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ARTICLE

Contrasting Early Marine Ecology of Chinook Salmon and Coho Salmon in Southeast Alaska: Insight into Factors Affecting Marine Survival

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Abstract
To identify processes potentially contributing to the differential marine survival rates of Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* originating from Southeast Alaska, we compared the early marine ecology of the two species during the critical first summer in marine waters. We predicted that the higher survival rates for coho salmon relative to Chinook salmon were related to the larger size, faster growth, or different habitat or species associations of coho salmon. Our size and growth expectations were largely substantiated: juvenile coho salmon were larger than juvenile Chinook salmon and had faster length-based growth, although weight-based growth rates were similar. The most obvious difference was in their distributions. Juvenile coho salmon overlapped spatially and temporally with abundant juvenile pink salmon *O. gorbuscha* and chum salmon *O. keta*, whereas juvenile Chinook salmon were geographically separated from other salmonids. This suggests that coho salmon benefited from a predation buffer that did not extend to Chinook salmon. Our results indicate that factors influencing marine survival of juvenile Chinook salmon and coho salmon in Southeast Alaska are attributable to species-specific differences in their early marine distribution patterns and species interactions.

Identifying the processes that control marine fish recruitment has been the focus of extensive research for over a century (Sinclair 1988) and has greatly increased our understanding of the factors influencing recruitment (Gallego et al. 2007). In general, recruitment is controlled by some combination of bottom-up (e.g., high feeding success or rapid growth) and top-down (predation) processes, which assert the greatest influence during the earliest stages of marine life (Hunter and Price 1992; Govoni 2005).

Marine mortality in anadromous Pacific salmon *Oncorhynchus* spp. is probably highest during the first few weeks or months of ocean residence, when juvenile salmon typically inhabit coastal waters (e.g., Pearcy 1992; Briscoe et al. 2005; Pyper et al. 2005). During this critical period, habitat

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characteristics such as temperature regimes, vertical mixing, prey availability, competitor abundance, and predator abundance are believed to affect survival (Nickelson 1986; Fisher and Pearcy 1988; Logerwell et al. 2003). Coherence in salmon survival trends within and between species suggests that these ocean conditions exert the greatest influence at regional scales (hundreds of square kilometers) as opposed to larger, ocean-basin scales (Pyper et al. 2005; Malick et al. 2009; Teo et al. 2009). However, the relation between particular habitat conditions and salmon marine ecology (and ultimately survival) is largely unknown. This limited understanding of processes controlling salmon recruitment hinders our ability to prudently manage these commercially and culturally important species.

The actual processes influencing recruitment success for a given salmon species are variable and complex. For example, rapid growth rates allow fish to quickly outgrow size-selective predation (Parker 1971; Holtby et al. 1990) and have been correlated with overall survival for Pacific salmon (e.g., Holtby et al. 1990; Beckman et al. 1999; Willette et al. 2001), Atlantic salmon *Salmo salar* (Salminen et al. 1995; Jonsson et al. 2003), and marine fish in general (Sogard 1997). Several recent studies have shown that individual juvenile salmon that survive to adulthood are typically larger than average (Beamish et al. 2004; Moss et al. 2005; Cross et al. 2009).

However, the mechanism that confers advantage to large size or rapid growth may not necessarily involve size-selective predation. For example, Pearcy (1992) noted that the size at which survival rapidly improves in common marine environments is species dependent, suggesting that age, experience, adaptability, or other factors are more important than absolute size. Beckman et al. (1999) demonstrated that rapid growth in salmon smolts was associated with high physiological quality, which may indirectly affect a fish's vulnerability to predation. Alternatively, Beamish and Mahnken (2001) argued that rapid growth and accumulation of energy reserves during the first summer in the ocean are essential for salmon to survive a second critical period during winter, when food resources are scarce.

A fish's vulnerability to predators may be equally complex. Studies have shown that predation on juvenile fishes, including juvenile salmon, results from interactions between ocean conditions and the distribution and abundances of predators and alternative prey, all of which vary at a range of temporal and spatial scales (Willette 1999; Emmett et al. 2005). Clearly, the factors that determine survival are complex, and no single variable has been identified as being consistently important.

Chinook salmon *O. tshawytscha* and coho salmon *O. kisutch* in Southeast Alaska provide a unique opportunity to explore the factors affecting marine survival because they share many life history traits, yet their marine survival rates are quite different. In this region, both species enter marine waters as yearling smolts (age 1.0) or as 2-year-old smolts (age 2.0; coho salmon only) at approximately the same size (70–100 mm fork length [FL]) and time (April–June; Halupka et al. 2000), suggesting that they are initially vulnerable to the same suite of factors affecting their survival. Diet overlap between the two species in marine habitats of Southeast Alaska is also high (Landingham et al. 1998; Weitkamp and Sturdevant 2008), indicating that they should be similarly affected by variations in prey availability.

However, marine survival rates for coho salmon during the ocean entry years of 1997–2000 (average survival = 12.4%) were more than 13 times those for Chinook salmon (0.9%; Figure 1; NSRAA 2003; Shaul et al. 2003; RMIS 2006) and were much higher than survival rates observed in other coho salmon populations (Shaul et al. 2007; Teo et al. 2009). Accounting for the longer life span and therefore higher natural mortality of Chinook salmon (following Coronado and Hilborn 1998) approximately doubles the estimated Chinook salmon survival rates, but they are still far lower than the estimates for coho salmon (Weitkamp 2004). Consequently, comparing the early marine ecology of Chinook salmon and coho salmon within Southeast Alaska allows us to identify possible aspects of ocean residency that may have led to the differential marine survival.

During summer, surface waters of the Alexander Archipelago (Southeast Alaska) are dominated by juvenile salmon, primarily pink salmon *O. gorbuscha* and chum salmon *O. keta* along with lower abundances of sockeye salmon *O. nerka*, Chinook salmon, and coho salmon (Orsi et al. 2000). The area is extremely productive for juvenile salmon (Orsi et al. 2004), leading to high survival rates for most salmon species originating from Southeast Alaska (Baker et al. 1996; Geiger et al. 2003; Heinl et al. 2003; McPherson et al. 2003; Shaul et al. 2003; Zadina et al. 2003). Comparison of the food habits of Chinook salmon and coho salmon from the area indicated that although diet overlap was high, coho salmon had more food in their stomachs and the number of empty stomachs was approximately 10 times lower for coho salmon than for Chinook salmon (Weitkamp and Sturdevant 2008).

In the present paper, we examine some factors that are potentially responsible for the disparity in marine survival rates for coho salmon and Chinook salmon by comparing the early marine ecology of the two species. Specifically, we compared abundance, distribution, species associations, size, body shape, and growth rate between these species during the first summer in the ocean (data collected during 1997–2000). Based on the factors believed to influence marine survival, we hypothesized that Chinook salmon and coho salmon should differ in their size, growth rate, and perhaps distribution or species associations, which would result in more favorable conditions (e.g., larger size, faster growth, or fewer competitors) and therefore higher survival for coho salmon relative to Chinook salmon. The large marine survival differences between Chinook salmon and coho salmon in Southeast Alaska despite their similar life history traits provide a unique opportunity to identify possible mechanisms responsible for success in marine environments.

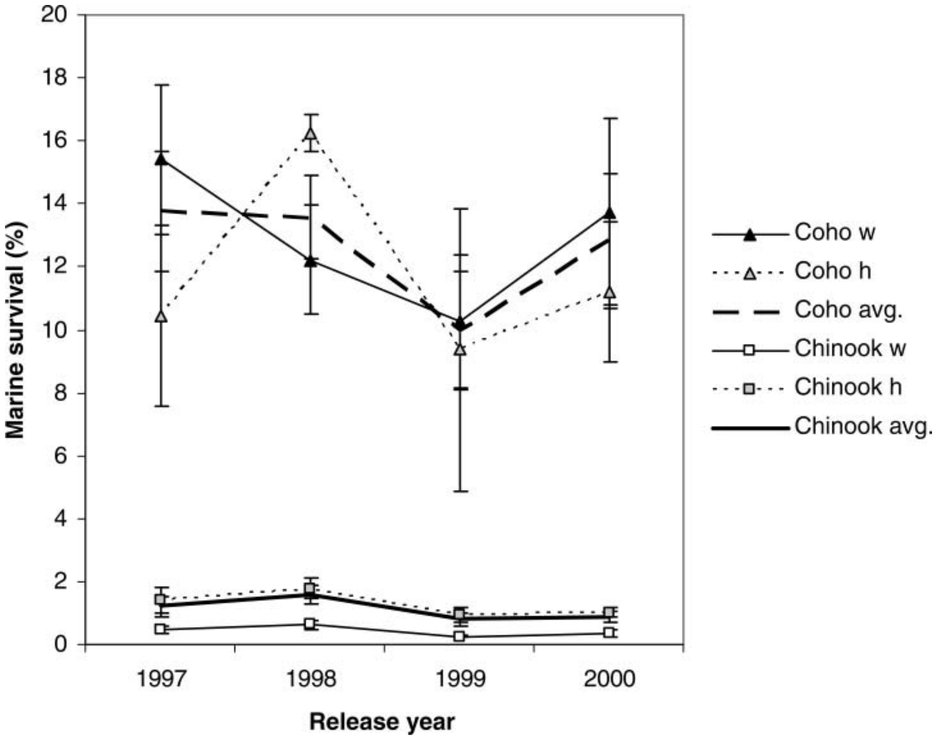

FIGURE 1. Estimated mean (±SD) marine survival of coho salmon and Chinook salmon (ocean entry years 1997–2000) from Southeast Alaska (h = hatchery origin; w = wild origin; avg. = average for hatchery and wild fish).

METHODS

Salmon Collection and Laboratory Analysis

Juvenile Chinook salmon and coho salmon were collected in 1997–2000 as part of the Southeast Coastal Monitoring (SECM) project in the northern region of Southeast Alaska (Orsi et al. 2000). Fish were sampled during daylight hours from late June to September at 11 stations (Figure 2). These stations were grouped into inshore and strait habitat types based on physical habitat characteristics and relative location along the salmon migration corridor. Inshore habitats were located near freshwater salmon sources (rivers and hatcheries) and had relatively cold, low-salinity surface waters due to extensive freshwater runoff. By contrast, strait habitats were typical of the many channels within the Alexander Archipelago through which juvenile salmon migrate to reach the ocean; these areas were intermediate in surface temperature and salinity between inshore (cold and low-salinity) waters and coastal (highly saline) waters (Orsi et al. 2000; Weitkamp and Sturdevant 2008). Although the SECM study includes coastal stations (outside of the Alexander Archipelago), the juvenile salmon caught at these stations were not included in our analyses because some of the fish originated from outside Southeast Alaska (Orsi et al. 2000).

Fish were sampled with a Nordic 264 rope trawl (18-m-deep, 24-m-wide mouth opening) towed at 1.5 m/s in surface waters; each haul lasted 20 min. The surface hauls have the potential to miss some juvenile Chinook salmon as these fish prefer to reside deep in the water column, a preference that increases with size (Orsi and Wertheimer 1995). However, we believe that this trawl effectively sampled juvenile Chinook salmon in our study area because at this stage of ocean residency, Chinook salmon would be within the expected depth range of the net (Weitkamp 2004). Furthermore, studies comparing catches made at the surface with those at greater depths (i.e., using similar nets) found that most juvenile salmon, including Chinook salmon, were near the surface (Beamish et al. 2000; Emmett et al. 2004).

