

mated number of spring Chinook juveniles caught by the number of kilometers trawled at each station. When examining interannual changes in overall CPUE, we included only transects that were sampled in at least 9 of 11 survey years. For May, these were the Grays Harbor, Columbia River and Cape Meares transects, and for June, the LaPush, Queets River, Grays Harbor, Willapa Bay, Columbia River, Cape Meares, and Newport transects.

The marking of hatchery releases is currently less than 100% for the Columbia River Basin [Table 1; Fish Passage Center (2005, www.fpc.org)]. Therefore, our unmarked juvenile Chinook salmon were considered a mixture of natural and unmarked hatchery fish. In order to calculate the potential number of naturally produced unmarked fish for each survey, we estimated the total number of hatchery fish by dividing the catch of marked fish by the marking rate (Table 1), and calculated the number of natural fish by subtracting the estimated number of hatchery fish from the total catch.

For trophic analysis, we analyzed up to 30 stomachs from each station following the methods of Daly et al. (2009). Stomach contents were identified to the lowest possible taxonomic category using a dissecting microscope. Prey were enumerated and weighed to the nearest 0.001 g. Prey were grouped into 13 categories that consistently contributed to more than 5% of salmon diets by weight: fish (unidentified fish and other fish that made up <5% of diet), cottids, pleuronectids, rockfishes (*Sebastes* spp.), *Ronquilus* sp., Pacific sand lance (*Ammodytes hexapterus*), osmerids (*Allosmerus elongatus* and other unidentified smelts), *Cancer* spp. larvae, copepods, other decapod larvae (non-*Cancer* spp. decapods), euphausiids, amphipods, and “other” (pteropods, mysids, polychaetes, gelatinous zooplankton, cephalopods, insects, and cirripede larvae). All diet analysis was based on percent weight of these prey categories.

Statistical analysis

The Cramér-von Mises nonparametric test was used to evaluate the spatial distribution differences between unmarked and hatchery salmon across the study area (Syrjala 1996). In the spatial analysis, a single test statistic Ψ was calculated for each survey (sampling month/year) between the two groups using a function called *Syrjala* in the *ecspa* package in the R

Table 1 Annual number of hatchery Columbia River basin spring Chinook salmon released, percentage of hatchery fish that were marked at release (Fish Passage Center (<http://www.fpc.org>)), and estimated total number of unmarked and hatchery marked Columbia River Basin spring Chinook salmon caught during May and June surveys. Provided are predicted numbers of fish of natural and hatchery origin which are based on the release marking rate. Listed are also the calculated percentage of the total Columbia River basin spring Chinook salmon catch predicted to be of natural origin for May and June

Year	Annual # hatchery released	Annual percent of hatchery released with mark	May survey				June survey				% of catch predicted to be of natural origin	
			Unmarked caught	Hatchery marked caught	Predicted natural origin	Predicted hatchery origin	Unmarked caught	Hatchery marked caught	Predicted natural origin	Predicted hatchery origin		
1999	30,841,098	61.3	101	140	12	229	5.1	49	88	0	144	0.0
2000	28,085,803	73.7	34	59	13	80	14.3	33	24	24	33	42.4
2001	25,610,529	74.6	16	41	2	54	3.9	11	12	7	15	31.5
2002	32,327,368	90.3	13	106	2	118	1.4	20	47	15	52	22.6
2003	33,128,752	89.1	8	77	0	86	0.0	50	60	42	68	38.5
2004	33,728,540	91.9	4	68	0	74	0.0	14	22	12	24	33.4
2005	33,779,499	93.4	0	4	0	4	0.0	8	5	7	5	57.2
2006	33,295,623	92.8	26	185	11	200	5.4	14	31	12	33	26.6
2007	31,155,813	89.3	29	199	5	222	2.1	7	45	1	50	2.2
2008	30,882,312	94.7	50	474	23	501	4.5	52	290	35	306	10.3
2009	32,262,276	93.5	31	376	5	402	1.2	28	79	23	85	21.1
Total catch			312	1729	5			285	704			
Overall average	31,372,510	85.9%					3.4%					26.0%

programming language (<http://cran.r-project.org/web/packages/ecespa/index.html>; last accessed 11 January 2011). A p-value is computed based on 9999 random permutations of the data. This test is designed to be sensitive to differences in the way the populations are distributed across the study area but insensitive to differences in abundance between the two populations.

We compared fork lengths and condition of hatchery and unmarked fish. We defined condition as the residuals from regressions of $\ln(\text{wet weight})$ on $\ln(\text{fork length})$ (Brodeur et al. 2004) and calculated these regressions for both groups combined in May ($n=2041$) and June ($n=989$) separately. Statistical analysis of differences in fork length and body condition between unmarked and hatchery fish was tested using a Kruskal-Wallis non-parametric test as both groups exhibited skewed data sets. The Kruskal-Wallis analysis of variance by ranks is a non-parametric test of medians which does not assume the data is normally distributed. These comparisons were made between all sampled years in May and June except 2005, when sample size was too low, and between months (all years together).

Spearman rank correlation analysis was used to identify relationships between the catch data of hatchery and unmarked salmon and their physical characteristics (fork length, body condition, and feeding intensity). We also tested whether the overall annual CPUE of hatchery fish correlated significantly ($P \leq 0.05$) with unmarked fish fork length, condition and feeding intensity.

