Abstract—We investigated estuarine spatial and temporal overlap of wild and marked hatchery chum salmon (*Oncorhynchus keta*) fry; the latter included two distinct size groups released near the Taku River estuary (Taku Inlet) in Southeast Alaska (early May releases of ~ 1.9 g and late May releases of ~ 3.9 g wet weight). Our objectives were to compare abundance, body size, and condition of wild chum salmon fry and hatchery chum salmon fry raised under early and late rearing strategies in different habitats of Taku Inlet and to document environmental factors that could potentially explain the distribution, size, and abundance of these chum salmon fry. We used a sampling design stratified into inner and outer inlet and neritic and littoral habitats. Hatchery fry were rare in the inner estuary in both years but outnumbered wild fry 20:1 in the outer estuary. Hatchery fry were significantly larger than wild fry in both littoral and neritic samples. Abundances of wild and hatchery fry were positively correlated in the outer inlet, indicating the formation of mixed schools of hatchery and wild fry. Spatial and temporal overlap was greatest between wild and early hatchery fry in the outer inlet in both habitats. The early hatchery release coincided with peak abundances of wild fry in the outer inlet, and the distribution of wild and early hatchery fry overlapped for about three weeks. Our results demonstrate that the timing of release of hatchery fry may affect interactions with wild fry.

Spatial and temporal distribution and the potential for estuarine interactions between wild and hatchery chum salmon (*Oncorhynchus keta*) in Taku Inlet, Alaska

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Salmonids have been reared and released from hatcheries since the nineteenth century (Olla et al., 1998) and enhancement facilities now exist worldwide (e.g., Mahnken et al., 1998; Kaeriyama, 1999; Zaporohzets and Zaporohzets, 2004). Many authors have expressed concern that large-scale salmonid hatcheries may diminish fitness and productivity of wild populations (Hilborn and Eggers, 2000; Einum and Fleming, 2001; Zaporozhets and Zaporozhets, 2004; Araki et al., 2007). Others have shown that hatchery releases support the recovery of declining populations (Heard et al., 1995; Brannon et al., 2004) and can enhance fisheries without impacting wild stocks (e.g., Bachen and Linley, 1995; Heard et al., 1995; Wertheimer, 1997). Hatchery salmonids can impact wild fish in a number of ways, such as through spawning interactions, genet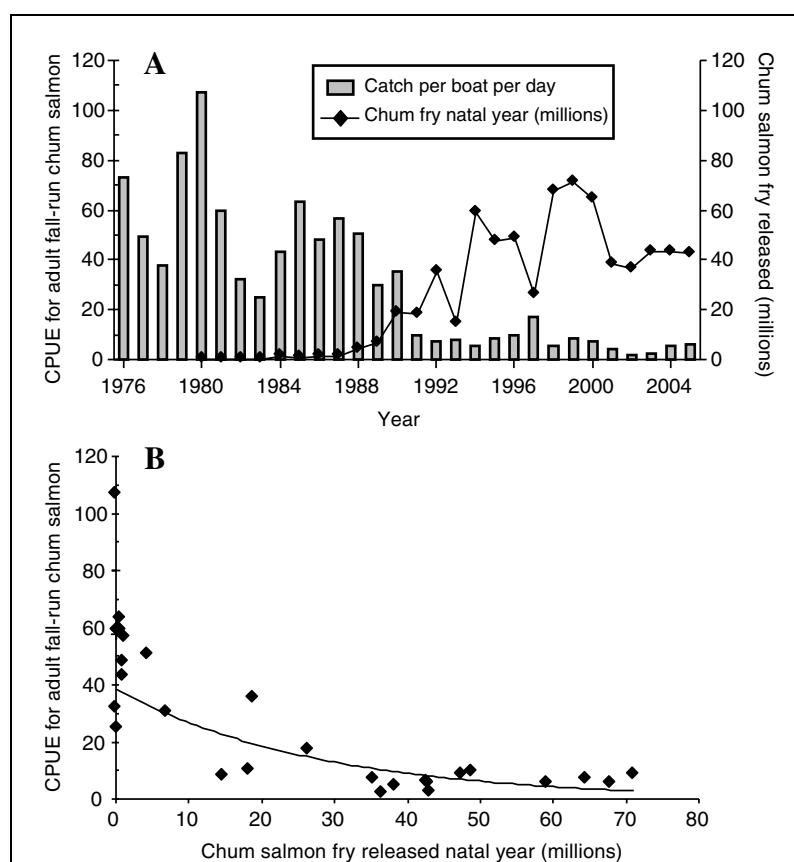ic interactions, inducing over-harvesting, and by trophic or behavioral interactions during estuarine and oceanic life-history phases (Levings et al., 1986; Bigler et al., 1996; Olla et al., 1998). Hatchery salmonids can also impact wild fry populations by either attracting predators that selectively eat smaller wild fry (Hargreaves and LeBrasseur 1986; Wertheimer and Thrower, 2007; Duffy and Beauchamp, 2008) or hatchery salmonids can benefit wild populations by buffering wild fry from predators (Willette et al., 2001; Briscoe et al., 2005). The potential for hatchery fish to affect wild fish increases with the degree of spatial and temporal overlap between fishes of similar life-history stages. Hatcheries often employ different rearing and release strategies to reduce these impacts, such as releasing fry away from streams that produce wild fish (Bachen and Linley, 1995; Heard et al., 1995) or releasing

fry later at a larger size to reduce overlap with wild fry, thus decreasing nearshore residency of hatchery fish and increasing survival of wild fish (Kaeriyama, 1999; Wertheimer and Thrower, 2007).

Douglas Island Pink and Chum (DIPAC), an enhancement hatchery near Juneau, Alaska, uses two different release strategies simultaneously for chum salmon (*Oncorhynchus keta*). These strategies provide an opportunity to study spatial and temporal overlap of wild fry with both hatchery fry that are released early at a smaller body size and those released later and at a larger size. Spatial and temporal overlap between these hatchery fry and wild fry in the Taku River estuary is likely because of the proximity of the release sites, and thus interactions are possible. Hatchery juveniles are released near Taku Inlet in the spring when wild fry are most abundant. The DIPAC hatchery has placed unique thermal marks (Orsi et al., 2004) on all groups of chum salmon fry released since 1991, and has used distinct marks by location for smaller earlier groups and for larger later groups. DIPAC is thought to have more than doubled the annual adult chum salmon catch in the region based on releases of over 100 million fry near Juneau each spring; over the past 5 years annual catches of returning adult chum salmon that were released from DIPAC have averaged approximately 2 million fish. At the same time, independent indices of wild chum salmon abundance from the Taku River have declined significantly, raising questions about stock interactions. Catch per unit of effort (CPUE) for wild chum salmon caught in the commercial gillnet

Figure 1

Trends in abundance of chum salmon (*Oncorhynchus keta*) near Taku Inlet, Alaska, as (**A**) annual commercial catch-per-boat-day (CPUE) of wild fall-run adults (4-year-old) and Douglas Island Pink and Chum (DIPAC) hatchery fry releases (millions of fish), and (**B**) adult chum salmon CPUE versus number of hatchery fry released near the inlet (regression of ln *CPUE*: r^2=0.77, P <0.01, df=24), 1976–2005. Fry data were shifted to four years later to match natal year to adult harvest year.

fishery in Taku Inlet is negatively related to the number of chum salmon fry released from DIPAC hatchery near Juneau during their natal year (Fig. 1; coefficient of determination from regression of ln adult catch against fry releases, r^2=0.77, P=0.01). This relationship indicates that releases of hatchery chum salmon fry may contribute to the decline of wild chum salmon.