Concurrent oceanographic and biological sampling at all stations included conductivity, temperature, and depth profiles; sea surface temperature and salinity measurements (both at 3-m depth); ambient light intensity; and vertical and oblique plankton net tows. Zooplankton standing stock in the top 20 m of the water column was estimated from shallow (20-m) vertical tows made at each station with a 50-cm-diameter, 243-μm-mesh North Pacific standard (NORPAC) plankton net. On board the vessel, zooplankton samples were concentrated and preserved in a 5% solution of formalin and seawater. In the laboratory, each NORPAC zooplankton sample was allowed to settle for 24 h in an Imhoff cone, and the zooplankton settled volume (mL) was then measured.

All collected fish were immediately identified to species, counted, and measured (FL; mm); juvenile salmon were individually tagged and bagged and were immediately frozen for later

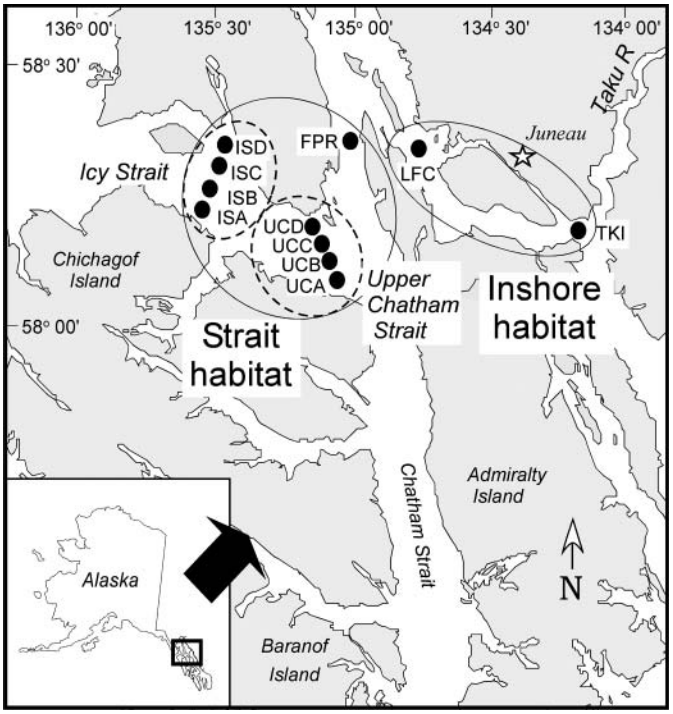

FIGURE 2. Locations of 11 stations (black circles) where juvenile Chinook salmon and coho salmon were sampled in marine waters of the northern region of Southeast Alaska. Stations represented two habitat types (strait habitat: 9 stations; inshore habitat: 2 stations), designated based on physical characteristics and fish community composition (ISA–ISD = Icy Strait sites A–D; UCA–UCD = Upper Chatham Strait sites A–D; FPR = False Point Retreat; LFC = lower Favorite Channel; TKI = Taku Inlet).

laboratory analysis. In the laboratory, thawed juvenile salmon were remeasured (FL; mm) and weighed (g), and their scales were removed for growth analysis.

Origins of Juvenile Salmon

Origin (natal source) information was used to validate our analyses because salmon survival rates are estimated for each river or hatchery of origin. Therefore, linking fish characteristics to survival rates can only be accomplished when fish represent the populations upon which the survival rates are based (i.e., those from Southeast Alaska). Accordingly, all juvenile salmon were checked for the presence of coded wire tags (CWTs). For each tagged juvenile salmon, we extracted the CWT, read the tag code, and then determined the release location, release date, and type of rearing (hatchery or wild) for that tag code (available from an online CWT database; RMIS 2006). We used this release information with the date and location of recovery of each tagged fish to calculate the number of days since release (i.e., recovery date minus release date); using the appropriate navigational chart, we also estimated the minimum marine distance traveled from the release site to the recovery site (point-to-point waterway distance). We also estimated the marine migration rate as the distance traveled divided by the days since release. Using the Mann–Whitney (MW) rank-sum test corrected for ties, we tested the hypothesis that tagged juvenile Chinook salmon and coho salmon had statistically similar days, distances, and migration rates between release and recovery. The MW rank-sum test corrected for ties relies on ranks rather than actual measurements to evaluate differences between two samples and is a nonparametric analog to the two-sample t-test (Zar 1984).

We could not determine the hatchery or wild origin of untagged fish because a large number of unmarked hatchery fish (i.e., those without adipose fin clips or CWTs) were released in Southeast Alaska (ADFG 2010). Because of this, unmarked fish represented unknown mixtures of both hatchery and wild fish. Although some hatcheries in Southeast Alaska were thermally marking juvenile Chinook salmon and coho salmon, most were not. Therefore, analysis of otoliths for thermal marks was not conducted because it would not have identified all hatchery individuals. The MW rank-sum test corrected for ties was applied to untransformed data for comparisons of migration metrics (time, distance traveled, and migration rate between release and recovery) between hatchery ($n = 32$) and wild ($n = 10$) coho salmon with CWTs. Unfortunately, the number of known wild Chinook salmon recovered ($n = 2$) was too low to permit meaningful comparisons of these metrics between wild and hatchery Chinook salmon. Likewise, the low number of known wild coho salmon caught each month prevented us from evaluating possible differences in size by origin.

Analytical Approach

The goal of all analyses was to explore how various aspects of the early marine ecology (e.g., abundance, distribution, species associations, size, and growth rate) differed between juvenile Chinook salmon and coho salmon and thereby detect mechanism(s) to explain the differential survival of the two species in Southeast Alaska. To simplify analyses and increase sample sizes, fish were grouped by species, month, or habitat. We did not include year as a variable in our analysis because although there were clear species differences in marine survival (Figure 1; analysis of variance [ANOVA]: $F = 207$, $P < 0.05$), neither origin (hatchery versus wild) nor interannual variation in marine survival was statistically significant (ANOVA: $F < 1.2, P > 0.10$). This finding was based on marine survival rates (arcsine–square-root-transformed survival; Sokal and Rohlf 1995) of hatchery and wild populations in Southeast Alaska for ocean entry years 1997–2000, which were examined by ANOVA with species, year, and origin as variables. Wild coho salmon used in the analysis were from the Auke Creek, Taku River, Unuk River, Berners River, Hugh Smith Lake, and Ford Arm Lake populations; hatchery coho salmon originated from Medvejie, Hidden Falls, and Deer Lake hatcheries (data from NSRAA 2003; Shaul et al. 2003; RMIS 2006). Wild Chinook salmon were from the Taku River and Unuk River populations; hatchery Chinook salmon were from Crystal and Whitman lakes and from the Hidden Falls, Medvejie, Tamgas Creek, Neets Bay, and Macaulay/Gastineau hatcheries (NSRAA 2003; Shaul et al. 2003; RMIS 2006). In addition, physical conditions (e.g.,

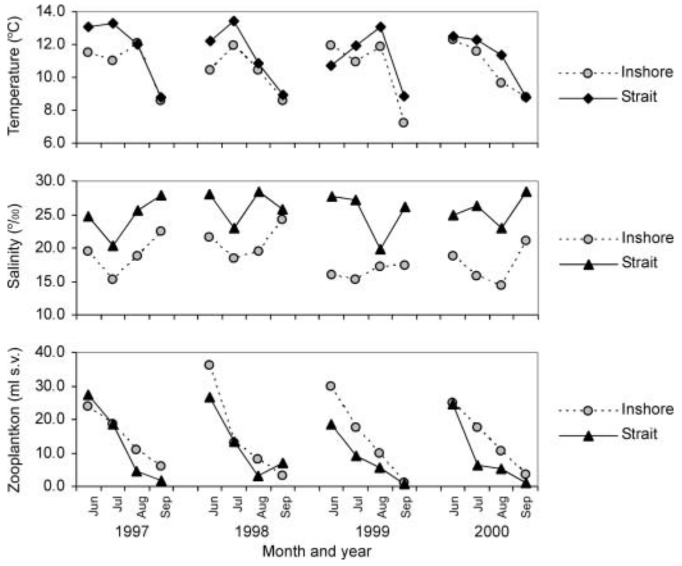

FIGURE 3. Surface (3 m) temperature, surface salinity, and zooplankton standing stock (mL settled volume [s.v.] from 20-m vertical hauls) measured in inshore and strait habitats (see Figure 2) of northern Southeast Alaska by the Southeast Coastal Monitoring study.

surface temperature, salinity, and zooplankton standing stock) were fairly consistent between years but displayed marked differences by habitat type and month (ANOVA: $F > 11$, $P < 0.05$; Figure 3). Consequently, our analyses focused on variation between species in each month and habitat type but not in individual years. Weitkamp (2004) provides a more thorough analysis of interannual variation in most traits, which was consistent with patterns observed when years were combined.

Distributions, abundance, and community associations.—Differences in the catch of juvenile Chinook salmon and coho salmon in time (month) and space (habitat type) were explored with ANOVA. To accomplish this, the two species were analyzed separately or together by using $\log_e(x+1)$ transformed catch per unit effort, where effort was one 20-min haul. For significant test results, differences were further evaluated by use of Bonferroni multiple comparison tests (Sokal and Rohlf 1995).

We employed two complementary methods to explore community associations of juvenile Chinook salmon and coho salmon. First, relationships within the larger fish community were evaluated by a cluster analysis based on the catch (number) of the 16 most frequently caught groups of fish (i.e., species or age-classes within species) in the 201 hauls conducted in inshore and strait habitats during June–September 1997–2000. This analysis relied on a resemblance matrix produced from Bray–Curtis similarities on square-root-transformed catch data for each species in each of the 201 hauls; Bray–Curtis similarities in this application ranged from 0% (no catches in common) to 100% (identical catches). The similarity matrix was used in hierarchical agglomerative clustering based on group-averaging linkages. The statistical validity of the resulting dendrogram was evaluated by the similarity profile algorithm, which tests for the significance of each node by permutation (Clarke et al. 2008). Similar dendrograms resulted from analyses with more (or fewer) species and different transformations, suggesting that the patterns were robust to the specific method used. This analysis was conducted with PRIMER-E software (Clarke and Gorley 2006).

Second, we explicitly compared the juvenile abundances of all salmon species (Chinook salmon, coho salmon, pink salmon, chum salmon, and sockeye salmon) in the 186 hauls in which at least one juvenile salmon was caught. This was accomplished by calculating pairwise Spearman's rank correlation coefficients (r_S) for the number of juveniles from each salmon species caught in each haul (Sokal and Rohlf 1995).