Diet composition of both unmarked and hatchery fish was evaluated using non-metric multidimensional scaling ordination (MDS) available on the PRIMER software package (Clarke and Warwick 2001). This analysis relied on a matrix constructed from pairwise Bray-Curtis similarity indices of diet composition between unmarked and hatchery salmon (Field et al. 1982). Diets by percent of weight of prey eaten were calculated for unmarked and hatchery fish at each station where a minimum of 3 fish from each group were caught. For both fish groups, diets were averaged by station, and the proportional diets were arc-sine square root transformed prior to analysis to achieve normality (Zar 1999). To test for significant differences in diet composition between unmarked and marked salmon, we utilized diets from individual fish at a sampling station for each month/year pair. The test used was analysis of similarities (ANOSIM),

a multivariate analog to analysis of variance (ANOVA) based on the matrix of pairwise Bray-Curtis similarity coefficients (Clarke 1993). The ANOSIM statistical significance is determined by permutation (Clarke 1993) where $P < 0.05$.

To examine differences in stomach fullness (i.e., feeding intensity) between unmarked and hatchery fish, we used an index of feeding intensity (IFI), where:

$$IFI = \frac{\text{stomach content weight}}{\text{total fish weight} - \text{stomach content weight}} \times 100.$$

Proportional feeding intensity values were arc-sine square root transformed to achieve normality (Zar 1999). There was a significant correlation between length and feeding intensity over the range of sizes examined. Therefore, we used multifactor ANCOVA, with length as a covariate, to test for differences in feeding intensity between groups. We also tested for interannual differences in feeding intensity of both unmarked and hatchery fish. When there were significant interannual differences in feeding intensity, we followed the ANCOVA with the Fisher's least significant difference multiple range test. Mean IGF-1 levels between marked and unmarked fish were assessed using a two-way ANOVA (fish origin and year) with May and June examined separately. Blood samples were obtained only in May in years 2006–2009. There were not enough unmarked fish bled from the June 2000–2007 samples for comparison of IGF-1 levels between groups. Significance was set at $P < 0.05$ for all analyses. We used STATGRAPHICS Centurion XV software for all univariate statistical analyses.

Results

Distribution and spatial overlap

We collected 2472 juvenile salmon that were genetically identified as Columbia River Basin spring Chinook during 11 years of research cruises in May and June (Table 1). Of these fish, approximately 3% had low stock-assignment probabilities and were not used in the analyses presented here. Of fish used for analyses, the percentage estimated to be natural origin Chinook was quite low, averaging only 3.4% ($\pm 4.1\%$)

in May and 26.0% ($\pm 17.3\%$) in June (Table 1). Ninety-eight percent of both unmarked and hatchery Chinook salmon were caught either along the Columbia River transect (primarily in May), or further north (in June; Fig. 1). There was similar seasonal and interannual variability in the numbers caught of both hatchery and natural Chinook salmon. Both groups were more abundant in May than in June and particularly more abundant in the year 2008, but nearly absent in 2005 (Fig. 2). The highest catches of salmon in May were typically along the Columbia River transect, but in June were along the Washington coast (Fig. 1).

Unmarked and hatchery Chinook salmon were closely associated spatially. At 82% of the sampled stations where we caught unmarked fish, we also caught at least one hatchery fish. Hatchery fish also numerically dominated the unmarked fish when they were caught together (Fig. 1). For example, hatchery Chinook salmon were equally or more abundant than unmarked salmon at 99% of the stations in May and 93% of the stations in June. The distributions of unmarked and hatchery fish were not different from each other for 80% of the sampling efforts (month/year pairs). Only in May 2001 and 2004, and June 2007 and 2009 were spatial distributions significantly different between unmarked and hatchery salmon (Cramér-von Mises; $P < 0.05$; Table 2). Too few fish were collected in 2005 to calculate meaningful spatial overlap values.

Physical characteristics

Hatchery fish in May and June were typically significantly longer than unmarked fish. On the other hand, in May unmarked fish caught in over half of the sampling years exhibited significantly greater body condition than hatchery fish. In June, body condition did not differ between the two groups. Also, the length and body condition of unmarked and hatchery salmon varied interannually and between the two months, except hatchery fish body condition did not change significantly between May and June.

In May, hatchery fish were found to be significantly longer than unmarked fish in half of our sampling years (Kruskal-Wallis (K-W) test, $P < 0.05$; Fig. 3a). In May, overall average fork length was 156.1 mm for unmarked fish vs. 171.0 mm for hatchery fish (Fig. 3a). In June, hatchery fish were

significantly longer than unmarked fish (K-W, $P < 0.05$) in all years except 1999 and 2000. From the June catches, unmarked fish averaged 150.7 mm fork length, while hatchery fish were 30 mm longer, averaging 184.9 mm fork length (Fig. 3b). In addition, hatchery fish collected during June surveys were significantly longer than those caught during May (K-W, $P < 0.0001$), yet unmarked Chinook salmon were significantly shorter in June than in May (K-W, $P = 0.02$; Fig. 3). Interannual variation in the size of both groups of fish generally followed a similar pattern (Fig. 3).

Seasonal and interannual differences in body condition were also observed between fish groups. In May 1999, 2001, 2002, and 2006–2008 unmarked fish had significantly higher condition factors than hatchery fish (K-W, $P < 0.05$; Fig. 4a). By June, the salmon groups did not have distinctly different body conditions. Condition of fish caught in May showed similar interannual trends, regardless of origin, with fish from 1999, 2003, and 2004 exhibiting the lowest values, although the differences were not statistically significant. Condition values for unmarked fish caught in June 2001 and 2007 were below the 11-year average (Fig. 4b); while values for hatchery fish were below average in 2001, 2003 and 2007 (Fig. 4b). Unmarked fish had significantly higher condition in May than in June (K-W, $P = 0.0002$; Fig. 4).