Four kinds of potential wild and hatchery interactions have been proposed, namely 1) marine phase ecological interactions, 2) spawning competition and interbreeding interactions, 3) induced overharvesting interactions, and 4) early estuarine phase ecological interactions. We considered interactions during the estuarine life-history phase as the most plausible mechanism for the decline in wild Taku River fall chum salmon runs because other salmon populations in Southeast Alaska have been stable, including Taku summer chum salmon runs, and because Pacific salmon populations are known to co-vary in response to ocean

conditions (Pyper et al., 2002; Mueter et al., 2005). The estuarine phase is known to be a period of high mortality with many variables influencing juvenile salmon growth and survival, including density and competition (e.g., Simenstad et al., 1982; Willette et al., 2001; Wertheimer and Thrower, 2007; Duffy et al., 2005). Thus, the goal of this study was to investigate habitat use and migration timing of wild and hatchery chum salmon fry in Taku Inlet to evaluate the potential for wild and hatchery fish to interact in this estuary. Specifically, our objectives were 1) to compare the abundance of wild and hatchery chum salmon fry raised under early and late rearing strategies in different habitats of Taku Inlet (inner and outer inlet locations, littoral and neritic habitats); 2) to compare the body size and condition of these groups of fry in different habitats; and 3) to document environmental factors that potentially could explain the distribution and size of chum salmon fry and the abundance of hatchery fry.
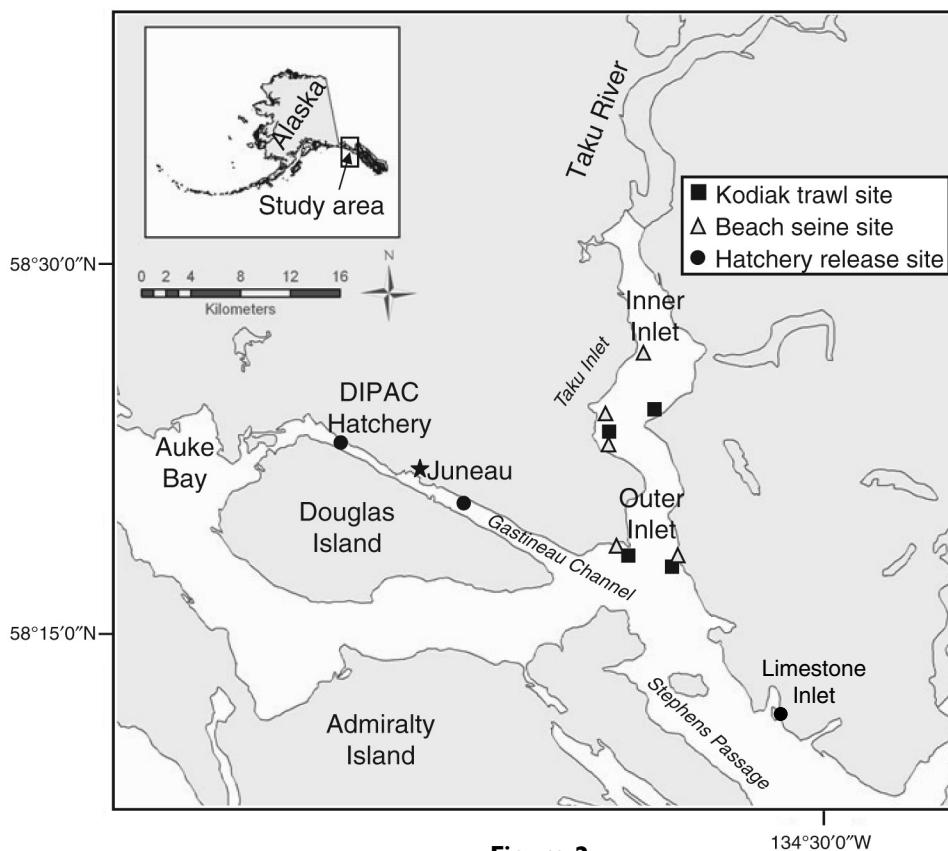
Figure 2

Sites sampled by beach seine (triangles) and Kodiak trawl (squares) in inner and outer Taku Inlet, Alaska, from late April to late June, 2004–05, and nearby hatchery release sites (circles) for chum salmon (*Oncorhynchus keta*) fry. Sampling began before the outmigration period for wild fry (late April to mid-June) and before hatchery releases of approximately 25 million "early" fry (released in early May at 1.9 g size) and 25 million "late" fry (released in late May at 3.9 g size) each year.

Background and study area

The Taku River enters the ocean 20 km south of Juneau, Alaska. About 90% of its 16,000 km^2 watershed is located in a roadless wilderness in British Columbia, Canada. Taku Inlet is a narrow fjord, 3–6 km wide by 18 km long (Fig. 2). In addition to chum salmon, the Taku River supports stable runs of sockeye (*O. nerka*), Chinook (*O. tshawytscha*), coho (*O. kisutch*), and pink salmon (*O. gorbuscha*). Migration timing of chum salmon fry in the Taku River is adapted to decreases in salinity and increases in sea surface temperature that typically occur from April through June (Meehan and Siniff, 1962; Murphy et al., 1997).

Annual production of chum salmon released by DIPAC at Limestone Inlet and Gastineau Channel near Taku Inlet increased from <1 million fry in 1982 to approximately 60 million fry in 1994 and production has generally remained above 40 million since then (Fig. 1). DIPAC has also released 50–60 million thermally marked fry annually in northern Southeast Alaska at sites distant from Taku Inlet. During this study,

26 million "early" fry were released May 7–17 at 1.9 g wet weight and 24 million "late" fry were released May 22–June 3 at 3.9 g in the vicinity of Taku Inlet in each year. These groups were produced from the same summer brood stock derived from coastal streams near Juneau and differed only in the rearing duration and the size and date at release.

Methods

Field sampling

Sampling was conducted from late April to late June, 2004–05, thus covering the outmigration period for chum salmon in Taku Inlet (Meehan and Siniff, 1962; Murphy et al., 1997). We conducted two 48-hour cruises per week, in which littoral and neritic habitats were sampled with different gear and at different times of day. We sampled littoral habitat throughout the inlet where it was feasible to use a 37-m long×3-m deep beach seine (3-mm bunt mesh) (Mortensen et al., 2000; Johnson and Thedinga,

2006). Beach gradient was 9–14% and substrate was predominantly gravel <5 cm. Three beaches were seined in the inner inlet and two in the outer inlet (Fig. 2). All five beach seine sites were sampled during daylight for a minimum of three times per week. At each beach seine site, sea surface temperature was measured with a thermometer and a water sample was collected to determine salinity.

We sampled neritic habitat with a two-boat Kodiak trawl at night (Moulton, 1997; Mortensen et al., 2000). The 6-m wide × 15-m long × 3-m deep surface trawl (3-mm codend mesh) was towed at the surface at 2 knots, 40–100 m offshore, parallel to the shoreline and at a bottom depth of 10–20 m. We trawled two nights per week at two sites in the outer inlet and two in the inner inlet (Fig. 2; 8 samples per week). Each tow lasted 10 minutes. At each trawl site, a temperature and salinity profile was taken with a Seabird SBE-19 Seacat conductivity-salinity-depth (CTD) profiler (Sea-Bird Electronics, Bellevue, WA).