Size and growth.—Differences in length or weight of juvenile salmon were compared by using two-sample t-tests formulated for unequal variances (Zar 1984) on $\log_e(x + 1)$ transformed data. Because salmon were growing rapidly throughout the summer, these comparisons were restricted to months and were made between species within habitats and within species between habitats. Because of distributional differences between Chinook salmon and coho salmon, however, analyses that tested for both habitat and species effects simultaneously (e.g., two-way ANOVA) were hampered by empty cells and low sample sizes and were abandoned in favor of single-factor tests (i.e., either habitat or month; Kruskal–Wallis H-test). Population growth rates and comparisons of size can be confounded by factors such as migration, stock-specific or origin-specific (hatchery or wild) size differences, and size-dependent survival. Differences in body shape between species and habitats were explored by using analysis of covariance (ANCOVA) on $\log_e(x + 1)$ transformed length and weight data with weight used as the covariate. Comparisons were made for all Chinook salmon and coho salmon (regardless of month), for all Chinook salmon and coho salmon in each month, and within species between habitats across months.

Growth rates were estimated at the population level for Chinook salmon and coho salmon and at the individual level for Chinook salmon only. Population-based growth rates were determined from the mean sizes (length or weight) observed during the four monthly sampling periods, and growth was estimated as the change in size within habitats between months. This method is based on the critical assumption that the fish collected in a particular habitat during a given month are the same (or similarly sized) stock groups as fish collected there in subsequent months. Because of this assumption, we restricted growth rate estimates to fish within a given habitat type (i.e., inshore or strait) rather than between habitats (e.g., as if fish moved from inshore habitat to strait habitat). Absolute changes in FL (G_L; mm/d) were calculated as

$$G_L = (L_y - L_x)/(t_y - t_x), \tag{1}$$

where L_y and L_x are FLs at times t_y and t_x. Instantaneous changes in weight (G_W; % body weight [BW]/d) were calculated as

$$G_W = \{100 \times [\log_e(W_y) - \log_e(W_x)]\}/(t_y - t_x), \quad (2)$$

where W_y and W_x are weights at times t_y and t_x (Ricker 1975). To provide adequate sample sizes, these estimates were based on data from fish caught in different years even though the fish were clearly not part of the same population. Weitkamp (2004) estimated year-specific growth rates when sufficient data were available ($n > 5$ fish) and found that they were similar in magnitude to estimates calculated across years, which suggests that this violation of the assumption did not unduly influence our results.

Individual growth rates were estimated from the scales of 182 juvenile Chinook salmon by using standard techniques (Davis et al. 1990). Scale analysis was also conducted on juvenile coho salmon (Briscoe et al. 2005) but was not conducted in a way that allowed back-calculation of fish size. Chinook salmon scales were collected from the preferred area of the body (Davis et al. 1990), mounted on slides, and analyzed with a video imaging system developed specifically for scale data collection (BioSonics Model OPR-512 optical pattern recognition system). Fish age and life history zones (e.g., freshwater and ocean growth) on the scales were assigned based on visual examination. The number and spacing of circuli within each zone were measured along the longest axis in the anterior (sculptured) field of the scale. The length of Chinook salmon at annulus formation (L_a) was estimated by using the Fraser–Lee back-calculation method (Ricker 1992),

$$L_a = [(L - 43.7895)/R] \times R_a + 43.7895, \quad (3)$$

where L is FL at capture, R is scale radius at capture, R_a is scale radius at annulus formation, and 43.7895 is the intercept from the R–L regression (i.e., the estimated FL at scale formation). The size at annulus formation is assumed to be the size at saltwater entry. Weights at various stages (e.g., annulus formation, saltwater entry, and penultimate circulus formation) were estimated from the equation $W = aL^b$, where W is weight (g) at capture, a is the intercept of the $\log_e(L)$–$\log_e(W)$ regression, and b is the slope of the regression. Differences in scale-based estimates of growth or size were compared between months and habitat types by use of ANOVA. Length-based growth data met normality assumptions, but L_a and instantaneous growth rate did not and therefore were $\log_e(x + 1)$ transformed. Significant test results ($P < 0.05$) were further evaluated by using Bonferroni multiple comparison tests (Sokal and Rohlf 1995).

Environmental variability.—We looked at the potential effects of environmental conditions (temperature, salinity, and zooplankton standing stock) on juvenile salmon distributions and size. The environmental conditions under which each individual Chinook salmon or coho salmon was caught were compared by using a MW rank-sum test for each environmental variable (Sokal and Rohlf 1995). We also examined whether juvenile salmon size (FL) was related to temperature by using linear regression. This comparison was made across all Chinook salmon and coho salmon and by month and habitat type (e.g., Chinook salmon caught in inshore habitats during June) to explore how the relationship varied. Similar patterns from the analysis of temperature on weight were explored by Weitkamp (2004).

RESULTS

Origins of Juvenile Salmon

The CWTs recovered from juvenile Chinook salmon and coho salmon indicated that all fish originated from Southeast Alaska (Table 1). In total, 69 CWTs (28 from Chinook salmon; 41 from coho salmon) were recovered from the 414 juvenile Chinook salmon and 1,107 juvenile coho salmon caught in strait and inshore habitats. The tags represented both hatchery fish ($n = 57$) and wild fish ($n = 12$) from Southeast Alaskan populations. Based on these findings, we concluded that untagged juvenile salmon used in our analysis were representative of Southeast Alaska stocks and their associated marine survival rates. Analysis of CWTs and thermal otolith marks from juvenile Chinook salmon and coho salmon from the SECM study in subsequent years further supported this conclusion (Orsi et al. 2002, 2003).

Despite the common origins, however, the time, distance, and marine migration rates from release to recovery differed greatly between tagged Chinook salmon and coho salmon. On average, juvenile Chinook salmon traveled a shorter distance after release than did coho salmon (72 versus 101 km), but it took them longer to do so (74 versus 45 d). Thus, the migration rate observed for coho salmon (4.2 km/d) was nearly four times that observed for Chinook salmon (1.2 km/d). All differences were statistically significant (MW rank-sum test: $Z > 2.7$, $P < 0.05$).

Because fish with CWTs were the only ones for which hatchery or wild origin was known, we explored whether the migration estimates varied by origin. We found that hatchery coho salmon traveled farther after release than did wild coho salmon (113 versus 84 km), but they spent longer doing so (53 versus 35 d), resulting in a lower rate of travel (3.3 versus 6.6 km/d). However, only the difference in distance traveled was statistically significant (Kruskal–Wallis test: $H = 9.1$, $P < 0.01$).

Chinook Salmon and Coho Salmon Abundance and Distribution

Based on monthly sampling (June–September 1997–2000) at 11 stations representing strait and inshore habitats, catches of juvenile Chinook salmon were both smaller and less frequent than those of juvenile coho salmon. Total catch of juvenile Chinook salmon (414 fish) was nearly one-third that of juvenile coho salmon (1,107 fish), and Chinook salmon were caught less often (in 43% of 201 hauls) than were coho salmon (66% of hauls). However, Chinook salmon and coho salmon constituted minor

TABLE 1. Origin (rearing type: H = hatchery; W = wild) and recovery data for coded-wire-tagged juvenile Chinook salmon and coho salmon that were recovered from strait (S) and inshore (I) habitats of northern Southeast Alaska. All release localities were within Southeast Alaska. The mean number of days, distance traveled, and migration rate between release and recovery are also presented.

Release location	Rearing type	Number recovered	Days since release	Distance from release site (km)	Migration rate (km/d)	Recovery habitat type
			Juvenile Chinook salmon			
Auke Bay	H	3	47	5	0.1	I
Fish Creek	H	10	64	11	0.2	I
Gastineau Channel	H	4	53	50	0.9	I
Kasnyku Bay	H	5	71	137	1.9	I, S
Little Port Walter	H	3	103	223	2.2	I, S
Medvejie Bear Cove	H	1	126	235	1.9	I
Taku River	W	2	137	60	0.4	I
			Juvenile coho salmon			
Auke Creek	W	2	42	65	1.5	S
Berners River	W	6	39	81	2.1	S
Chilkat River	W	1	30	120	4.0	S
Duck Creek	H	1	42	75	1.8	S
Gastineau Channel	H	12	44	103	2.3	I, S
Kasnyku Bay	H	11	37	125	3.4	S
Sheep Creek	H	7	66	93	1.4	I, S
Taku River	W	1	45	100	2.2	S

percentages of the juvenile salmon community (total catch = 22,702 juvenile salmonids), contributing only 1.8% (Chinook salmon) and 4.9% (coho salmon) of the juvenile salmonid catch. In contrast, chum salmon exhibited a much higher abundance at 45.0% (10,227 fish) of the salmonid catch, pink salmon contributed 42.9% (9,739 fish), and sockeye salmon contributed 4.9% (1,215 fish).

There were spatial and temporal differences in abundance and distribution between juvenile Chinook salmon and coho salmon (Figure 4). Catches of Chinook salmon were highest in inshore habitats (ANOVA: $F = 99.6$, $P < 0.01$) and remained relatively high throughout the summer, whereas Chinook salmon catches in strait habitats were low in June and July but increased by September; this resulted in a significant month × habitat interaction ($F = 2.9$, $P < 0.05$). In contrast, catches of juvenile coho salmon were highest in strait habitats in June and July but declined in August and September; a similar pattern but at much lower levels was observed for coho salmon in inshore habitats (ANOVA: $F > 10.1$, $P < 0.05$).

Fish Community Associations

The cluster analysis indicated that juvenile Chinook salmon and coho salmon had fundamentally different associations with other fish species based on their positions in the resulting dendrogram (Figure 5). Juvenile Chinook salmon loosely grouped with Pacific spiny lumpsuckers *Eumicrotremus orbis* (similarity = 26%) and crested sculpin *Blepsias bilobus* (similarity = 35%), the latter of which are often associated with jellyfish (Orsi et al. 2006). By contrast, juvenile coho salmon clustered with other juvenile salmon (pink salmon, chum salmon, and sockeye salmon) with a similarity of 46%. These two clusters were separated from each other at a similarity of only 15%, suggesting that they had little in common. The similarity profile test indicated

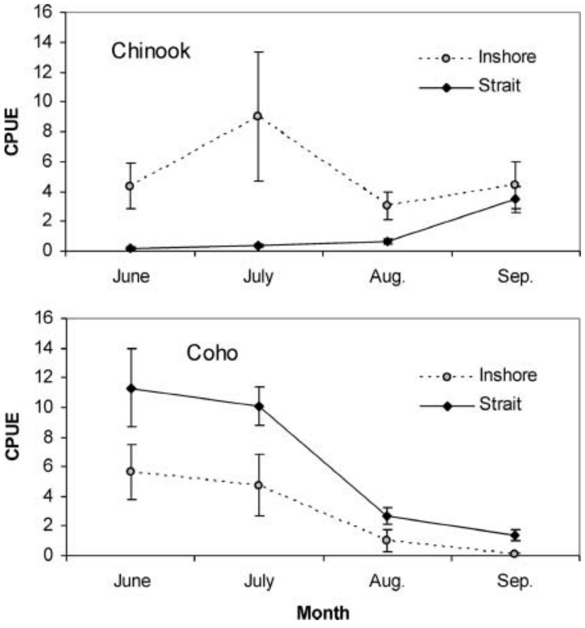

FIGURE 4. Mean (±SD) catch per unit effort (CPUE; fish per 20-min haul) for juvenile Chinook salmon and coho salmon within inshore and strait habitats of northern Southeast Alaska (data presented for each month are averaged across years).