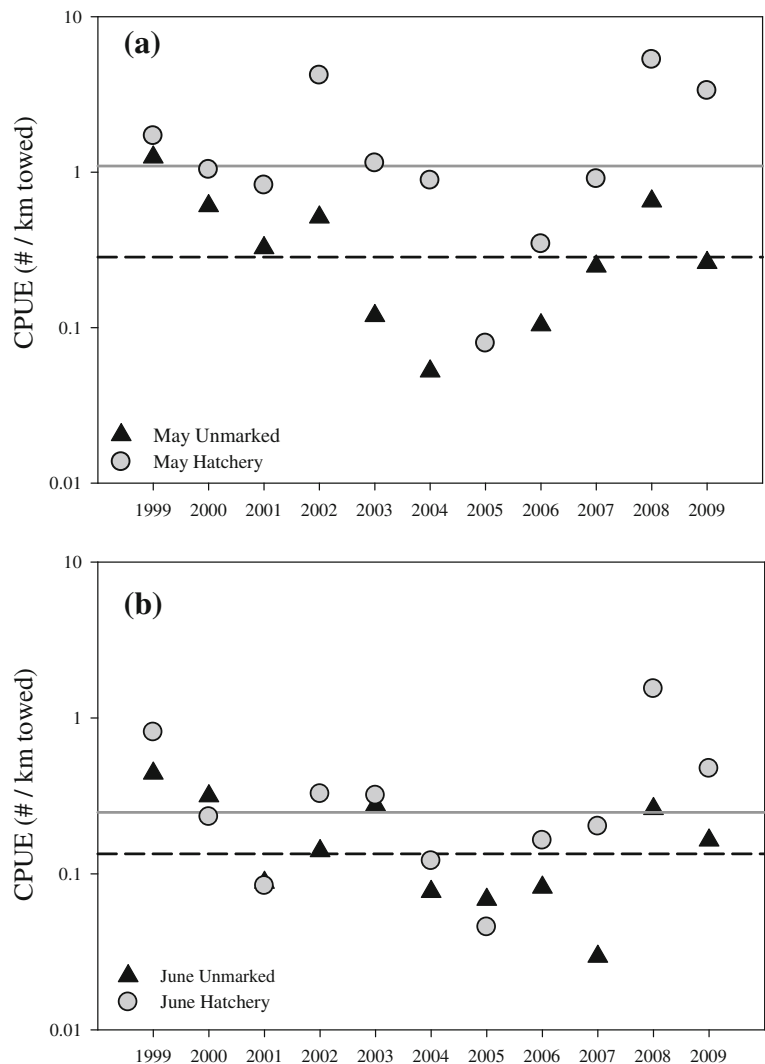
Physical characteristics and CPUE

The length and body condition, as well as feeding success (or feeding intensity) of unmarked salmon was not impacted by the number (as measured by CPUE) of hatchery fish present (Spearman rank correlation $P > 0.05$). Instead, we found that unmarked and hatchery fish were longer during years of higher CPUE (unmarked $r = 0.746$; $P = 0.02$; hatchery $r = 0.721$ $P = 0.03$). In addition, in years when there were higher catches of unmarked fish, we also caught significantly more hatchery fish ($r = 0.764$; $P = 0.02$).

Diet characteristics

Diets of unmarked and hatchery Chinook salmon were very similar. Dietary analysis of 275 unmarked and 855 hatchery salmon showed that during May and June, these fish were highly piscivorous (>80% of

Fig. 2 Overall annual (May and June) catch per unit effort (CPUE) calculated for consistently sampled transects of unmarked (*black circles*) and hatchery (*gray circles*) fish caught in May (a) and June (b). Overall mean reference line (*dashed black*) for unmarked and (*gray*) hatchery. Y-axis in scale of \log_{10}



diet) and ate similar prey types in similar proportions, regardless of origin (Fig. 5). We also observed shifts in the types of fish prey eaten between May and June and between years, yet these shifts were consistent for both hatchery and unmarked salmon. MDS plots revealed numerous instances where unmarked and hatchery diets from the same station grouped closely together, and additionally that the diets from both groups were well mixed in the ordination space, again suggesting that the diets of both groups were similar (Fig. 6).

High similarity in diets between unmarked and hatchery fish occurred at the finest spatial scale sampled. We tested for diet composition differences at the station level using ANOSIM and found few significant differences for any month/year pair be-

tween unmarked and hatchery diets. Out of the 14 sampling pairs, only in June 2000 and May 2006 were unmarked fish significantly different in diet composition than hatchery fish (ANOSIM $P < 0.05$; Table 2).

Feeding intensity was similar for both unmarked and hatchery fish. For both salmon origin types during each sampling year we did not find a difference in feeding intensity between May and June ($P = 0.69$), so we combined the monthly feeding intensity data and then tested for annual differences between unmarked and marked fish. Overall, the average annual feeding intensity for unmarked fish was 1.1% which was similar for hatchery fish (1.0%; Fig. 7). Only in 2000 was there a significant difference in feeding intensity, when hatchery fish

Table 2 Interannual spatial (p-values from Cramér-von Mises test) and diet differences (calculated by analysis of similarities; ANOSIM) between unmarked and marked Chinook salmon during the months of May and June. Analysis of the diet

composition was derived from a subset of the catch data where we had at least three unmarked and marked Chinook salmon diets examined per sampling effort. Values in bold are significant at $P < 0.05$

Year	May		June	
	Spatial Distribution P-value	Diet composition P-value	Spatial Distribution P-value	Diet composition P-value
1999	0.35	0.17	0.58	0.66
2000	0.12	0.56	0.51	0.01
2001	0.03	0.90	0.10	0.47
2002	0.24	0.30	0.26	0.50
2003	0.35	0.90	0.59	0.68
2004	0.02	–	0.64	–
2005	–	–	–	–
2006	0.55	0.04	0.40	–
2007	0.20	0.50	0.03	–
2008	0.20	0.95	0.25	0.88
2009	0.20	–	0.04	–

had fuller stomachs than unmarked fish (ANCOVA with FL as a covariate; $P=0.04$). Also, hatchery fish exhibited significant interannual variability in feeding intensity (ANCOVA; $P=0.0003$; Fig. 7), but not unmarked fish. Lastly, the percentage of empty stomachs ($<0.05\%$ BW) was similar in both unmarked and hatchery fish (7.8 and 7.2%, respectively).