Fish from both beach seine and trawl sets were processed in the same manner and fish treatment followed a protocol approved by the University of Alaska Fairbanks Animal Care and Use Committee (IACUC no. 05-19). All captured fish were anesthetized with tricaine methanesulfonate (MS-222), identified to species, and counted; nontarget species were released after identification. A maximum of 60 chum salmon per set was euthanized with excess MS-222 and either preserved in 10% formaldehyde-seawater solution or frozen for subsequent laboratory analysis. Preserved fry were transferred to 50% isopropyl to maintain the integrity of the otolith.

Laboratory processing

Each preserved or frozen fish was weighed to the nearest 1.0 mg wet weight (wt), and measured to the nearest 1.0 mm fork length (FL). Otoliths were removed and fry were identified by origin from the presence and type of thermal marks. Each year DIPAC placed a unique thermal mark on fry released near Taku Inlet: one mark for Gastineau Channel early fry, one for Gastineau Channel late fry, and one for Limestone Inlet fry(Fig. 2). Early and late hatchery fry were released from Limestone Inlet in both years but the two groups were given the same thermal mark. All fry caught from Limestone Inlet releases before release of the late hatchery fry were assumed to be early hatchery. All fry without thermal marks were assumed to be wild. Inferences about the distribution of late hatchery fry from Limestone Inlet after they were released were based on Gastineau Channel late-hatchery-fry data.

Data analysis

We analyzed data from 2004 and 2005 separately. Sampling sites were pooled by littoral or neritic habitat for inner or outer inlet locations. The inner inlet sites were closest to the mouth of the river (the source of wild fish)

and the outer inlet sites were closer to the hatchery release sites (Fig. 2), and therefore there was an *a priori* expectation that hatchery fry would be more abundant in the outer inlet. The inner and outer inlets were stratified because sea surface temperature and salinity were noticeably higher in the outer inlet location and the probability of encountering hatchery fry was greater in the outer inlet. Data on early fry from both hatchery release sites were pooled for analysis for two reasons: first, early hatchery fry from Gastineau Channel and Limestone Inlet were released at almost the same time and were similar in size; and second, the fry from both release sites were commonly found on both the east and west sides of the inlet (Fig. 2). We conducted three types of analyses: 1) spatial and temporal analyses to compare the abundances of wild and hatchery chum salmon fry; 2) spatial and temporal analyses to contrast the body sizes of hatchery and wild chum salmon fry; and 3) analyses to correlate the distribution and size of wild chum fry with hatchery fry distribution, sea surface temperature, and salinity.

Spatial and temporal distribution of relative abundance

Total catch of chum salmon for each set (seine or trawl) was apportioned by hatchery origin or wild origin according to the proportion of thermally marked fry in the sample. We calculated CPUE of wild and hatchery salmon separately as the mean number of chum salmon captured per set by week in the inner or outer inlet locations (Fig. 2). We plotted CPUE as an indicator of fry abundance. The proportions of wild and hatchery fry in the catch were calculated by week through the season and plotted separately by habitat and location. We could not determine when individual wild fry entered the estuary, but hatchery fry were assumed to have resided in the area since time of release.

Spatial and temporal change in body size of hatchery and wild salmon

Mean fork length and weight of wild, early hatchery, and late hatchery chum salmon fry were plotted by week over the course of the emigration period by location and habitat. The change in the mean size of each fish stock over time was calculated as an indirect measure of apparent growth. Although we acknowledge that immigration, emigration, and size-selective mortality are confounding effects on growth, we could not account for these changing processes. We determined apparent growth rate using the slope of the regression of fork length on date caught (day of the year). Fork length of fry of all origins was plotted into four histograms per year by location and habitat. Differences in length among location (inner, outer) and habitat type (littoral, neritic) for each year were analyzed with a one-way analysis of variance (ANOVA) for wild fry. The ANOVA compared length of wild fry by location and habitat. Fork length of early hatchery fry was analyzed by using the same ANOVA procedure. We used *t*-tests to examine length

for late hatchery fry between habitat types because no late hatchery fry were caught in the inner inlet. For all these analyses, fork length was ln-transformed because some of the frequency distributions were not normally distributed.

Distribution, size, and condition of wild chum salmon fry in relation to temperature, salinity, and chum salmon abundance

Because of the small sample size of wild chum salmon in neritic trawls, analyses of the distribution and size of wild chum salmon were conducted only with data from littoral habitat. Correlation analysis and stepwise multiple regressions were used for fry in littoral habitat to determine the relationships of wild fry abundance, weight, and condition factor (defined below), with sea surface temperature, salinity, time (date), and total chum salmon abundance. Sea surface temperature and salinity were included in analyses because the behavior and distribution of outmigrating salmon fry in estuaries often reflects evolutionary adaptations to hydrographic conditions in the estuary (reviewed by Salo, 1991; Murphy et al., 1997). To account for morphological changes that occur with ontogeny, condition factor was calculated as the residual of the regression of ln weight versus ln fork length (Jakob et al., 1996). Data from sets made before the release of hatchery fry were excluded from the analysis in order to address our goal of determining if wild fish distribute themselves differently in the presence of hatchery-released fish. Separate analyses were conducted for each year, by location, and habitat. A forward-backward stepwise regression was used with an alpha of 0.10 to include variables in the equation and an alpha of 0.10 to exclude the significance of β, by using the following equation:

$$\text{Wild abundance} = \beta_H \text{ hatchery abundance} + \beta_T \text{ SST} + \beta_S \text{ salinity} + \beta_d \text{ date} + \varepsilon, \quad (1)$$

where $abundance$ = ln ($catch$+1);
SST = sea surface temperature; and
$date$ = day of the year.

We added 1 to all catches because zeros would become undefined upon transformation. The same approach was used to relate weight of wild fry to wild fry abundance, hatchery fry abundance, sea surface temperature, and salinity. The stepwise regression used the following equation:

$$\text{Weight of wild fry} = \beta_W \text{ wild abundance} + \beta_H \text{ hatchery abundance} + \beta_T \text{ SST} + \beta_S \text{ salinity} + \beta_d \text{ date} + \varepsilon, \quad (2)$$

where $Weight = ln$ weight (g).

Finally, we analyzed the relationship between condition factor of wild fry and wild abundance, hatchery abundance, sea surface temperature, and salinity using the same techniques. The stepwise multiple regression equation used to analyze condition factors of individual wild fry was the following:

$$\text{Condition factor} = \beta_W \text{ wild abundance} + \beta_H \text{ hatchery abundance} + \beta_T \text{ SST} + \beta_S \text{ salinity} + \beta_d \text{ date} + \varepsilon. \quad (3)$$

No colinearity was found in these models (Sokal and Rohlf, 1995).

Results

Spatial and temporal distribution of relative abundance

Littoral habitat   Hatchery fry were most abundant in littoral habitat in the week following the early hatchery releases in both years, on 10 May 2004 and on 17 May 2005 (Fig. 3, A and B). Both hatchery and wild fry were generally less abundant in 2004 than in 2005. During both years, hatchery chum salmon represented over 95% of the catch in the outer inlet, but in the inner inlet represented only 11% in 2004 and 1% in 2005 (Fig. 4). Abundance of wild and early hatchery chum salmon fry in littoral habitat declined within two weeks in late May in both the inner and outer inlet. Abundance of late hatchery fry declined within one week of their release in late May, but unlike early hatchery chum salmon, late hatchery fry were never caught by beach seine in the inner inlet.