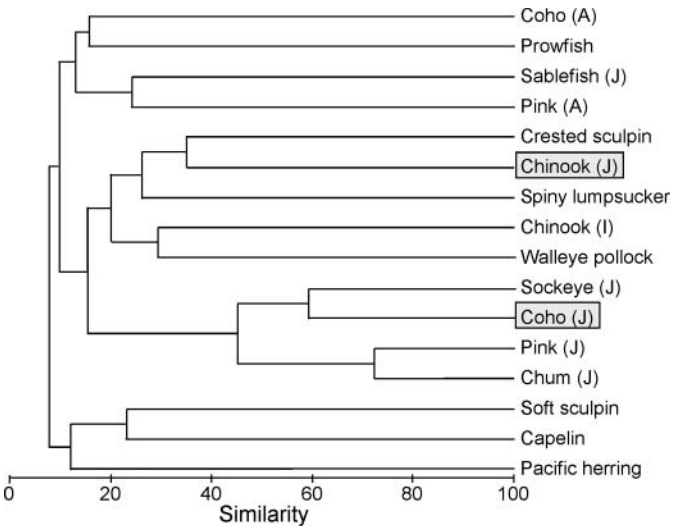

FIGURE 5. Cluster analysis (with % similarity) of the 16 most abundant groups of fish caught within inshore and strait habitats of northern Southeast Alaska during summer in 1997–2000 (age-class designations: A = adult; I = immature; J = juvenile). Species without specified age-classes consist of multiple age-classes. Species include coho salmon *O. kisutch* (coho), prowfish *Zaprora silenus*, sablefish *Anoplopoma fimbria*, pink salmon *O. gorbuscha* (pink), crested sculpin *Blepsias bilobus*, Chinook salmon *O. tshawytscha* (Chinook), Pacific spiny lumpsucker *Eumicrotremus orbis*, walleye pollock *Theragra chalcogramma*, sockeye salmon *O. nerka* (sockeye), chum salmon *O. keta* (chum), soft sculpin *Psychrolutes sigalutes*, capelin *Mallotus villosus*, and Pacific herring *Clupea pallasii*. All clusters were significant ($P < 0.05$).

that all major and minor clusters were statistically significant ($P < 0.05$).

Distinct associations between Chinook salmon and coho salmon were also produced when only the abundances of juvenile salmon in each haul were considered. Large catches of juvenile coho salmon often coincided with large catches of pink salmon, chum salmon, and sockeye salmon ($r_S = 0.35$–0.46, $P < 0.05$; Figure 6), but juvenile Chinook salmon were rarely caught together with coho salmon ($r_S = -0.34$, $P < 0.05$) or with juveniles of the other three salmonid species ($r_S = -0.21$ to -0.31, $P < 0.05$). This indicates little spatial or temporal overlap between coho salmon and Chinook salmon at the finest spatial scale (i.e., one trawl haul of about 1.8 km).

Pacific herring, similar to juvenile Chinook salmon, were primarily caught in inshore habitats (97% of 2,444 individuals caught), suggesting potential habitat overlap. However, the cluster analysis indicated that juvenile Chinook salmon and Pacific herring clusters were widely separated and had little in common (similarity = 8%). For hauls in which at least one Chinook salmon or Pacific herring was caught ($n = 101$), the Chinook salmon catch was independent of Pacific herring catch ($r_S = -0.02$, $P > 0.10$). Although both species occupied inshore habitats, their distributions were quite different at fine spatial and temporal scales. Taken as a whole, both the cluster and correlation analyses indicated that whereas juvenile coho salmon were caught in strait habitats together with abundant juvenile pink salmon, chum salmon, and sockeye salmon, juvenile Chinook salmon traveled alone in inshore habitats.

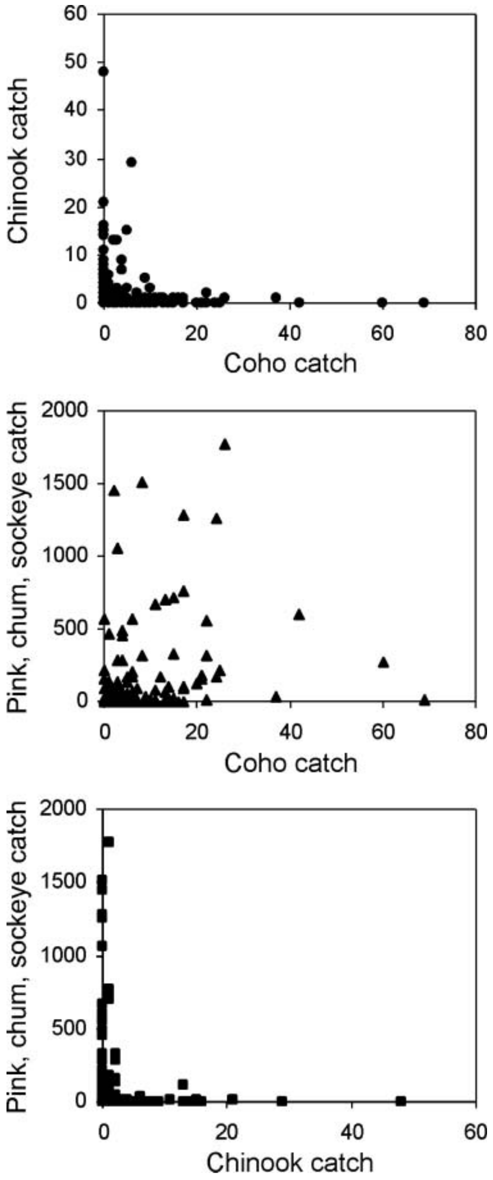

FIGURE 6. Plots of juvenile salmon catch per haul (in 186 hauls that contained at least one juvenile salmon) within inshore and strait habitats of northern Southeast Alaska: Chinook salmon versus coho salmon (top panel); pink salmon, chum salmon, and sockeye salmon versus coho salmon (middle panel); and pink salmon, chum salmon, and sockeye salmon versus Chinook salmon (bottom panel).

Size Comparisons

Length and weight data were available from 336 juvenile Chinook salmon and 897 coho salmon that were caught in inshore and strait habitats. Juvenile coho salmon were consistently longer and weighed more than juvenile Chinook salmon in any

TABLE 2. Results of two-sample *t*-tests comparing fork length (FL) and weight of juvenile Chinook salmon and coho salmon sampled from strait and inshore habitats of northern Southeast Alaska. Comparisons were made between the two species, between the two habitat types within each species, and between the two species within each habitat type. Nonsignificant ($P > 0.05$) test statistics are in bold italics. Catch of coho salmon in inshore habitats during August and September was insufficient for analysis ($n < 5$ fish).

Comparison	Month	FL: *t*-value	Weight: *t*-value
Chinook salmon vs. coho salmon (both habitats)	Jun	4.0	4.4
	Jul	14.0	9.4
	Aug	6.6	4.4
	Sep	7.0	5.2
Chinook salmon inshore vs. strait	Jun	8.0	6.8
	Jul	5.1	5.8
	Aug	10.0	9.8
	Sep	13.9	14.5
Coho salmon inshore vs. strait	Jun	5.6	5.4
	Jul	2.7	***1.9***
Inshore Chinook salmon vs. inshore coho salmon	Jun	***0.1***	***0.0***
	Jul	***0.8***	***0.8***
Strait Chinook salmon vs. strait coho salmon	Jun	3.7	2.6
	Jul	***0.3***	***1.4***
	Aug	***0.6***	2.0
	Sep	3.1	***1.1***

given month (Table 2; Figure 7; $t > 4.4$, $P < 0.05$). This size difference increased from 15 mm and 18 g in June to 33 mm and 58 g in September. For both species, individuals in inshore habitats were smaller than individuals in strait habitats (Table 2; Figure 7). Therefore, juvenile Chinook salmon were smaller in areas where they were abundant (inshore habitats) than in areas where they were not abundant (strait habitats). In contrast, juvenile coho salmon were larger in areas where they were abundant (strait habitats) than in areas where they were not abundant (inshore habitats). Size comparisons between the two species within habitats, however, suggested that neither species was consistently larger than the other within a particular habitat.

The shape of juvenile salmon also varied; Chinook salmon generally weighed more for a given length than did coho salmon (ANCOVA test of means [TOM]: $F_{\text{TOM}} = 70$, $P < 0.05$). This shape difference increased with fish size (ANCOVA test of slope: $F = 125$, $P < 0.05$) and was significant for all months ($F_{\text{TOM}} > 79$, $P < 0.05$) except June ($F_{\text{TOM}} = 0.6$, $P = 0.42$). Accordingly, by September, a 300-mm-long Chinook salmon would weigh 18% more than a coho salmon of identical length (381 versus 323 g, respectively). Chinook salmon in strait habitats also weighed more for a given length than Chinook salmon in inshore habitats ($F_{\text{TOM}} = 21$, $P < 0.05$), but comparable habitat-specific differences in body shape were not observed for coho salmon ($F_{\text{TOM}} = 2.5$, $P = 0.11$).

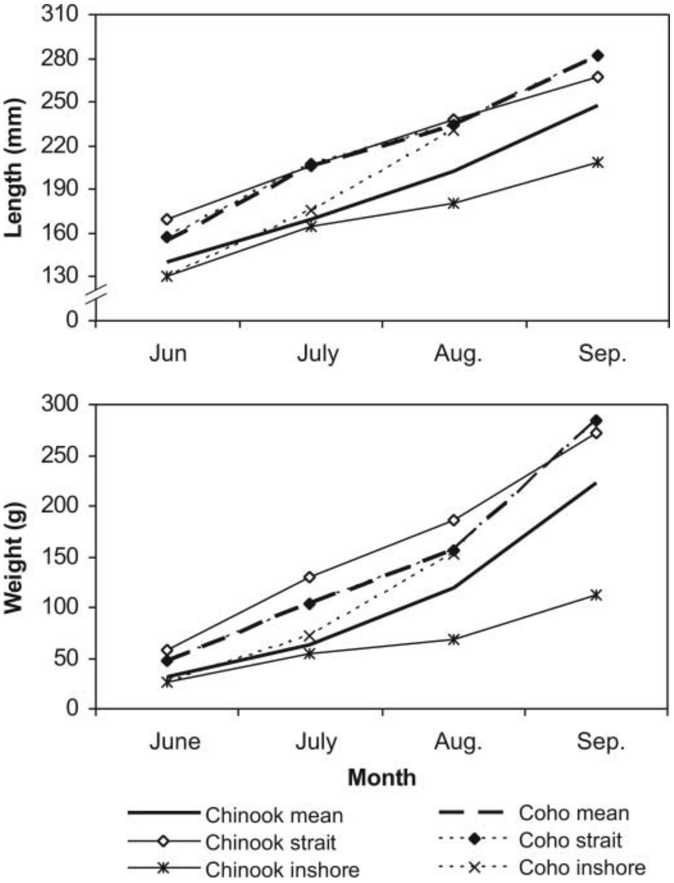

FIGURE 7. Mean fork length and weight of juvenile Chinook salmon and coho salmon caught in inshore habitat, strait habitat, and both habitat types (mean) within northern Southeast Alaska.