Growth rates

There were no significant differences in recent growth, as assessed by IGF-1 levels between unmarked and hatchery fish, in either May or June (ANOVA; $P > 0.05$; Fig. 8). However, average IGF-1 levels did differ between years, with lower values found in May 2006 and 2007 as compared to May 2008 and 2009; demonstrating that marine growth may vary interannually.

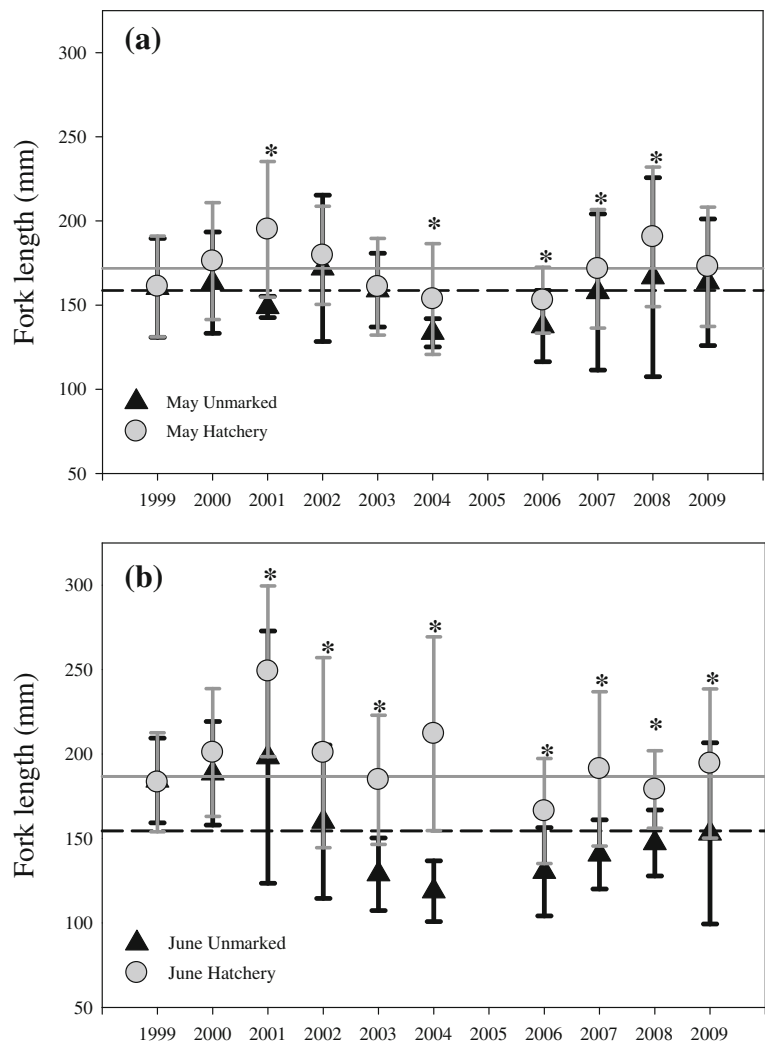
Discussion

Interaction between natural and hatchery fish may influence marine mortality of juvenile salmon. Distribution and abundance patterns, physical and diet characteristics and recent marine growth rates each suggested that unmarked and hatchery Columbia River Basin spring Chinook salmon had a high degree

of similarity in use of the coastal marine environment. Unmarked and hatchery fish were found to be highly sympatric in the ocean and ate similar types of prey in similar proportions. Feeding intensity and growth of unmarked and hatchery fish were for the most part not significantly different, and both groups exhibited similar interannual patterns in abundance, fork length, condition, and growth. We did document, however, that fish of hatchery origin, especially in June, were significantly longer than unmarked fish and that unmarked fish had better body condition than hatchery fish in May.

Unmarked and marked juvenile spring Chinook salmon had similar spatial distributions (only 4 of 20 year/month comparisons showed significantly different distributions). High marine spatial overlap of wild and hatchery fish has been previously documented through coded-wire data recoveries of wild Chinook salmon which indicated similar distributions to those of fish from nearby hatcheries (Weitkamp 2010). Both groups of Chinook salmon were collected along the Columbia River transect, or further north, with few fish collected to the south. These results were consistent with data from coded-wire tagged fish (primarily of hatchery origin), which show a fast northward migration of Columbia River Basin spring Chinook salmon (Trudel et al. 2009). However, there appeared to be temporal differences in

Fig. 3 Interannual average fork length (with standard deviation bars) for unmarked (*black triangles*) and hatchery (*gray circles*) fish in May (a) and June (b). Data not shown for 2005 due to low sample size. Overall mean reference line (*dashed black*) for unmarked salmon and mean reference line (*gray*) for hatchery salmon is shown. Significant difference between unmarked and hatchery fish is noted with an asterisk