The greatest spatial and temporal overlap among chum salmon fry in littoral habitat occurred between wild and early hatchery fry in the outer inlet. Little potential existed for wild and early hatchery chum salmon fry to interact in inner Taku Inlet because hatchery fry were rare in this location. Similarly, little chance existed for wild and late hatchery fry to interact because the latter were not observed in the inner inlet and migrated from the outer inlet within one week of their release. The early hatchery release coincided with peak abundance of wild fry in the outer inlet and the distribution of these stocks overlapped for about 3 weeks. Wild chum salmon were present in littoral habitat from the beginning of sampling on 19 April through 21 June in both years. Abundance of wild chum salmon fry peaked in the inner inlet during the week of 17 May 2004 and the week of 3 May 2005 (Fig. 3A). Abundance of wild chum salmon fry peaked in the outer inlet in the week of 17 May 2004 and 10 May 2005 (Fig. 3B).

Neritic habitat   Hatchery fry were most abundant in neritic habitat in the outer inlet during the weeks of 17–31 May. Both hatchery and wild fry were generally less abundant in 2004 than in 2005. By location, hatchery chum salmon represented over 98% of the catch in the outer inlet during both years, whereas in the inner inlet they represented 93% in 2004 and 24% in 2005 (Fig. 4). Most of the hatchery chum salmon from neritic
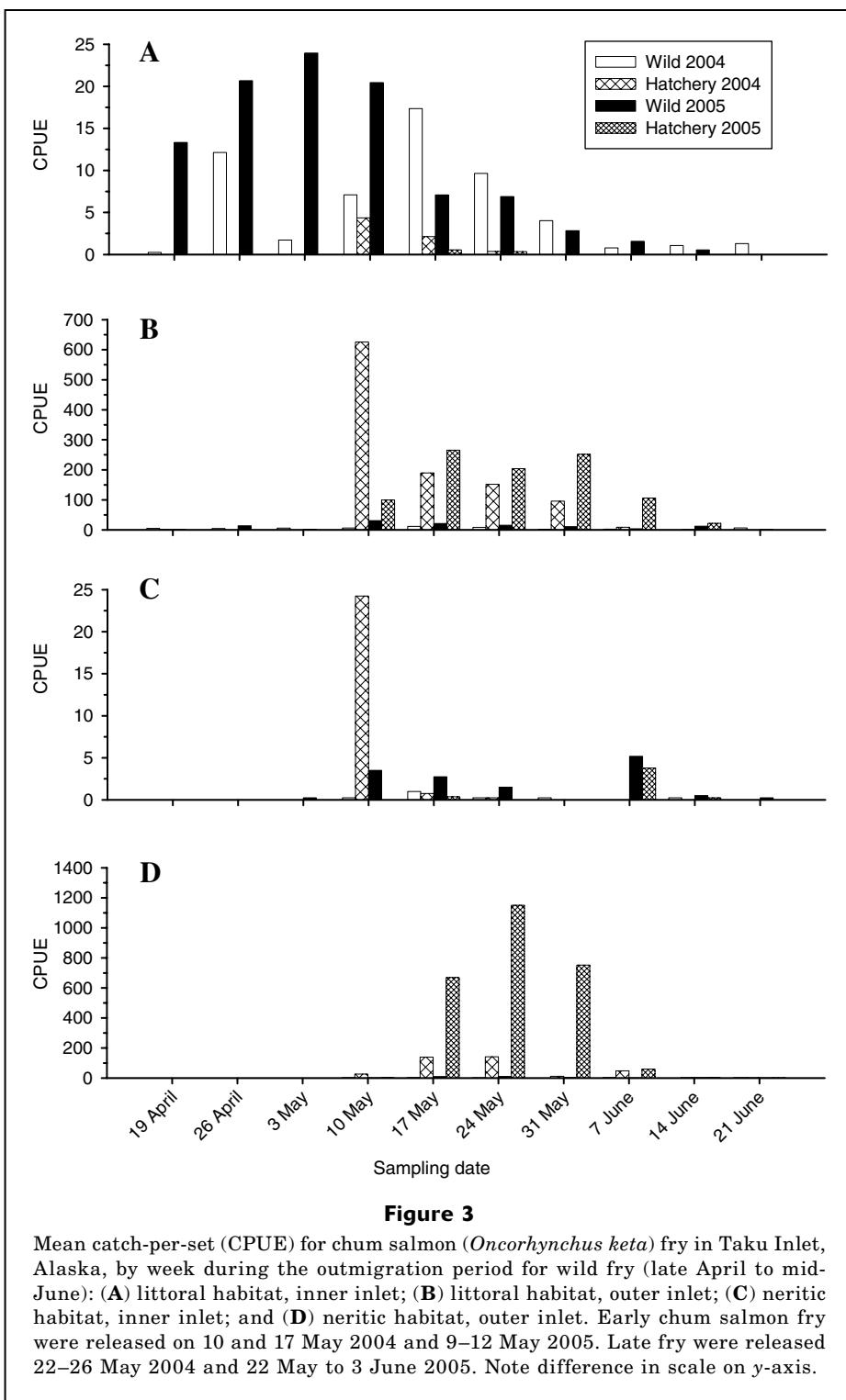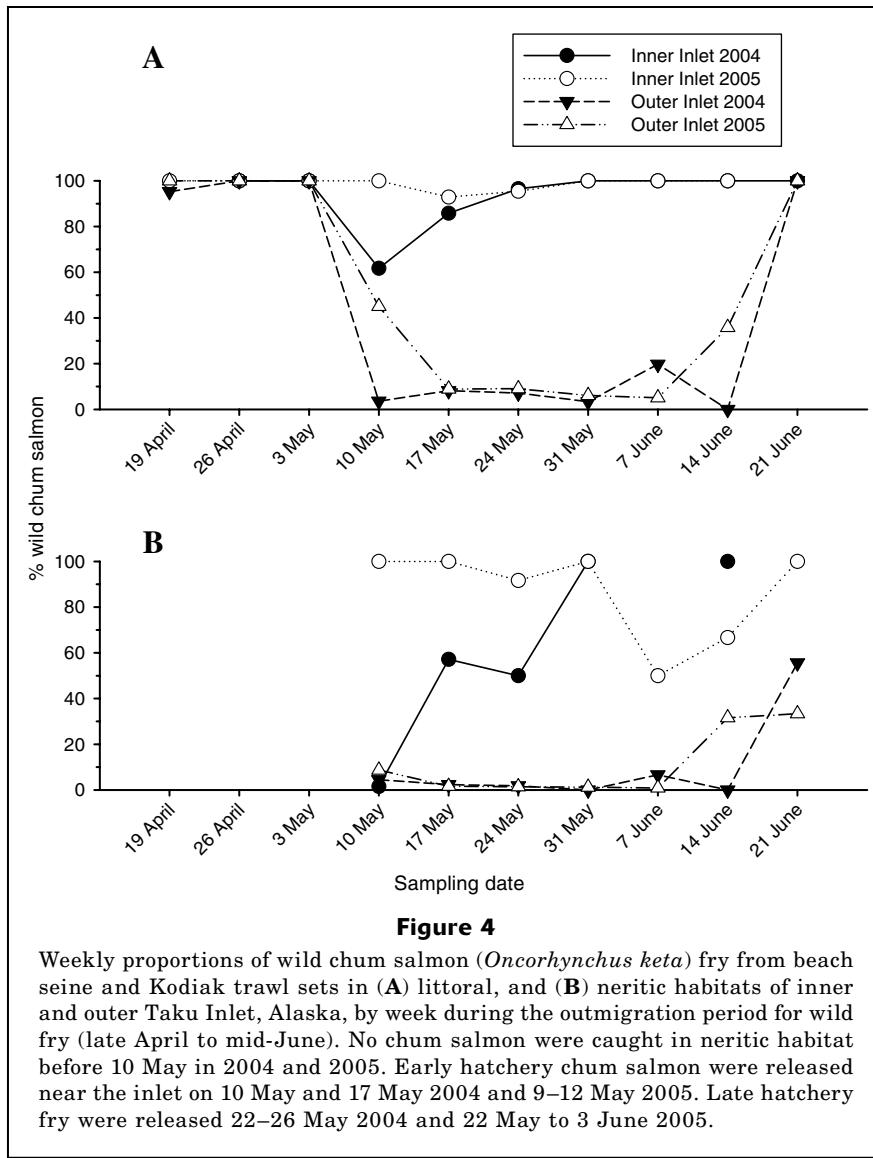
Figure 3