Growth Rates

Growth rates were estimated at the population level (i.e., based on changes in mean fish size each month) and individual level (determined from scales for Chinook salmon only). Population-based growth rates of juvenile salmon were positive throughout the summer (June–September) but were lower overall for Chinook salmon (0.9 mm/d, 1.6% BW/d) than for coho salmon (1.3 mm/d, 1.9% BW/d; Figure 8). Growth rates were generally highest early in the summer (June–July: 1.2–2.1 mm/d, 2.6–4.3% BW/d), were lowest in midsummer (July–August: 0.5–1.1 mm/d, 0.9–1.9% BW/d), and increased by late summer (August–September: 0.8–1.4 mm/d, 1.1–1.7% BW/d). Growth rates in each habitat type were generally similar for each species except that during midsummer (July–August), the Chinook salmon growth rate was greater in strait habitats than in inshore habitats.

Because the assumption that the fish measured each month were the same individuals is unlikely to be absolutely true, these population growth rates are approximate at best. Given this caveat, Chinook salmon and coho salmon growth rates, especially growth in weight, were surprisingly similar. The

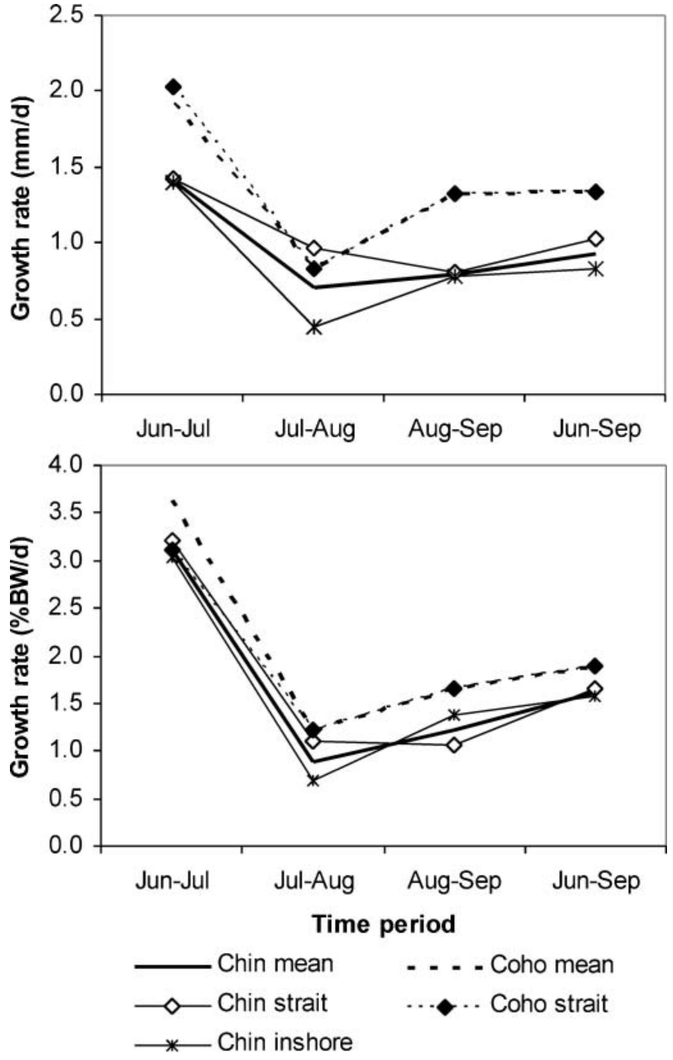

FIGURE 8. Population-based growth rates of juvenile Chinook salmon (Chin) and coho salmon, presented as changes in fork length or body weight (BW) for monthly intervals during summer. Growth rates for coho salmon in inshore habitats were anomalously high during June–July (2.0 mm/d, 4.1% BW/d) and are not shown; growth rates in August and September were not estimated due to low abundances after July ($n < 5$).

unusually high growth rates for coho salmon in inshore habitats during June (4.1% BW/d) probably reflect relatively small sample sizes (10 fish in June; 24 fish in July) and possible violations of the aforementioned assumption.

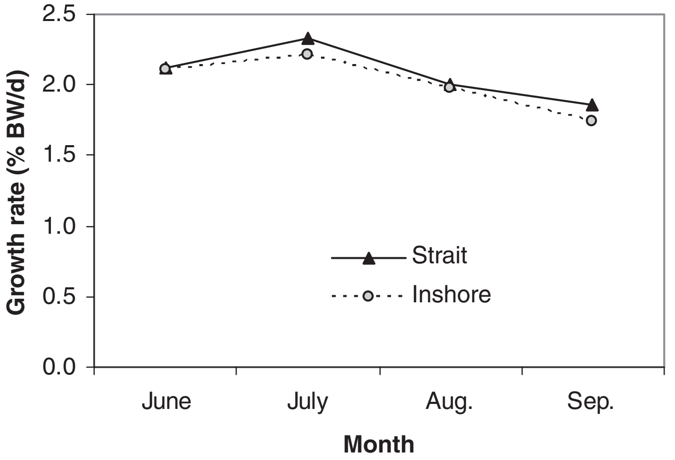

FIGURE 9. Individual-based growth rates (body weight [BW]) of juvenile Chinook salmon as estimated from scale analysis for fish collected in inshore and strait habitats of northern Southeast Alaska.

Growth rates of individual Chinook salmon as estimated from scale features were similar to population-based growth rates in both magnitude and seasonal patterns, suggesting that population-based growth rate estimates were not drastically different from true growth rates. For example, average individual-based growth rates after ocean entry (1.0 mm/d, 2.0% BW/d) were only slightly higher than population-based growth rates throughout the summer (June–September: 0.9 mm/d, 1.6% BW/d); individual-based growth rates were also highest in early summer (June–July: 2.3% BW/d; Figure 9) and declined by late summer (August–September: 1.8% BW/d; Figure 9; ANOVA: $F = 9.3$, $P < 0.05$). Similar to the population-based growth rates, individual-based growth rates in length were also higher for fish captured in strait habitats than for those captured in inshore habitats (ANOVA: $F = 38$, $P < 0.05$); however, weight growth rates were similar between the two habitat types (ANOVA: $F = 1.0$, $P > 0.10$).

The scale analysis also revealed several differences between Chinook salmon collected in inshore habitats and strait habitats. In particular, the value of L_a (assumed to be length at ocean entry) was significantly greater for Chinook salmon collected in strait habitats (125.2 mm FL) than for those collected in inshore habitats (112.1 mm FL), regardless of the month of capture (ANOVA: $F = 21.4$, $P < 0.05$). In addition, relative to Chinook salmon caught in strait habitats, the scales of Chinook salmon caught in inshore habitats during late summer (August–September) had more growth that was intermediate (circulus spacing = 29 μm) between relatively slow freshwater growth (25 μm) and fast marine growth (39 μm; ANOVA: $F > 3.5$, $P < 0.05$).

Environmental Variation

Temperature, salinity, and zooplankton standing stock were typically higher in strait habitats (where most coho salmon were caught) than in inshore habitats (where most Chinook salmon were caught; Figure 3). Accordingly, waters where juvenile Chinook salmon were caught were significantly colder (10.2°C), were less saline (21.7‰), and had a lower zooplankton standing stock (settled volume = 11.5 mL) than waters where juvenile coho salmon were caught (12.2°C, 25.0‰, and 15.4 mL, respectively; MW rank-sum test: $Z > 3.4$, $P < 0.05$).

We also explored whether temperature was associated with the body length of juvenile salmon. Examined across all individuals of a given species (Chinook salmon or coho salmon), temperature was significantly and negatively related to length, although the relationship was not particularly strong in either case (Chinook salmon: $r^2 = 0.29$, $F = 137$, $P < 0.05$; coho salmon: $r^2 = 0.05$, $F = 52$, $P < 0.05$). When examined by month and habitat type, however, strong seasonal and spatial trends in the data weakened the relation between temperature and fish length. That is, temperatures were coldest in September, when fish were largest, and were typically colder in inshore habitats, where fish were usually smaller relative to those in strait habitats. Changes in the strength and direction of the relationship between temperature and body length at different spatial and temporal scales suggest that temperature had relatively little consistent influence on juvenile salmon length.

DISCUSSION

We evaluated abundance, distribution, species associations, size, shape, and growth rates of juvenile Chinook salmon and coho salmon during their first summer in Southeast Alaska marine environments to explore possible mechanisms responsible for the higher marine survival rates of coho salmon relative to Chinook salmon. We expected that higher marine survival rates in coho salmon would be due to their larger size, faster growth, and perhaps beneficial species associations during the critical first summer in the ocean. Our expectations were not entirely supported by the data, despite the 10-fold difference in marine survival between these two species in Southeast Alaska.

Size, Growth, and Survival

Our expectations for differential sizes between Chinook salmon and coho salmon were supported by the data, but differential growth rates were less clear. Overall, coho salmon were larger than Chinook salmon in any given month (Figure 7) and grew faster (population-based growth rates; Figure 8), as we had expected. However, population-based growth rates were approximate at best, and individual Chinook salmon growth rates in weight (2.0% BW/d) actually exceeded the population-based growth rates observed for coho salmon (1.9% BW/d), reflecting the tendency of Chinook salmon to grow more in body girth than in length. Seasonal changes in the abundance of Chinook salmon suggested that some fish moved from inshore habitats to strait habitats in September; recovery of tagged fish from the same hatcheries in both inshore and strait habitats validated this movement (Table 1). However, the decrease in abundance within the inshore habitats may also reflect mortality; population-based growth rates estimated as if Chinook salmon moved from inshore habitats to strait habitats were extremely high ($\geq$3.8% BW/d; Weitkamp 2004). Consequently, while coho salmon were definitely larger than Chinook salmon overall, differences in the species' growth rates were less clear. Growth rates reported here for both species are comparable to estimates from the Pacific Northwest (Table 3), suggesting that juveniles in Southeast Alaska do not have a regional growth advantage.

Our size estimates and population-based growth rates depend on the assumption that we were measuring the same group of fish

TABLE 3. Comparison of estimated growth rates in fork length (FL) and body weight (BW) during the first summer of ocean residence for yearling (age-1.0) Chinook salmon and coho salmon in marine environments. Growth rates were estimated from scales of individual fish (individual) or from changes in mean size of fish in the population between time periods (population). Blank cells indicate that no data were available.

Location	Method	FL (mm/d)	Weight (%BW/d)	Source[a]
		Chinook salmon		
Southeast Alaska	Individual	0.9	2.0	This study
	Population	0.9	1.6	
	Population	1.1–1.4		Trudel et al. 2007
Strait of Georgia	Population	0.8–0.9	0.7–2.1	Healey 1980
Washington, Oregon coasts	Population	0.7–0.9		Trudel et al. 2007
		Coho salmon		
Southeast Alaska	Population	1.3	1.9	This study
	Population	1.3–1.5		Trudel et al. 2007
West Coast of Vancouver Island	Population	1.2–1.3		Trudel et al. 2007
Strait of Georgia	Population	0.7–1.0		Beamish et al. 2008
Puget Sound	Population		1.7	Mathews and Buckley 1976
Washington, Oregon coasts	Individual and population	1.3–1.8	1.5–2.6	Fisher and Pearcy 1988, 2005
	Population	1.2–1.3		Trudel et al. 2007
Southern Oregon, northern California coasts	Individual[b]	1.1–1.7	1.8–2.8	Brodeur et al. 2004

[a] Growth rates from Trudel et al. (2007) were estimated based on their Figure 5; those from Beamish et al. (2008) were estimated based on FLs provided in their Table 6.
[b] Estimates do not include individuals that were identified as jacks (precocious males).