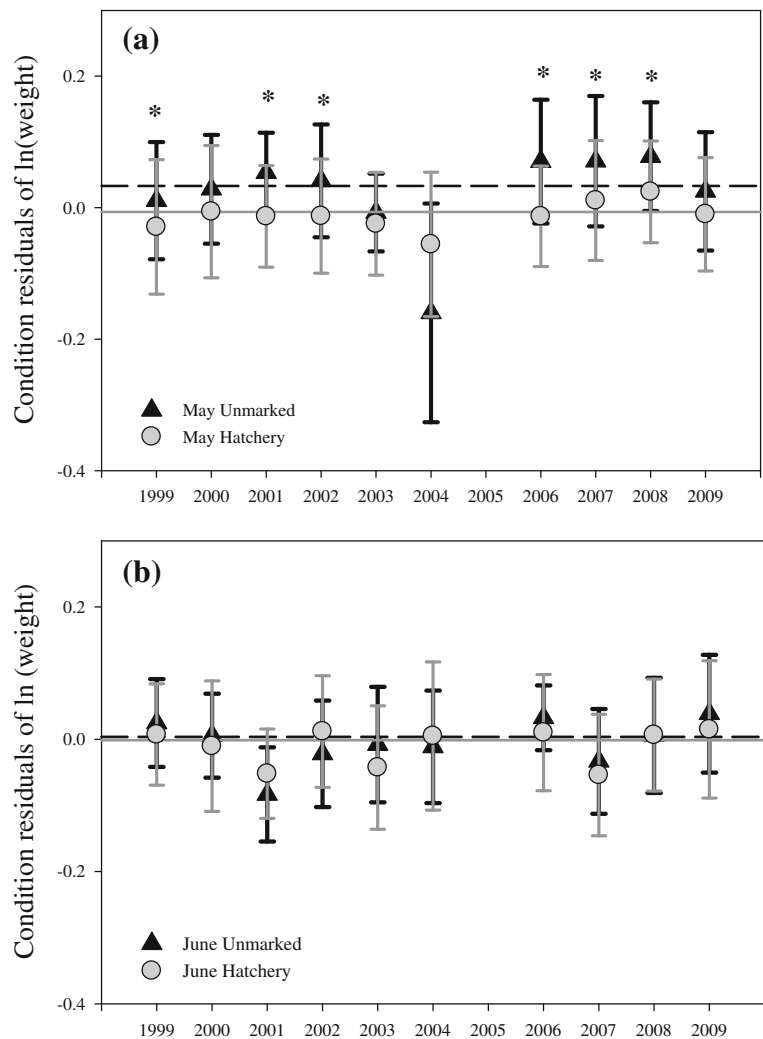
peak abundance in the ocean, with hatchery fish found in the greatest abundance in May and presumed natural fish found in the greatest abundance in June.

Both the strong numerical dominance of hatchery Chinook salmon and the high spatial overlap between unmarked and hatchery fish were consistent throughout our 11-year study. Although hatchery fish were caught in the same trawls as unmarked fish, and in higher numbers, the small-scale spatial overlap between the two groups is unknown. The trawls we used sampled a large volume of water (mean=1.5 million m³), and fish caught in a single tow could have been either highly dispersed or aggregated within the sampling volume. Detection of any small-scale spatial overlap that may lead to behavioral interactions would also require knowledge of the

horizontal and vertical distribution of both wild and hatchery juveniles. This information could be obtained using acoustic tags and a large receiving array (e.g., Clemens et al. 2009), which were beyond the scope of the present study. Previous collections of juvenile salmon in the marine environment have used purse seines, which sample about one-fifth the volume of our trawl net (Percy and Fisher 1986). The smaller sampling scale of a purse seine may enhance perception of finer spatial interactions between unmarked and hatchery salmon.

The larger fork length consistently exhibited by the hatchery salmon could have a negative impact on the smaller and less abundant unmarked fish. Ontogenetic changes in diets of Chinook salmon have been documented in the marine environment, with larger

Fig. 4 Average interannual condition residuals (with standard deviation bars) for unmarked (*black triangles*) and hatchery (*gray circles*) fish in May (**a**) and June (**b**). Data not shown for 2005 due to low sample size. Overall mean reference line (*dashed black*) for unmarked salmon and mean reference line (*gray*) for hatchery salmon is shown. Significant difference between unmarked and hatchery fish is noted with an asterisk