Mean catch-per-set (CPUE) for chum salmon (*Oncorhynchus keta*) fry in Taku Inlet, Alaska, by week during the outmigration period for wild fry (late April to mid-June): (**A**) littoral habitat, inner inlet; (**B**) littoral habitat, outer inlet; (**C**) neritic habitat, inner inlet; and (**D**) neritic habitat, outer inlet. Early chum salmon fry were released on 10 and 17 May 2004 and 9–12 May 2005. Late fry were released 22–26 May 2004 and 22 May to 3 June 2005. Note difference in scale on *y*-axis.

habitat in the inner inlet in 2004 were caught in one set on 10 May.

As in littoral habitat, the greatest spatial and temporal overlap of chum salmon in neritic habitat occurred between wild and early hatchery fry in the outer inlet. Peak abundance of wild chum salmon in neritic habitat trailed behind the peak in littoral habitat by 1 to 2 weeks (Fig. 3,C and D). With one exception, no chum fry of any origin were caught in neritic habitat until the weeks of 17 May 2004 and 10 May 2005 (Fig. 3). Wild fry were most abundant in neritic habitat in both the inner and outer inlet during the week of 17 May

Figure 4

Weekly proportions of wild chum salmon (*Oncorhynchus keta*) fry from beach seine and Kodiak trawl sets in (**A**) littoral, and (**B**) neritic habitats of inner and outer Taku Inlet, Alaska, by week during the outmigration period for wild fry (late April to mid-June). No chum salmon were caught in neritic habitat before 10 May in 2004 and 2005. Early hatchery chum salmon were released near the inlet on 10 May and 17 May 2004 and 9–12 May 2005. Late hatchery fry were released 22–26 May 2004 and 22 May to 3 June 2005.
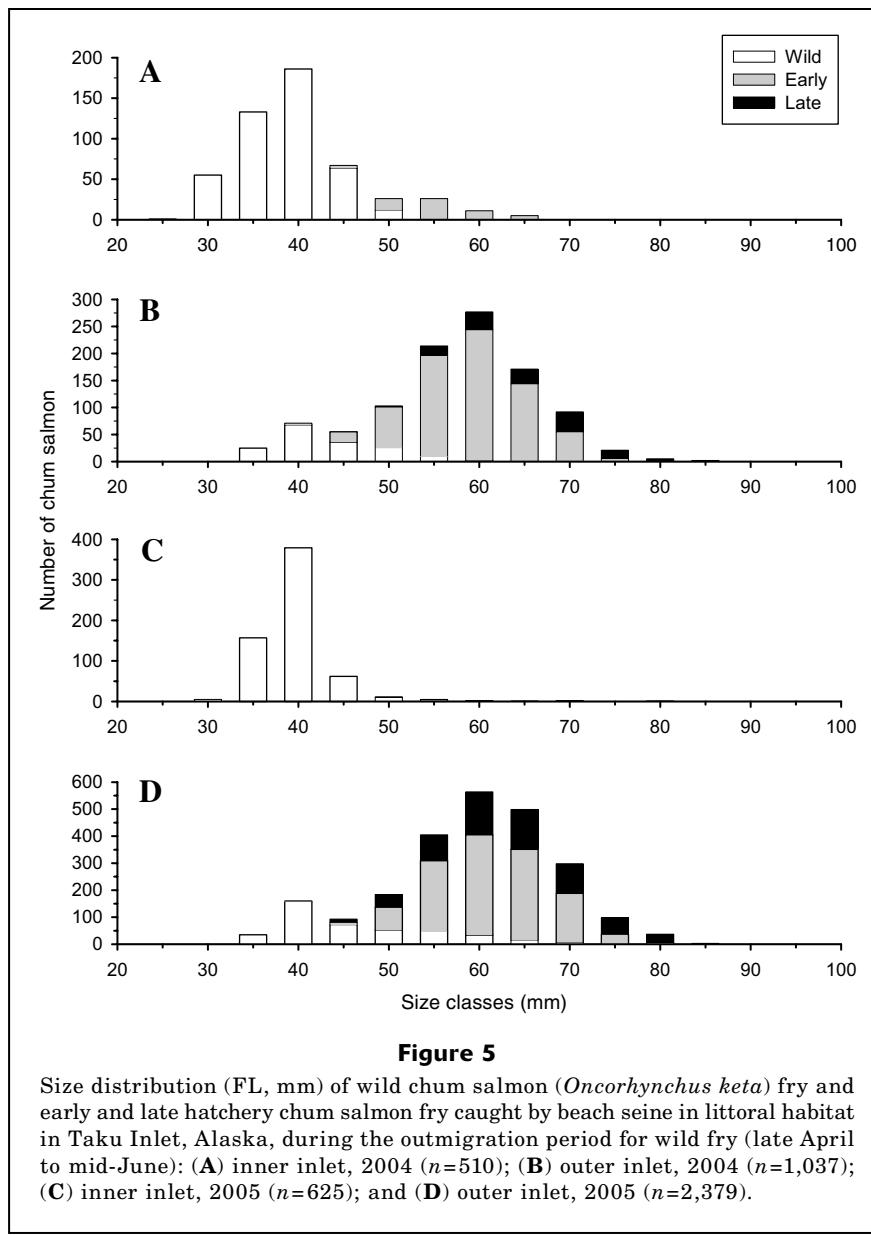
(Fig. 3). The proportion of wild fry was greatest in the inner inlet (Fig. 4), but abundance of both wild and hatchery chum salmon was greatest in the outer inlet.