(or a similarly sized group) each month. However, we know that Southeast Alaska hatchery fish at the time of release are typically larger (120–140 mm FL; RMIS 2006) than equivalent-aged wild fish (70–100 mm FL; Murphy et al. 1997; Halupka et al. 2000; Shaul et al. 2003; Pahlke et al. 2010), and recent studies suggest that hatchery fish are likely to maintain this size advantage over wild fish during the first summer in the ocean (Sweeting and Beamish 2009; Daly et al., in press). Other than the 69 individuals with CWTs, determinations of the hatchery or wild origin of individuals were not possible; therefore, we could not estimate the relative abundance of either group. Consequently, a change in the relative proportions of large hatchery fish and small wild fish between months would have been mistakenly interpreted as growth. Without more information on the origins of individual fish in our samples, we cannot estimate the degree to which this confounding factor influenced our growth estimates.

Moreover, two available estimates of the proportions of hatchery and wild salmon in our samples suggest very different ratios. Based on the presence of otolith thermal marks, Orsi et al. (2002–2004) estimated that most of the Chinook salmon (61–100%) but few of the coho salmon (5–11%) captured during the SECM study in 2001–2003 were of hatchery origin. However, only a few Southeast Alaskan hatcheries were thermally marking juvenile Chinook salmon and coho salmon at that time (ADFG 2010), so some of the unmarked fish were undoubtedly of hatchery origin, resulting in underestimates of hatchery proportions. By contrast, comparisons of estimated smolt production suggest that for Chinook salmon and especially for coho salmon, hatchery smolts should have outnumbered wild smolts either in the northern portion of Southeast Alaska (from which most of the tagged salmon originated; Table 1) or in Southeast Alaska as a whole (Table 4; McNair 1998–2001; Shaul et al. 2003; McPherson et al. 2010; Pahlke et al. 2010). The ratio of hatchery to wild smolts ranges from 1.3:1.0 (Chinook salmon in Southeast Alaska) to 7.3:1.0 (coho salmon in Southeast Alaska; Table 4) and is still large (>0.5:1.0) if wild production estimates (which are minimum values) are doubled. Clearly, the marking of hatchery fish is critical to obtain a full understanding of how salmon origin influences salmon marine ecology.

Furthermore, despite the caveats about population-based growth rates being confounded by the presence of hatchery fish, we do not believe that this factor had a large influence on our estimates. In particular, population- and individual-based growth rates estimated for Chinook salmon were similar, which would be unlikely if population-based growth rates had been biased by changes in the hatchery fish proportion between months. Although we did not have comparable individual-based growth rates for coho salmon, population-based growth rates for this species were consistent between years (Weitkamp 2004), which would not be expected if the ratio of hatchery to wild fish varies between years, as it undoubtedly does. Finally, our growth rates are similar in magnitude to those observed elsewhere in the North Pacific (Table 3), suggesting that our estimates were no more confounded than those presented in other studies.

TABLE 4. Estimated production of wild and hatchery Chinook salmon and coho salmon smolts for Southeast Alaska and for only the northern region of Southeast Alaska (NSE Alaska) during ocean entry years 1997–2000. Data are from McNair (1998–2001), Shaul et al. (2003), McPherson et al. (2010), and Pahlke et al. (2010).

Region	Chinook salmon smolts (millions)	Coho salmon smolts (millions)
Wild smolt production[a]		
Southeast Alaska	5.1	2.3
NSE Alaska	1.7	1.5
Hatchery production[b]		
Southeast Alaska	6.7	16.7
NSE Alaska	3.3	4.1
Ratio of hatchery : wild production		
Southeast Alaska	1.3:1.0	7.3:1.0
NSE Alaska	1.9:1.0	2.7:1.0

[a] Chinook salmon wild smolt production was estimated from the Taku River (McPherson et al. 2010) for NSE Alaska and from the Taku and Stikine rivers for Southeast Alaska; we used average smolt production for 2000–2004 because estimates for 1997–1999 were not available (Pahlke et al. 2010). Coho salmon wild smolt production was estimated from Auke Creek, Berners River, and Taku River for NSE Alaska and from those three systems plus Ford Arm Lake, Hugh Smith Lake, and Unuk River for Southeast Alaska (Shaul et al. 2003).

[b] Hatchery production (both species) for NSE Alaska was tallied from releases at Hidden Falls, Medvejie, Macaulay, Burro Creek, Little Port Walter, and Auke Creek hatcheries and their satellite facilities. Hatchery production for Southeast Alaska included those hatcheries plus the releases from Whitman Lake, Neets Bay, Burnett Inlet, Bell Island, Port Armstrong, Snettisham, Deer Mountain, Gunnuk Creek, Sheldon Jackson, Tamgas Creek, Klawock, and Crystal Lake hatcheries and their satellite facilities (McNair 1998–2001).

The degree to which larger size and rapid growth contribute to the high marine survival rates of juvenile coho salmon is also unclear. Briscoe et al. (2005) and LaCroix et al. (2009) determined that marine growth rates were largely independent of marine survival for Southeast Alaska coho salmon. However, Lum (2003) found that the largest coho salmon smolts emigrating from Auke Creek (near Juneau) had the highest survival rates during the 1990s, although this advantage dissolved for smolts emigrating after the peak migration time, when marine survival rates declined regardless of smolt size. In contrast, a similar study conducted a decade earlier (Shaul and Van Alen 2001) and a recent study that examined hatchery coho salmon near Auke Creek (Linley 2001) found no evidence for size-based survival differences.

It is also unclear whether the smaller size of juvenile Chinook salmon in inshore habitats contributes to their lower survival rates. Presumably, smaller individuals are more vulnerable to predators. However, chum salmon marine survival rates from several hatcheries in the northern region of Southeast Alaska (3.1–4.5% for releases in 1983–1999) were considerably higher than those of Chinook salmon (average = 1.6%) released from the same facilities during the same years (NSRAA 2003). This survival difference occurred even though (1) chum salmon were released at a much smaller size (nearly an order of magnitude smaller by weight) than yearling Chinook salmon smolts and (2) the two species returned from the ocean at similar ages. Thus, low Chinook salmon marine survival rates may be attributable not only to their small size (compared with that of coho salmon) but also to other factors that influence survival.

Distributions, Species Associations, and Survival

One factor that exhibited unexpectedly large differences between the two species was distribution: juvenile Chinook salmon were largely confined to inshore habitats, particularly during the early part of the summer (June and July), whereas juvenile coho salmon were primarily caught in strait habitats. Because of these distributional differences, coho salmon were surrounded by and caught together with juvenile pink salmon and chum salmon, which were both an order of magnitude more abundant than coho salmon but were also smaller in size (Jaenicke and Celewycz 1994; Orsi et al. 2000). By contrast, Chinook salmon were largely caught by themselves or with Pacific spiny lumpsuckers or crested sculpin; these latter species are neither abundant (fewer than 45 individuals of either species were caught over the 4 years) nor relatively elongated like juvenile salmon, making them unlikely substitute prey for predators that target juvenile salmon. Pacific herring also used inshore habitats, but their catches were not correlated with those of Chinook salmon, suggesting that they provide a limited predation buffer at best.

These fine-scale distributional differences suggest that coho salmon in strait habitats may benefit from a predation buffer that does not extend to the inshore habitats occupied by Chinook salmon. By the time Chinook salmon occupy strait habitats (i.e., later in the summer), most of the other juvenile salmon have left the area, effectively removing the predation buffer. Positive (i.e., buffering) rather than negative (i.e., competition) consequences of the high spatial and temporal overlap between coho salmon and abundant pink salmon and chum salmon are suggested by the limited diet overlap between these species (Landingham et al. 1998; Brodeur et al. 2007), the low incidence of empty stomachs among all juvenile salmonids in Southeast Alaska (Brodeur et al. 2007), and the extremely high productivity in the region (Orsi et al. 2004).

Buffers against predation are believed to be important for juvenile salmon survival in marine (e.g., Willette 1999; Emmett et al. 2005) and freshwater (e.g., Ruggerone 1992) systems. Recent analyses provide strong support for the presence of predation buffers benefiting Southeast Alaskan coho salmon (Briscoe et al. 2005; LaCroix et al. 2009). These studies found that regional abundances of juvenile chum salmon, pink salmon, or both explained the greatest variance in coho salmon survival or commercial catch (a proxy for marine survival), providing the best fit for any parameter explored. In contrast, Malick et al. (2009) found little evidence for widespread positive correlations between pink salmon and chum salmon fry abundances (either hatchery or wild) and coho salmon marine survival rates in Southeast Alaska. However, Malick et al. (2009) only considered local pink salmon and chum salmon abundances (i.e., around the mouths of natal streams for coho salmon) rather than regional abundances (northern portion of Southeast Alaska). If we are correct in our hypothesis that predation buffering in strait habitats is important for coho salmon survival, then it occurs at a time when juvenile pink salmon and chum salmon from many populations are intermingled (Orsi et al. 2000–2004) and when local population densities near stream mouths may or may not be important. Furthermore, many studies have documented strong positive correlations in marine survival trends between Southeast Alaska coho salmon populations (Shaul et al. 2003; Briscoe et al. 2005; Malick et al. 2009; Teo et al. 2009), consistent with regional-scale factors controlling marine survival, such as predation buffers in areas (e.g., strait habitats) inhabited by juvenile salmon from many rivers.

If coho salmon are indeed benefiting from a predation buffer provided by juvenile pink salmon and chum salmon, then coho salmon probably profit from the extensive production of chum salmon at Southeast Alaska hatcheries, which released 364 million fry annually during 1997–2000 (McNair 1998–2002). For example, of the juvenile chum salmon caught during the SECM study in 2000–2002, approximately half (44–59%) were of hatchery origin (Orsi et al. 2001–2003).

If differential predation on juvenile Chinook salmon and coho salmon is at least partially responsible for the differential marine survival, then knowledge of the predator species and their abundances is clearly important. Unfortunately, little is known about avian or marine mammal predation on juvenile salmon in Southeast Alaska's marine waters. Piscine predators caught by the SECM study included adult coho salmon, sablefish, spiny dogfish *Squalus acanthias*, and walleye pollock (Orsi et al. 2000; Sturdevant et al. 2009). Additional research on both the seasonal timing of predation and the size of prey consumed by predators will be required in order to gain a full understanding of the potentially different predation rates on juvenile Chinook salmon and coho salmon.

Our results suggest that major processes controlling survival may be both habitat specific and species specific: the survival of Chinook salmon residing in inshore habitats and the survival of coho salmon occupying strait habitats are potentially influenced by two different suites of factors. Coho salmon may receive greater protection from predation by the presence of millions of smaller juvenile pink salmon and chum salmon, while Chinook salmon probably do not benefit from this predation buffer and therefore may suffer greater predation-related mortality.