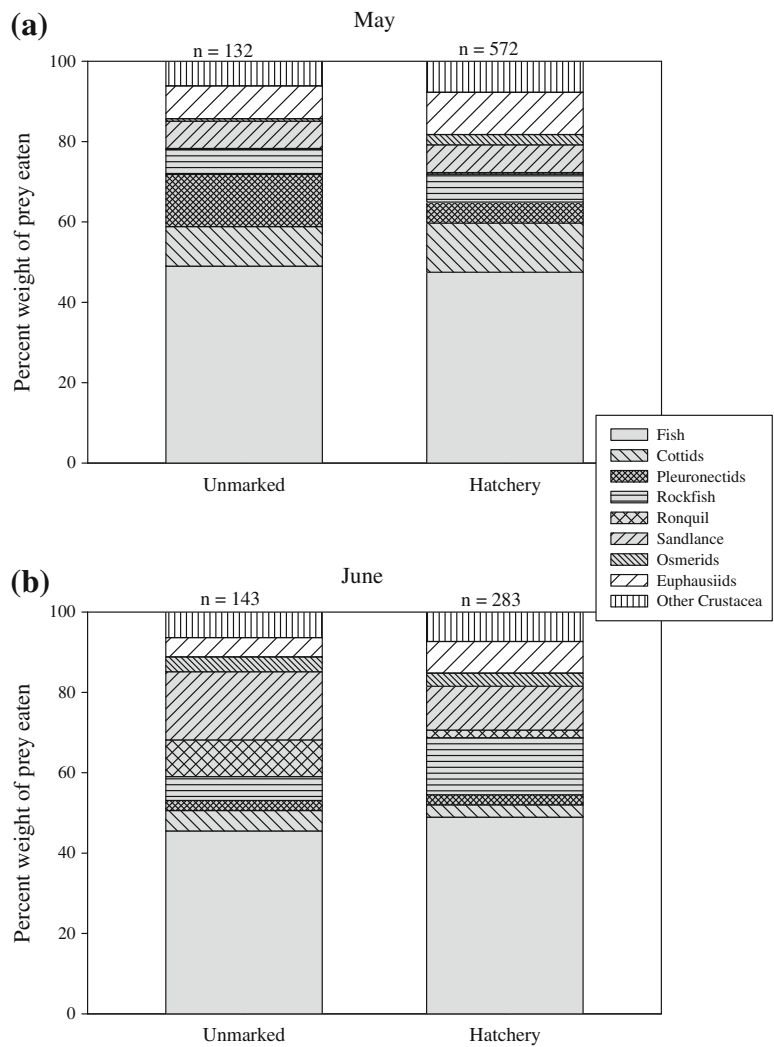


salmon eating larger prey and having a higher rate of piscivory (Daly et al. 2009; Duffy et al. 2010). Even though the hatchery Chinook salmon in our study were larger, (on average 35 mm longer in June) their diets and stomach fullness were not typically different from the unmarked fish, a result similar to that found by Sweeting and Beamish (2009) for hatchery and wild coho salmon (*Oncorhynchus kisutch*). Hatchery Chinook salmon exhibited significant increases in body length between May and June, likely indicating rapid early marine growth and extended residence in our sampling area. In contrast, many small unmarked fish (100–120 mm FL) were collected in June but not in May, suggesting a delayed seaward migration of natural as compared to hatchery smolts. The delayed migration of small unmarked smolts into ocean waters

well into June confounded our ability to observe early marine growth in the unmarked fish based solely on size differences. Also, higher proportions of the salmon caught during our May surveys were of hatchery origin, with a decline in the hatchery proportion seen in June. This suggests that either the peak migration to marine environments is earlier for hatchery than for unmarked fish, or that hatchery fish are migrating from our sampling area more quickly. Genetic analyses of samples collected beyond our study area, or additional tagging of natural juveniles, are needed to provide more information on the migration patterns of Columbia River Basin spring Chinook salmon.

Competition between two groups can occur when spatial and dietary resources overlap, but there must

Fig. 5 Average percent weight of prey eaten for unmarked and hatchery fish in May (a) and June (b) with overall sample size at top of each bar. Fish prey are grey with individual patterns, and invertebrates have different patterns with no fill color

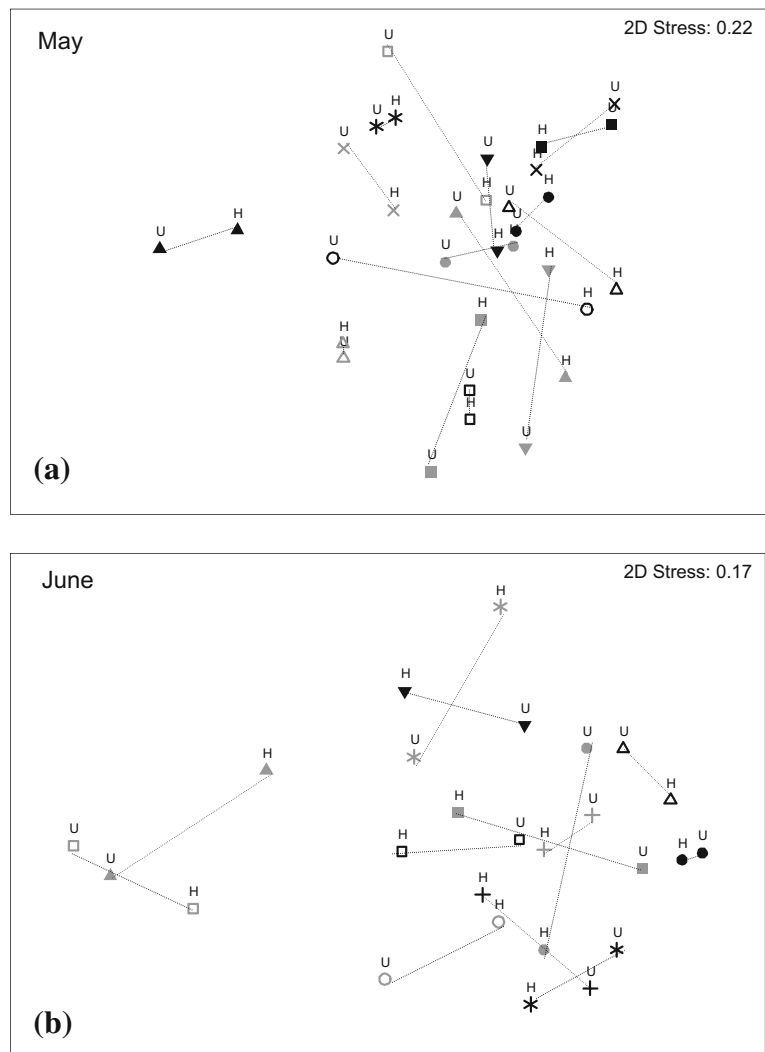


also be a limit to one or both of these resources. Diets of unmarked and hatchery juvenile salmon were found to be highly similar at the smallest spatial scale we examined (fish caught together in the same tow). This may imply that, at least within our smallest sampling scale, both groups of fish are utilizing the available prey field with significant overlap. Our finding of high similarity between unmarked and hatchery spring Chinook salmon diets has been previously documented for hatchery and wild juvenile coho salmon in the Strait of Georgia (Sweeting and Beamish 2009) and for hatchery and wild juvenile pink salmon (*O. gorbuscha*) in the Gulf of Alaska (Armstrong et al. 2008). Yet our finding of high overlap in diets did not necessarily imply that competition was occurring between our two groups.

For example, in years when some prey (e.g., euphausiids) are extremely abundant, diet overlap among all predators is high as they utilize these readily available prey resources (Brodeur and Pearcy 1992).