Spatial and temporal change in body size of hatchery and wild salmon

Littoral habitat Early and late hatchery fry both were on average about four times heavier and about 15 mm FL longer than wild fry in littoral habitat (Fig. 5). Early hatchery fry were similar in size to late hatchery fry by the time the latter were released (Fig. 6). For wild fry in the inner inlet, mean weight and length were 0.39 g and 36.5 mm FL in 2004 and did not increase throughout the season (Fig. 6; regression probability that slope of size over time=0, P=0.62). In 2005, weight and length of wild fry did increase significantly (P=0.03), but the increases were relatively small, from 0.38 to 0.48 g and from 37 to 42 mm FL (Fig. 6). In the outer inlet, by contrast, wild fry more than doubled in weight and mean length increased significantly (P<0.01) through the season in both years, from 37 to 50 mm FL (Fig. 6). For early hatchery fry, mean length in the inner inlet increased significantly (P=0.02) over time from 51 to 54 mm FL in 2004, but did not change in 2005 (P=0.94). In the outer inlet, mean weight of early hatchery fry increased significantly (P<0.01) by 80% in both years and mean length increased significantly (P<0.01) from 52 to 60 mm FL in 2004 and from 53 to 63 mm FL in 2005 (Fig. 6). For late hatchery fry, mean length in littoral habitat in the outer inlet did not change significantly in either 2004 (P=0.24) or 2005 (P=0.08).
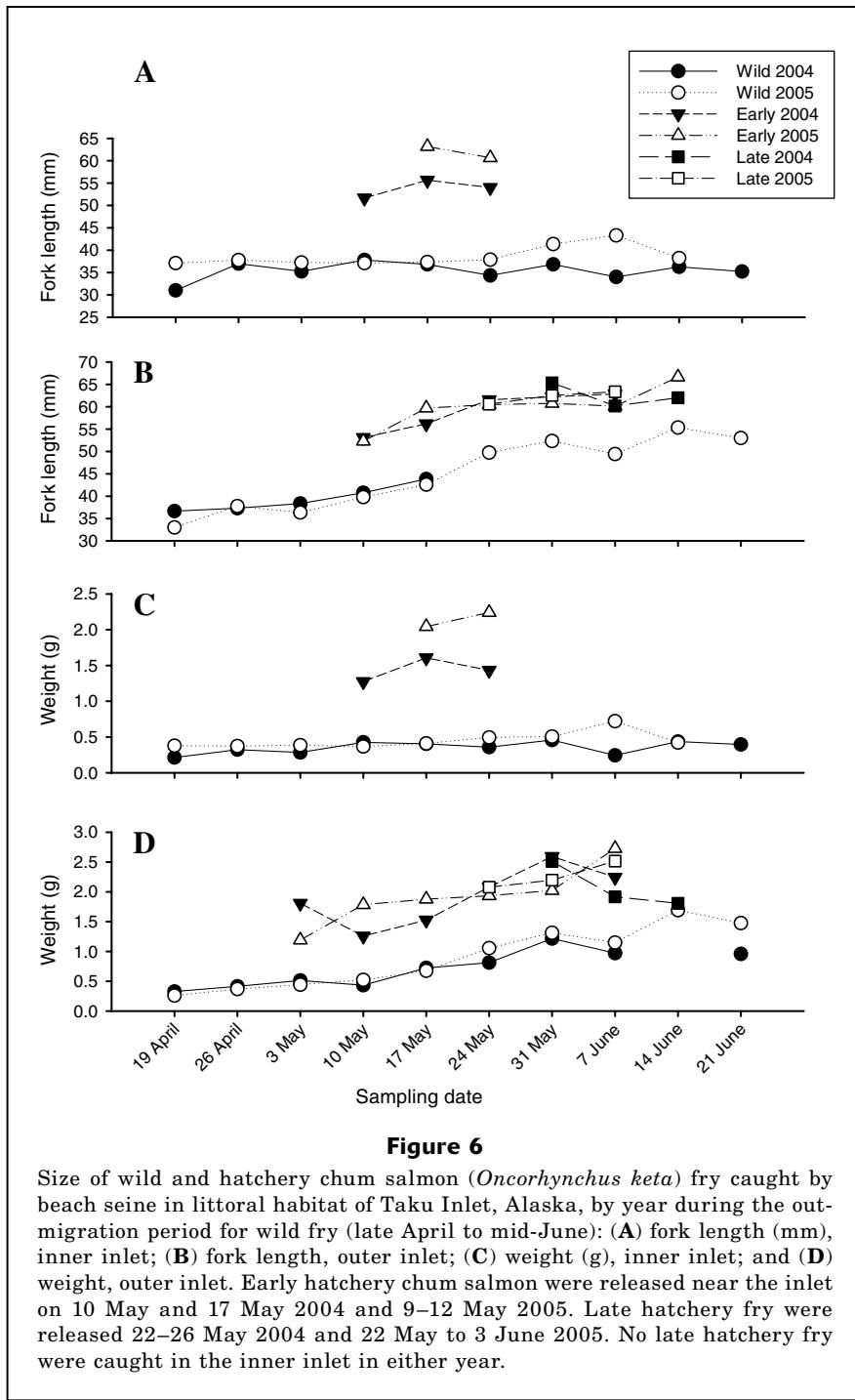
Neritic habitat Hatchery chum salmon fry in neritic habitat were longer than wild fish in the inner and outer

Figure 5

Size distribution (FL, mm) of wild chum salmon (*Oncorhynchus keta*) fry and early and late hatchery chum salmon fry caught by beach seine in littoral habitat in Taku Inlet, Alaska, during the outmigration period for wild fry (late April to mid-June): (**A**) inner inlet, 2004 (*n*=510); (**B**) outer inlet, 2004 (*n*=1,037); (**C**) inner inlet, 2005 (*n*=625); and (**D**) outer inlet, 2005 (*n*=2,379).

inlet in both years (Fig. 7). Late and early hatchery fry had similar fork length distributions in the outer inlet in both years. For wild fry, mean length in the inner inlet increased significantly over time in both years (Fig. 8), from 39 to 49 mm FL in 2004 (P=0.05) and from 36 to 47 mm FL in 2005 (P<0.01). In the outer inlet, mean length of wild fry increased significantly (P<0.01), from 42 to 66 mm FL in 2004 and from 41 to 74 mm FL in 2005. For early hatchery fry, mean length in the inner inlet increased significantly (P<0.01) from 54 to 62 mm FL in 2004, but sample size was too small for analysis in 2005. In the outer inlet, mean length of early hatchery fry increased significantly (P<0.01) in both years, from 53 to 69 mm FL in 2004 and from 59 to 67 mm FL in 2005. For late hatchery fry, mean length actually decreased significantly (P<0.01) in 2004 from 71 to

66 mm, but there was no significant change (P=0.56) in length in 2005 (Fig. 8).

Comparisons of habitats   In both years, wild chum salmon fry in neritic habitat were larger in the outer inlet than in the inner inlet and larger in neritic habitat than in littoral habitat (Fig. 9; ANOVA: 2004: P<0.01, F=84.7; 2005: P<0.01, F=139.7). As with wild fry, early hatchery fry in 2004 were larger as they shifted from littoral habitat to neritic habitat (ANOVA: P<0.01, F=19.4); no significant differences were observed in 2005. Too few early hatchery fry were sampled in the neritic habitat in the inner inlet in 2005 to include in these analyses. In the outer inlet, fork length of late hatchery fry was significantly greater in neritic habitat than in littoral habitat in 2004 (t=1.97,
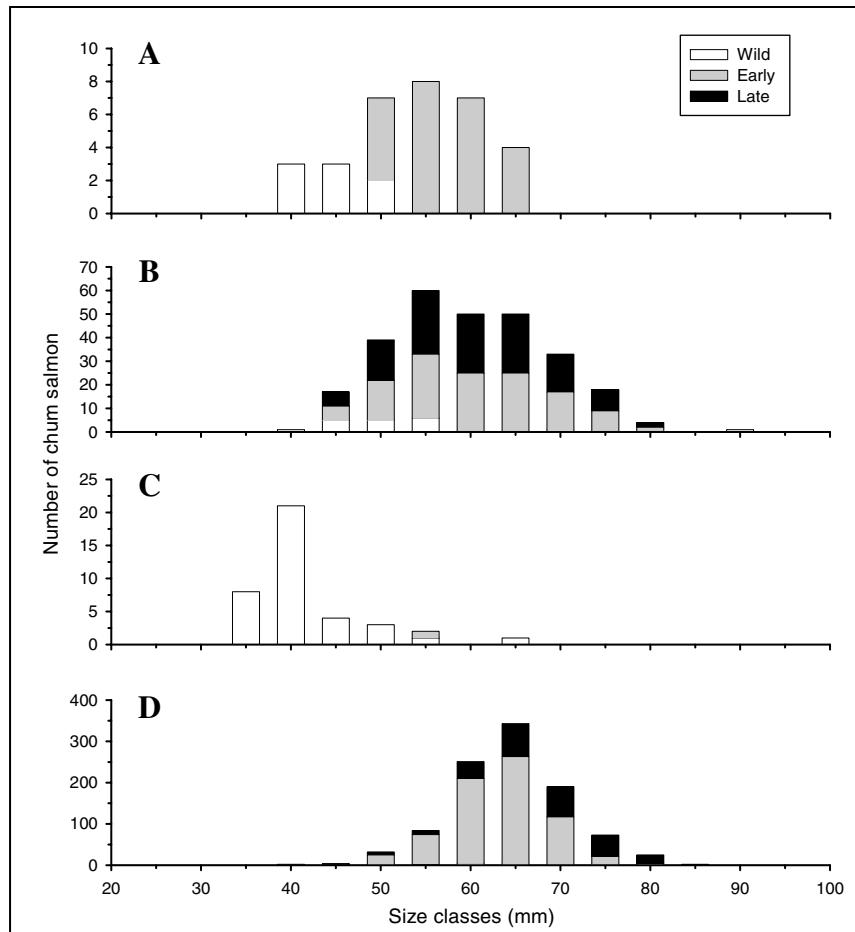
Figure 6