Contrasting Life History Strategies of Chinook Salmon and Coho Salmon

If indeed the high marine survival rates of coho salmon result from predation buffers that do not extend to Chinook salmon because of habitat use differences, then this raises the perplexing question of why Chinook salmon behave as they do, especially if it results in such low marine survival rates. Our results from the first summer in the ocean, when paired with differences observed both before and after this period, suggest fundamentally different habitat utilization patterns between the two species throughout their life cycles. The Chinook salmon strategy must be successful for it to exist (Thorpe 1999); however, the particular advantage conferred by this strategy under the current highly productive ocean conditions is unclear.

Although Chinook salmon and coho salmon in Southeast Alaska share many life history traits that probably subject them to similar factors influencing their marine survival rates (e.g., size and timing at ocean entry, as discussed earlier), there are also substantial differences. For example, coho salmon inhabit thousands of mainland and island river basins, whereas Chinook salmon are largely restricted to large mainland rivers in the eastern portion of the region (Baker et al. 1996). The two species also have different ocean migrations. Juvenile coho salmon are largely absent from Southeast Alaska during the fall and winter (Fisher et al. 2007; Morris et al. 2007), only returning in summer as maturing adults. By contrast, some Southeast Alaskan Chinook salmon populations move rapidly to oceanic waters, while others remain within Southeast Alaska for most of their marine life history phase (Orsi and Jaenicke 1996; Halupka et al. 2000; Fisher et al. 2007; Trudel et al. 2009).

Our work indicates that there are additional life history differences early in the marine residency period. The obvious distributional differences between the two species suggest extensive habitat partitioning. By occupying different habitats (i.e., Chinook salmon in inshore habitats and coho salmon in strait habitats), the two species minimize potentially competitive interactions, which may be important given their high overlap in diets (Weitkamp and Sturdevant 2008). Similar subtle distributional differences have been observed for juvenile Chinook salmon and coho salmon in coastal waters of the northern California Current, which indicates that the patterns we observed in Southeast Alaska are not unique. For example, several studies have shown that although yearling Chinook salmon and coho salmon have generally similar distributions, yearling Chinook salmon are located in shallower water closer to shore than juvenile coho salmon (e.g., Brodeur et al. 2004; Bi et al. 2007; Fisher et al. 2007; Peterson et al. 2010). However, how these differences influence the survival of the two salmon species in this region has not been determined.

Chinook salmon and coho salmon also appear to use these habitats differently in Southeast Alaska. Most juvenile coho salmon spend 1–2 months in protected waters of the study area before leaving for oceanic waters by mid- to late summer. By contrast, juvenile Chinook salmon linger in protected waters for at least the summer if not longer (Orsi and Wertheimer 1995; Orsi and Jaenicke 1996; Halupka et al. 2000). These patterns are apparent from our catch data (Figure 4) and from our CWT recoveries: on average, the migration rate of tagged juvenile coho salmon was four times that of tagged Chinook salmon (Table 1).

Analysis of scales also indicated finer-scale variation within this general pattern of lingering by Chinook salmon in protected habitats. The smaller size at ocean entry and the presence of intermediate growth regions on scales of individuals occupying inshore habitats suggest that these fish and the Chinook salmon residing in strait habitats use different pathways. The pathways probably diverge prior to ocean entry and continue in marine environments such that larger individuals occupy strait habitats and smaller individuals occupy inshore habitats. Although these patterns are intriguing, many questions remain, such as (1) whether Chinook salmon caught in inshore habitats and strait habitats represent similar stocks (suggesting within-population "bet-hedging" via multiple strategies) or different stocks (indicating a genetic basis to the patterns) and (2) which freshwater areas were associated with these differential growth rates and thus led to the discrepancies in size at ocean entry. Annual scale growth in Chinook salmon can exhibit a strong dependency on the previous year's growth (Ruggerone et al. 2007). Thus, size at ocean entry may be reflected in growth (and perhaps survival) throughout the life span of Chinook salmon. Clearly, this is an interesting line of research to pursue but is beyond the scope of the present study.

Furthermore, low marine survival rates of Chinook salmon in Southeast Alaska potentially place some populations' persistence at risk. However, Chinook salmon typically have nearly twice the fecundity (5,401 eggs/female) and a considerably larger egg size (300 mg/egg) than coho salmon (2,878 eggs/female and 220 mg/egg; Quinn 2005). Larger egg size may result in higher egg-to-smolt survival for Chinook salmon, while higher overall fecundity allows Chinook salmon to persist at comparable or perhaps higher overall survival rates than coho salmon despite the considerably lower marine survival rates (Quinn 2005). This tactic is apparently less susceptible to the boom-and-bust cycles exhibited by pink salmon, chum salmon, sockeye salmon, and coho salmon in Southeast Alaska, which have reached record abundances in recent years (e.g., Geiger et al. 2003; Heinl et al. 2003; McPherson et al. 2003; Shaul et al. 2003; Zadina et al. 2003). Although it is entirely speculative, perhaps the benefits of the strategy employed by Chinook salmon are greatest when marine productivity is low. In this situation, lingering in inshore habitats may provide a safeguard against otherwise hostile open-ocean conditions, thus allowing the strategy to succeed.

In summary, we compared the early marine ecology of juvenile Chinook salmon and coho salmon to investigate potential processes that may have led to the higher marine survival rates of coho salmon relative to Chinook salmon in Southeast Alaska. Our results indicate that fairly minor differences in spatial or temporal distribution led to large differences in community composition that potentially provided a substantial predation buffer to coho salmon but not to Chinook salmon. Thus, the mechanisms regulating survival may be both habitat specific and species specific. Our results also indicate that during the early marine phase, Chinook salmon adopt a size-dependent strategy characterized by a tendency for small individuals to linger in protected habitats after juveniles of other salmon species have departed.

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REFERENCES

ADFG (Alaska Department of Fish and Game). 2010. Mark, tag, and aging lab database. ADFG. Available: tagotoweb.adfg.state.ak.us. (November 2010).

Baker, T. T., A. C. Wertheimer, R. Burkett, D. R. Dunlap, D. M. Eggers, E. I. Fritts, A. J. Gharrett, R. A. Holmes, and R. L. Wilmot. 1996. Status of Pacific salmon and steelhead escapements in southeastern Alaska. Fisheries 21:6–18.

Beamish, R., D. Noakes, G. McFarlane, W. Pinnix, R. Sweeting, and J. R. King. 2000. Trends in coho marine survival in relation to the regime concept. Fisheries Oceanography 9:114–119.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Transactions of the American Fisheries Society 133:26–33.

Beamish, R. J., R. M. Sweeting, K. L. Lange, and C. M. Neville. 2008. Changes in the population ecology of hatchery and wild coho salmon in the Strait of Georgia. Transactions of the American Fisheries Society 137:503–520.

Beckman, B. R., W. W. Dickhoff, W. S. Zaugg, C. Sharpe, S. Hirtzel, R. Schrock, D. A. Larsen, R. D. Ewing, A. Palmisano, C. B. Schreck, and C. V. Mahnken. 1999. Growth, smoltification, and smolt-to-adult return of spring Chinook salmon from hatcheries on the Deschutes River, Oregon. Transactions of the American Fisheries Society 128:1125–50.

Bi, H., R. E. Ruppel, and W. T. Peterson. 2007. Modeling the pelagic habitat of salmon off the Pacific Northwest (USA) coast using logistic regression. Marine Ecology Progress Series 336:249–265.

Briscoe, R. J., M. D. Adkison, A. Wertheimer, and S. G. Taylor. 2005. Biophysical factors associated with the marine survival of Auke Creek, Alaska, coho salmon. Transactions of the American Fisheries Society 134:817–828.

Brodeur, R. D., E. A. Daly, M. V. Sturdevant, T. W. Miller, J. H. Moss, M. Thiess, M. Trudel, L. A. Weitkamp, J. L. Armstrong, and E. C. Norton. 2007. Regional comparisons of juvenile salmon feeding in coastal marine waters off the West Coast of North America. Pages 183–203 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Brodeur, R. D., J. P. Fisher, D. J. Teel, R. L. Emmett, E. Casillas, and T. W. Miller. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the northern California Current. U.S. National Marine Fisheries Service Fishery Bulletin 102:25–46.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER version 6: user manual/tutorial. PRIMER-E, Plymouth, UK.

Clarke, K. R., P. J. Somerfield, and R. N. Gorley. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 330:55–80.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 55:2067–2077.

Cross, A. D., D. A. Beauchamp, J. H. Moss, and K. W. Myers. 2009. Interannual variability in early marine growth, size-selective mortality, and marine survival for Prince William Sound pink salmon. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 1:57–70.

Daly, E. A., R. D. Brodeur, J. P. Fisher, L. A. Weitkamp, D. J. Teel, and B. R. Beckman. In press. Spatial and trophic overlap of hatchery marked and unmarked Columbia River basin spring Chinook salmon during early marine life with implications for competition between hatchery and naturally produced fish. Environmental Biology of Fishes. DOI: 10.1007/510641-011-9857-4.

Davis, N. D., K. W. Myers, R. V. Walker, and C. K. Harris. 1990. The Fisheries Research Institute's high-seas salmonid tagging program and methodology for scale pattern analysis. Pages 863–879 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

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

Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2005. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Progress in Oceanography 68:1–26.

Fisher, J., M. Trudel, A. Ammann, J. A. Orsi, J. Piccolo, C. Bucher, E. Casillas, J. A. Harding, B. MacFarlane, R. D. Brodeur, J. F. Morris, and D. W. Welch. 2007. Comparisons of the coastal distributions and abundances of juvenile Pacific salmon from central California to the northern Gulf of Alaska. Pages 31–80 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA in years of differing coastal upwelling. Canadian Journal of Fisheries and Aquatic Sciences 45:1036–1044.

Fisher, J. P., and W. G. Pearcy. 2005. Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in spacing of scale circuli. U.S. National Marine Fisheries Service Fishery Bulletin 103:34–51.

Gallego, A., E. W. North, and P. Petitgas. 2007. Introduction: status and future of modeling physical-biological interactions during the early life of fishes. Marine Ecology Progress Series 347:121–126.

Geiger, H. J., M. R. Cartwright, J. H. Clark, J. Conitz, S. C. Heinl, K. Jensen, B. Lewis, A. J. McGregor, R. Riffe, G. Woods, and T. P. Zadina. 2003. Sockeye salmon stock status and escapement goals in Southeast Alaska. Alaska Department of Fish and Game, Regional Information Report 1J03-04, Juneau.

Govoni, J. J. 2005. Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. Scientia Marina 69(Supplement 1):125–137.

Halupka, K. C., M. D. Bryant, M. F. Willson, and F. H. Everest. 2000. Biological characteristics and population status of anadromous salmon in Southeast Alaska. U.S. Forest Service General Technical Report PNW-GTR-468.

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. Pages 203–229 *in* W. J. McNeil and D. C. Himsworth, editors. Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.

Heinl, S. C., T. P. Zadina, A. J. McGregor, and H. J. Geiger. 2003. Chum salmon stock status and escapement goals in Southeast Alaska. Alaska Department of Fish and Game, Regional Information Report 1J03-08, Juneau.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181–2194.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology (Washington, D.C.) 73:724–732.