Conditions do exist for potential competition between naturally produced and hatchery Chinook salmon, as they are found together and eat the same foods. However, direct measurements of food resources available to juvenile Chinook salmon in marine waters are logistically challenging, and robust estimates of prey availability—and whether prey are limiting—are not easily attainable (Brodeur et al. 2011). This lack of prey resource information prevented us from determining whether there was direct competition between the two groups of salmon. We

Fig. 6 Results of non-metric multidimensional scaling ordination (MDS) for percent weight of prey eaten by unmarked and hatchery salmon at sampling stations when there were ≥ 3 unmarked and hatchery diets available. Pairs of sampling station are connected by dotted lines and labeled either unmarked (U) or hatchery (H). Individual stations (one unmarked and one hatchery) have the same symbol and color type



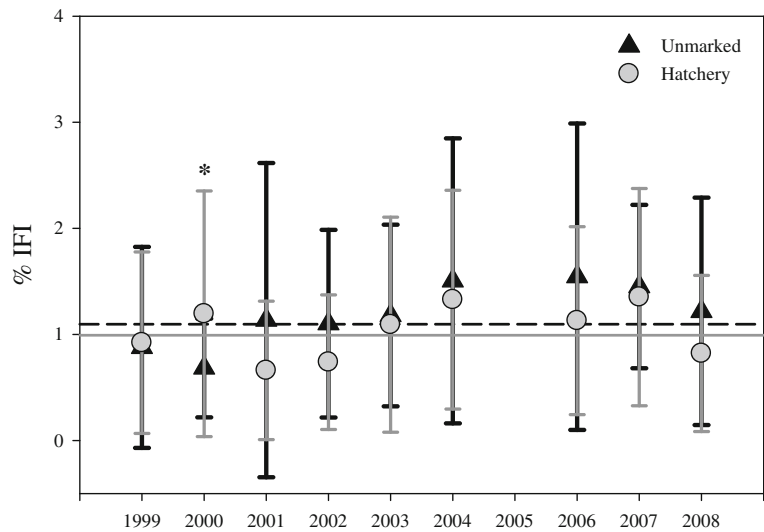
observed that feeding intensity and growth was similar between unmarked and hatchery Chinook salmon, which suggests that they are adapting to the marine environment equally. In addition, marine diets of juvenile salmon have been shown to strongly shift between seasons and years (Brodeur et al. 2007; Weitkamp and Sturdevant 2008; Daly et al. 2009), and our data suggest that both hatchery and unmarked fish are tracking prey resources similarly.

Juvenile Chinook salmon are numerically a relatively minor component of the pelagic fish community in the Northern California Current (NCC) during most years (Brodeur et al. 2005). However, Miller and Brodeur (2007) found that for the region off southern Oregon, the feeding habits of yearling juvenile Chinook salmon overlapped the most with other

salmonids (coho, chum (*O. keta*) and steelhead (*O. mykiss*), as well as adult Chinook salmon) but their diets had low overlap with the more numerous pelagic fishes. In May and June, high numbers of hatchery-reared coho salmon also enter the Northern California Current, where they are found to have high spatial (Bi et al. 2008) and dietary overlap (Daly et al. 2009) with Chinook salmon.

We also found interannual fluctuations in catch per unit effort, average length, body condition, diet composition, feeding intensity, and growth of Columbia River Basin Chinook salmon; yet for the most part, these fluctuations followed a similar pattern between unmarked and hatchery fish. Both groups of fish were typically the least abundant, smallest, and in poorest condition during the same years. Unmarked

Fig. 7 Annual (May and June combined) averages of feeding intensity (as a percent of prey of body weight) for unmarked (black triangles) and hatchery (gray circles) fish. Data are not shown for 2005 due to low sample size. Overall mean reference line (dashed black) for unmarked salmon and mean reference line (gray) for hatchery salmon is shown. Significant differences between unmarked and hatchery fish are noted with an asterisk



and hatchery fish followed a synchronous fluctuation in numerous biological characteristics, which suggested that both were reacting to variable food availability and ocean conditions in a similar manner. Increased competition with fish of hatchery origin may negatively affect listed natural salmon in the marine environment especially during poor ocean conditions. Yet the effects of ocean conditions upon both populations seemed similar and may have made it difficult to observe competition effects between the two groups.

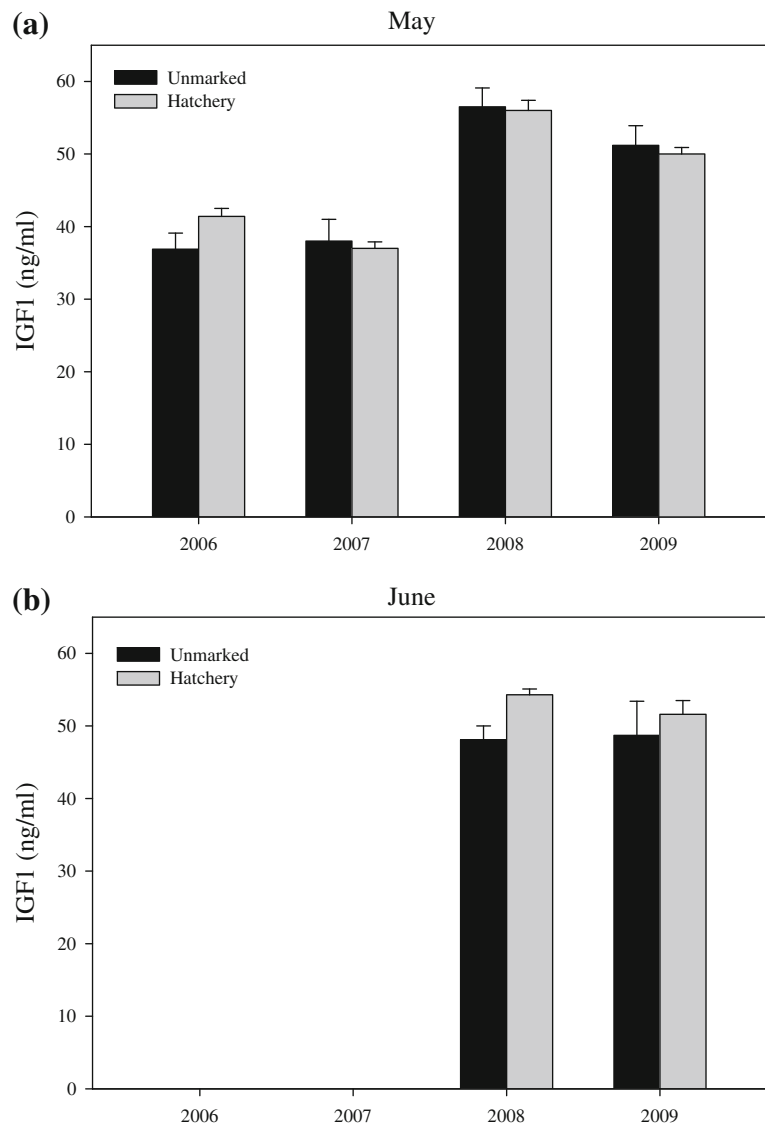
Of the five spring Chinook salmon ESUs in the Columbia River Basin, four are considered endangered or threatened (NMFS 2009). Predicting survival of naturally produced populations during less productive ocean conditions might be made more complicated by high hatchery production rates (Beamish et al. 1997; Levin et al. 2001; Scheuerell and Williams 2005; Martinson et al. 2008; Buhle et al. 2009). Martinson et al. (2008) found density dependent sockeye salmon growth during poor ocean conditions, even at low population abundances, resulting from increased competition for resources. Ruggerone and Goetz (2004) found that all 13 Chinook salmon stocks they examined in Puget Sound had lower survival, as well as reduced growth and delayed maturation, in years of high pink salmon (*O. gorbuscha*) abundance.