Size of wild and hatchery chum salmon (*Oncorhynchus keta*) fry caught by beach seine in littoral habitat of Taku Inlet, Alaska, by year during the out-migration period for wild fry (late April to mid-June): (**A**) fork length (mm), inner inlet; (**B**) fork length, outer inlet; (**C**) weight (g), inner inlet; and (**D**) weight, outer inlet. Early hatchery chum salmon were released near the inlet on 10 May and 17 May 2004 and 9–12 May 2005. Late hatchery fry were released 22–26 May 2004 and 22 May to 3 June 2005. No late hatchery fry were caught in the inner inlet in either year.

P=0.028), but no significant differences were found in 2005 (P=0.54).

Distribution, size, and condition of wild chum salmon fry in relation to temperature, salinity, and chum salmon abundance

Sea surface temperature and salinity followed patterns expected in Southeast Alaska in the spring during snowmelt (Meehan and Siniff, 1962; Murphy et al., 1997). Sea surface temperature generally increased throughout the season in littoral and neritic habitats in all locations and was warmer in the outer inlet than the inner inlet. Sea surface temperature ranged from 3° to 8°C in late April and increased to 7–12°C in late May and June in the inner inlet; in the outer inlet, it ranged from 4° to 9°C in late April and increased to 9–14°C in late May and June. Sea surface temperature
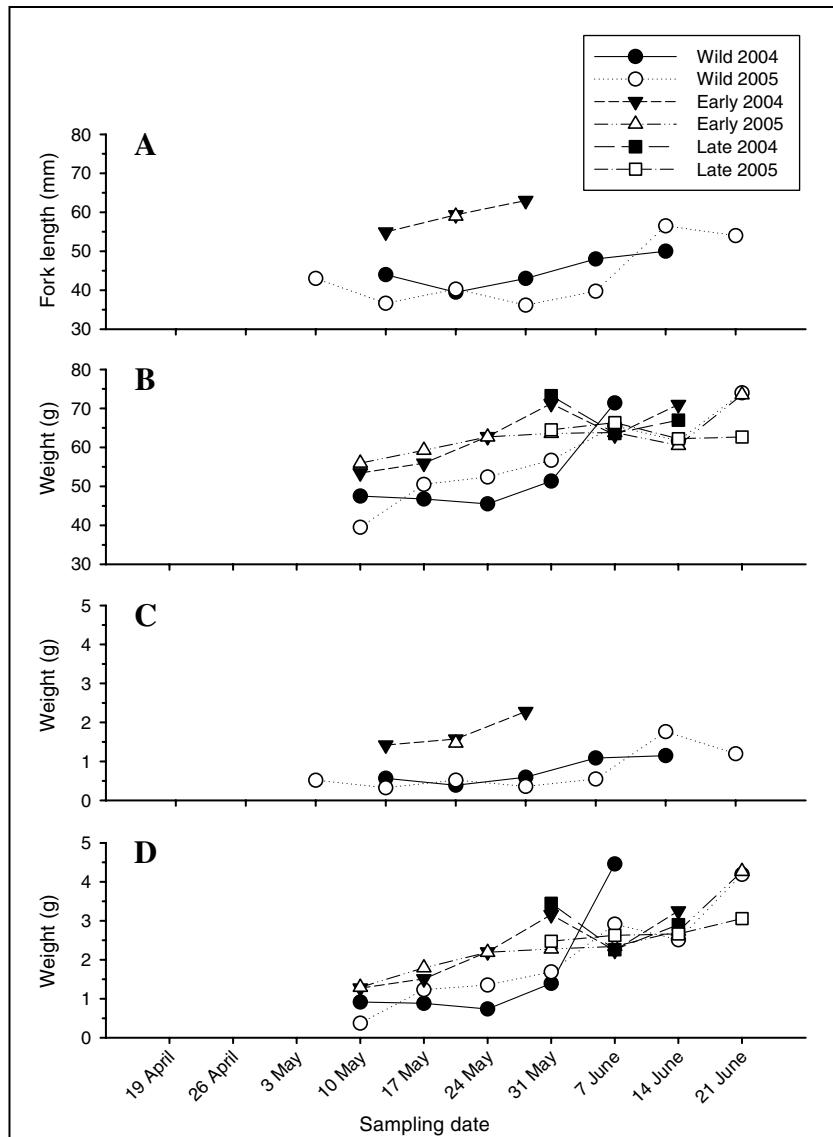
Figure 7

Size distribution (FL, mm) for chum salmon (*Oncorhynchus keta*) fry caught by Kodiak trawl in neritic habitat in Taku Inlet, Alaska, during the outmigration period for wild fry (late April to mid-June) by year: (**A**) inner inlet, 2004 (n=32); (**B**) outer inlet, 2004 (n=273); (**C**) inner inlet, 2005 (n=30); and (**D**) outer inlet, 2005 (n=1,006).

tended to be warmer in 2005 than in 2004, particularly after early hatchery fry were released. Salinity was also greater in the outer inlet than in the inner inlet in both littoral and neritic habitats. Salinity generally declined from 30 to 15 from April through mid-May in the outer inlet and remained relatively constant through the end of the season in both years, whereas in the inner inlet salinity declined from 15 to 5 over the same period.

Because of the small sample of wild chum salmon in neritic trawls, regression analysis of abundance, size, and condition of wild fish was limited to littoral habitats. In general, wild fry were more abundant and individuals were larger than hatchery fry. Abundance of wild fry was positively related to the abundance of hatchery fry in the inner inlet in 2004 and in the outer inlet in both years (Table 1). Abundance of wild fry was not related to salinity or sea surface temperature in either year.

Size (wet weight) of wild fry in the inner inlet was positively correlated with abundance of both wild and hatchery fry in 2004, but weight was negatively correlated with the abundance of wild fry and not correlated with the abundance of hatchery fry in 2005 (Table 2). Multiple regression analyses indicated that both wild and hatchery fry abundances were significant variables explaining the variation in weight in 2004; in 2005, neither parameter was significant when time (date) was included in the model (Table 2). Temperature was positively correlated with weight in both years but was not significant in the multiple regression models.