Jaenicke, J. W., and A. G. Celewycz. 1994. Marine distribution and size of juvenile Pacific salmon in Southeast Alaska and northern British Columbia. U.S. National Marine Fisheries Service Fishery Bulletin 92:79–90.

Jonsson, N., B. Jonsson, and L. P. Hansen. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. Journal of Applied Ecology 40:900–911.

LaCroix, J. J., A. C. Wertheimer, J. A. Orsi, M. V. Sturdevant, E. A. Fergusson, and N. A. Bond. 2009. A top-down survival mechanism during early marine residency explains coho salmon year-class strength in Southeast Alaska. Deep-Sea Research Part II: Topical Studies in Oceanography A56:2560–2569.

Landingham, J. H., M. V. Sturdevant, and R. D. Brodeur. 1998. Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. U.S. National Marine Fisheries Service Fishery Bulletin 96:285–302.

Linley, T. J. 2001. Influence of short-term estuarine rearing on the ocean survival and size at return of coho salmon in southeastern Alaska. North American Journal of Aquaculture 63:306–311.

Logerwell, E. A., N. J. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 126:554–568.

Lum, J. L. 2003. Effects of smolt length and emigration timing on marine survival and age at maturity of wild coho salmon (*Oncorhynchus kisutch*) at Auke Creek, Juneau, Alaska. Master's thesis. University of Alaska, Fairbanks.

Malick, M. J., M. D. Adkison, and A. C. Wertheimer. 2009. Variable effects of biological and environmental processes on coho salmon marine survival in Southeast Alaska. Transactions of the American Fisheries Society 138:846–860.

Mathews, S. B., and R. Buckley. 1976. Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*). Journal of the Fisheries Research Board of Canada 33:1677–1684.

McNair, M. 1998. Alaska salmon enhancement program, 1997, annual report. Alaska Department of Fish and Game, Regional Information Report 5J98-03, Juneau.

McNair, M. 1999. Alaska salmon enhancement program, 1998, annual report. Alaska Department of Fish and Game, Regional Information Report 5J99-02, Juneau.

McNair, M. 2000. Alaska salmon enhancement program, 1999, annual report. Alaska Department of Fish and Game, Regional Information Report 5J00-02, Juneau.

McNair, M. 2001. Alaska salmon enhancement program, 2000, annual report. Alaska Department of Fish and Game, Regional Information Report 5J01-01, Juneau.

McNair, M. 2002. Alaska salmon enhancement program, 2001, annual report. Alaska Department of Fish and Game, Regional Information Report 5J02-04, Juneau.

McPherson, S., D. R. Bernard, J. H. Clark, K. A. Pahlke, E. Jones, J. Der Hovanisian, J. Weller, and R. P. Ericksen. 2003. Stock status and escapement goals for Chinook salmon stocks in Southeast Alaska. Alaska Department of Fish and Game, Special Publication 03-01, Anchorage.

McPherson, S., E. L. Jones, S. J. Fleischman, and I. M. Boyce. 2010. Optimal production of Chinook salmon from the Taku River through the 2001 year class. Alaska Department of Fish and Game, Fishery Manuscript 10-03, Anchorage.

Morris, J. F., M. Trudel, M. E. Thiess, R. M. Sweeting, J. Fisher, S. A. Hinton, E. A. Fergusson, J. A. Orsi, E. V. Farley, and D. W. Welch. 2007. Stock-specific migrations of juvenile coho salmon derived from coded-wire tag recoveries on the Continental Shelf of western North America. Pages 81–104 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Moss, J. H., D. A. Beauchamp, A. D. Cross, K. W. Myers, E. V. Farley, J. M. Murphy, and J. H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Transactions of the American Fisheries Society 134:1313–1322.

Murphy, M. L., J. F. Thedinga, and K. V. Koski. 1997. Downstream migrations of juvenile Pacific salmon (*Oncorhynchus* spp.) in a glacial transboundary river. Canadian Journal of Fisheries and Aquatic Sciences 54:2837–2846.

Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon in the Oregon production area. Canadian Journal of Fisheries and Aquatic Sciences 43:527–535.

NSRAA (Northern Southeast Regional Aquaculture Association). 2003. Hatchery survival data. Available: www.nsraa.org. (October 2003).

Orsi, J. A., E. A. Fergusson, W. R. Heard, D. G. Mortensen, M. V. Sturdevant, A. C. Wertheimer, and B. L. Wing. 2002. Survey of juvenile salmon in the marine waters of southeastern Alaska, May–August 2001. North Pacific Anadromous Fish Commission, Document 630, Vancouver.

Orsi, J. A., E. A. Fergusson, M. V. Sturdevant, B. L. Wing, W. R. Heard, A. C. Wertheimer, and D. G. Mortensen. 2003. Survey of juvenile salmon in the marine waters of southeastern Alaska, May–August 2002. North Pacific Anadromous Fish Commission, Document 702, Vancouver.

Orsi, J. A., E. A. Fergusson, M. V. Sturdevant, B. L. Wing, A. C. Wertheimer, and W. R. Heard. 2006. Annual survey of juvenile salmon and ecologically related species and environmental factors in the marine waters of southeastern Alaska, May–August 2005. North Pacific Anadromous Fish Commission, Document 955, Vancouver.

Orsi, J. A., and H. W. Jaenicke. 1996. Marine distribution and origin of prerecruit Chinook salmon, *Oncorhynchus tshawytscha*, in southeastern Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 94:482–497.

Orsi, J. A., M. V. Sturdevant, J. M. Murphy, D. G. Mortensen, and B. L. Wing. 2000. Seasonal habitat use and early marine ecology of juvenile Pacific salmon in southeastern Alaska. North Pacific Anadromous Fish Commission Bulletin 2:111–122.

Orsi, J. A., M. V. Sturdevant, A. C. Wertheimer, B. L. Wing, J. M. Murphy, D. G. Mortensen, E. A. Fergusson, and B. K. Krauss. 2001. Survey of juvenile salmon in the marine waters of southeastern Alaska, May–August 2000. North Pacific Anadromous Fish Commission, Document 536, Vancouver.

Orsi, J. A., and A. C. Wertheimer. 1995. Marine vertical distribution of juvenile Chinook and coho salmon in southeastern Alaska. Transactions of the American Fisheries Society 124:159–169.

Orsi, J. A., A. C. Wertheimer, M. V. Sturdevant, E. A. Fergusson, D. G. Mortensen, and B. L. Wing. 2004. Juvenile chum salmon consumption of zooplankton in marine waters of southeastern Alaska: a bioenergetics approach to implications of hatchery stock interactions. Reviews in Fish Biology and Fisheries 14:335–359.

Pahlke, K. A., P. Richards, and P. Etherton. 2010. Production of Chinook salmon from the Stikine River, 1999–2002. Alaska Department of Fish and Game, Fishery Data Series 10-03, Anchorage.

Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28:1503–1510.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.

Peterson, W. T., C. A. Morgan, J. P. Fisher, and E. Casillas. 2010. Ocean distribution and habitat associations of yearling coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon in the northern California Current. Fisheries Oceanography 19:508–525.

Pyper, B. J., F. J. Mueter, and R. M. Peterman. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of northeast Pacific salmon. Transactions of the American Fisheries Society 134:86–104.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191.

Ricker, W. E. 1992. Back-calculation of fish lengths based on proportionality between scale and length increments. Canadian Journal of Fisheries and Aquatic Sciences 49:1018–1026.

RMIS (Regional Mark Information System). 2006. Coded wire tag database. Pacific States Marine Fisheries Commission, Regional Mark Processing Center, Portland, Oregon. Available: www.rmpc.org. (September 2006).

Ruggerone, G. T. 1992. Threespine stickleback aggregations create a potential predation refuge for sockeye fry. Canadian Journal of Zoology 70:1052–1056.

Ruggerone, G. T., J. L. Nielsen, and B. Agler. 2007. Retrospective analysis of AYK Chinook salmon growth. Arctic Yukon Kuskokwim Sustainable Salmon Initiative, 2007 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Product, Anchorage. Available: ayk.ssi.org. (September 2010).

Salminen, M., S. Kuikka, and E. Erkamo. 1995. Annual variability in survival of sea-ranched Baltic salmon, *Salmo salar* L.: significance of smolt size and marine conditions. Fisheries Management and Ecology 2:171–184.

Shaul, L., S. McPherson, E. Jones, and K. Crabtree. 2003. Stock status and escapement goals for coho salmon stocks in Southeast Alaska. Alaska Department of Fish and Game, Southeast Region, Special Publication 03-02, Anchorage.

Shaul, L., L. Weitkamp, K. Simpson, and J. Sawada. 2007. Trends in abundance and size of coho salmon in the Pacific Rim. North Pacific Anadromous Fish Commission Bulletin 4:93–104.

Shaul, L. D., and B. Van Alen. 2001. Status of coho salmon stocks in the northern boundary area through 1998. Alaska Department of Fish and Game, Regional Information Report 1J01-01, Juneau.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129–1157.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd edition. Freeman, New York.

Sturdevant, M. V., M. F. Sigler, and J. A. Orsi. 2009. Sablefish predation on juvenile Pacific salmon in the coastal marine waters of Southeast Alaska. Transactions of the American Fisheries Society 138:675–691.

Sweeting, R. M., and R. J. Beamish. 2009. A comparison of the diets of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia from 1997–2007. North Pacific Anadromous Fish Commission Bulletin 5:255–264.

Teo, S. L. H., L. W. Botsford, and A. Hastings. 2009. Spatio-temporal covariability in coho salmon (*Oncorhynchus kisutch*) survival, from California to Southeast Alaska. Deep- Sea Research II: Topical Studies in Oceanography A56:2570–2578.

Thorpe, J. E. 1999. Flexible life-history strategies: a context for understanding migration in salmonids. Bulletin of the Tohoku National Fisheries Research Institute 62:151–164.

Trudel, M., J. Fisher, J. A. Orsi, J. F. Morris, M. E. Thiess, R. M. Sweeting, S. Hinton, E. A. Fergusson, and D. W. Welch. 2009. Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. Transactions of the American Fisheries Society 138:1396–1391.

Trudel, M., S. R. Jones, M. E. Thiess, J. F. Morris, D. W. Welch, R. M. Sweeting, J. H. Moss, B. L. Wing, E. V. Farley, J. M. Murphy, R. E. Baldwin, and K. C. Jacobson. 2007. Regional variation in marine growth and energy accumulation of juvenile Chinook salmon and coho salmon along the West Coast of North America. Pages 205–232 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Weitkamp, L. A. 2004. Ocean conditions, marine survival, and performance of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in Southeast Alaska. Doctoral dissertation. University of Washington, Seattle.

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

Willette, T. M. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Canadian Journal of Fisheries and Aquatic Sciences 56:364–376.

Willette, T. M., R. T. Cooney, V. Patrick, D. M. Mason, G. L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fisheries Oceanography 10(Supplement 1):14–41.

Zadina, T. P., S. C. Heinl, A. J. McGregor, and H. J. Geiger. 2003. Pink salmon stock status and escapement goals in southeast Alaska and Yakutat. Alaska Department of Fish and Game, Regional Information Report 1J03-06, Juneau.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.