Reduction of suitable marine habitat for juvenile salmon has been shown to occur during years with poor ocean conditions (Bi et al. 2008). Yet the number of hatchery fish released is consistent each year, regardless of ocean conditions. Thus, resource

limitation and competition, if it occurs, could be greater during years with poor ocean conditions and presumably reduced carrying capacity (Brodeur et al. 1992). Our results showed that both unmarked and hatchery Columbia River Basin spring Chinook salmon exhibited reductions in abundance, condition, and fork length in similar years. The reduced abundance and size we saw among hatchery and unmarked Chinook salmon in years 2003–2006 coincided with years of low adult returns two years later (<http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/g-forecast.cfm>, last accessed 6 June 2010). In order to more fully understand marine mortality, especially during years of poor ocean conditions, sampling over a shorter time frame and earlier in the summer may help us to better understand early marine mortality and potential competition between hatchery and wild salmon when resources are more likely to be limited.

During the first 3 years of our study (1999–2001), the percentages of marked fish (known hatchery origin) in our catch was relatively low (58.5–73.1%). This coincided with years of lower fin-clipping rates at hatcheries (Table 1), suggesting that a high proportion of the unmarked fish were of hatchery origin in these years. Hatchery clipping rates that are less than 100% complicated our comparisons between naturally produced and hatchery fish, since the origin of individual unmarked fish was uncertain. The lack of ability to fully separate hatchery and naturally produced salmon reduced our ability to fully distinguish potential differences in their biological

Fig. 8 Insulin like growth factor 1 (IGF-1) levels (ng/ml) with standard error shown for unmarked (*black*) and hatchery (*gray*) fish for May (a) and June (b)



characteristics. Catches in May of fish that were predicted to be of natural origin were so low, that the statistical power of our comparisons to detect significant difference between the two groups was also low. On the other hand, by June, natural origin fish made up a greater proportion of the catch; and our result confirmed the pattern of high spatial and diet overlap between the two groups and greater length of hatchery fish seen in May.

Similarly, another potential bias within our analysis of Chinook salmon may have been introduced by variability of stock structure or population differences within the stocks that we reported upon. Differences among populations in the five ESUs could have

influenced our comparisons between unmarked and marked fish. However, comparing characteristics between unmarked and hatchery fish by individual stock group would be difficult due to the low catches of unmarked fish, which would reduce the sample size for comparisons.

Investigation of juvenile salmon ocean ecology is difficult, as these fish are dispersed over large areas of the California Current. In addition, different populations of juvenile Chinook salmon intermingle in the ocean environment. A critical element of our analysis was genetic identification of fish to specific stock groups, which was not possible until relatively recently. Also important to our study was the ability to identify, with

varying degrees of certainty, the origin of Columbia River Basin spring Chinook salmon. Integrating spatial and diet habits, as well as physical and growth characteristics of both unmarked and hatchery collected under variable ocean conditions is complex.

Further research of interactions between natural and hatchery produced fish would be greatly enhanced by the complete marking of all fish of hatchery origin. In addition, reducing or varying the output level of hatchery fish within the Columbia River Basin, or suppressing the release of high numbers of hatchery fish into predicted poor ocean habitat could provide direct insight into the carrying capacity of the ocean environment. Varying the number of hatchery fish released in response to perceived ocean conditions could assist us in understanding potential density dependent growth suppression and competition between hatchery and endangered and threatened naturally-produced salmon.

Acknowledgments Support for our research is through the Bonneville Power Administration and we are grateful for their long term funding of our efforts. We also thank the members of the Estuarine and Ocean Ecology group including Bob Emmett, Bill Peterson and Ed Casillas from NMFS and Cheryl Morgan along with numerous others from OSU who assisted in field collections, laboratory analysis, and database creation. David Kuligowski and Don Van Doornik (NMFS) collected the genetics data used in this study and Kathy Cooper ran IGF-I assays. Megan O'Connor (OSU) assisted with the R programming. We would also like to thank Bill Pearcy, Barry Berejikian, and two anonymous reviewers for their comments which greatly improved the manuscript.

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