Weight of wild fry in the outer inlet was not correlated with either hatchery or wild fry abundance in 2004; only date was significant in the multiple regression analysis for the year (Table 2). In 2005, weight was negatively correlated with wild fry abundance and not correlated with hatchery fry abundance. However, when date was included in the multiple regression model,
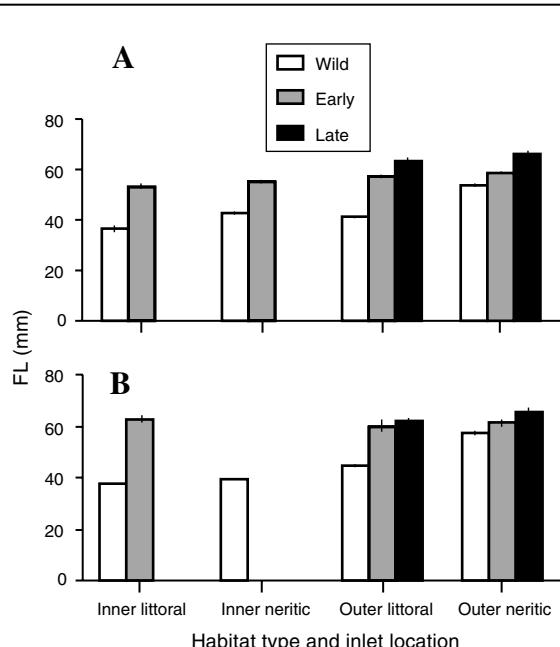
Figure 8

Fork length (FL, mm) and weight (g) of hatchery and wild chum salmon (*Oncorhynchus keta*) fry caught by Kodiak trawl in neritic habitats of Taku Inlet, Alaska, during the outmigration period for wild fry (late April to mid-June): (**A**) fork length (mm), inner inlet; (**B**) fork length, outer inlet; (**C**) weight (g) inner inlet; (**D**) weight, outer inlet. Early hatchery chum salmon were released near the inlet on 10 May and 17 May 2004 and 9–12 May 2005. Late hatchery fry were released 22–26 May 2004 and 22 May to 3 June 2005. No late hatchery fry were caught in the inner inlet in either year.

wild fry abundance had no significant effect on weight, whereas hatchery fry abundance had a significant positive effect on weight (Table 2). Sea surface temperature and salinity were positively and negatively correlated with weight, respectively, but neither variable was significant in the multiple regression analysis.

Condition factor of wild fry in the inner inlet was not correlated with either wild or hatchery fry abundance in 2004 (Table 3). In the multiple regression analysis, however, when salinity (which had the highest bivariate correlation) was included into the model, wild abundance had a significant and positive effect on condition factor. Hatchery abundance was not significant in the model. In 2005 in the inner inlet, condition factor was significantly correlated with wild fry abundance, but not with hatchery fry abundance (Table 3). In the

multiple regression analysis, wild abundance and date significantly affected condition factor in the inner inlet in 2005, and hatchery abundance had no significant effect.

Figure 9

Fork length (mm) of chum salmon (*Oncorhynchus keta*) fry in Taku Inlet, Alaska, during the outmigration period for wild fry (late April to mid-June), by location and habitat in (**A**) 2004 and (**B**) 2005. Sample size for early hatchery fry in neritic habitat in the inner inlet in 2005 was too small to be included in analysis. No late hatchery fish were caught in the inner inlet during either year. Vertical bars represent standard error about the mean.

Condition factor of wild fry in the outer inlet was positively correlated with wild fry abundance but not with hatchery fry abundance in 2004 (Table 3). In the multiple regression analysis, wild fry abundance had a significant and positive effect on condition factor. Date also had a significant and positive effect, whereas salinity had a negative effect. Abundance of hatchery fry was not significant in the model in 2004. In 2005, condition factor of wild fry was not correlated with wild fry abundance but was positively correlated with hatchery fry abundance. In the multiple regression, hatchery fry abundance had a significant positive effect on condition factor, whereas wild fry abundance had a significant negative effect when included in the model with hatchery fry abundance (Table 3).

Discussion

The objectives for this study were 1) to determine the abundance and spatial and temporal overlap of wild chum salmon fry and hatchery chum salmon fry subjected to early and late rearing strategies in different habitats of Taku Inlet; 2) to compare the body size and condition of these groups of fry; and 3) to document environmental factors that potentially could explain the distribution, size, and abundance of fry. The ultimate goal for this study was to evaluate the potential for interactions between wild and hatchery chum salmon in Taku Inlet. Our results indicated that the greatest spatial and temporal overlap between wild and hatchery chum salmon fry occurred between wild and early hatchery fry in littoral and neritic habitats of the outer inlet. Both wild and early hatchery salmon were captured together in the same habitats in Taku Inlet for up to four weeks. Hatchery production corresponded with a 20-fold increase in overall abundance of chum salmon fry in the outer inlet, indicating a substantially increased likelihood of density-dependent interactions at this time (Simenstad et al., 1982; Levings et al., 1986; Willette,

Table 1

Relationships of wild chum salmon (*Oncorhynchus keta*) fry abundance to environmental factors and to hatchery chum salmon fry abundance from beach-seine collections in littoral habitat by inner and outer location in Taku Inlet, Alaska, during the outmigration period for wild fry (late April to mid-June), 2004–05, determined with stepwise multiple regressions (Eq. 1) and correlation analyses. SST = sea surface temperature; NS = not significant.

| | | Significance of regression parameters | | Bivariate correlations with wild fry abundance | | | |
| | | | | Inner | | Outer | |
		Inner	Outer	r	P	r	P
2004	hatchery abundance	Positive P<0.01	Positive P<0.01	0.365	<0.01	0.645	<0.01
	SST	NS	NS	0.198	0.110	0.027	0.865
	salinity	NS	NS	−0.246	0.047	0.099	0.526
2005	hatchery abundance	NS	Positive P<0.01	0.097	0.460	0.626	<0.01
	SST	NS	NS	−0.314	0.025	−0.200	0.205
	salinity	NS	NS	0.272	0.035	0.056	0.695

2001; Fukuwaka et al., 2007). Early hatchery fry were also notably larger than wild fry and larger fry are known to be favored in interactions among chum salmon fry (Olla et al., 1998). By comparison, the low overlap between the stocks in inner Taku Inlet is not surprising, given that hatchery chum salmon would have to migrate against a salinity-temperature gradient that they are adapted to follow seaward (Salo, 1991). The observation that apparent growth of wild fry was greatest in the outer inlet where hatchery fish were most abundant,

and the lack of a negative relationship between condition of wild fry and hatchery fry abundance, would indicate that hatchery fry were not substantially depleting food resources available to wild fry and that negative, density-dependent interactions were not occurring or were not detected in this study. It should be noted, however, that apparent growth is potentially a biased measure of actual growth because of the continuous influx of small wild fry, shorter residence of larger fry, and size selective mortality, which have been documented for chum salmon

Table 2

Relationships of wild chum salmon (*Oncorhynchus keta*) fry weight to environmental factors and to hatchery chum salmon fry abundance from beach-seine collections in littoral habitat by inner and outer location in Taku Inlet, Alaska, during the out-migration period for wild fry (late April to mid-June), 2004–05, determined with stepwise multiple regressions (Eq. 2) and correlation analyses. SST = sea surface temperature; NS = not significant.

| | | Significance of regression parameters | | Bivariate correlations with wild fry abundance | | | |
| | | | | Inner | | Outer | |
		Inner	Outer	r	P	r	P
2004	date	NS	Positive P<0.01	−0.105	0.048	0.393	<0.01
	wild abundance	Positive P=0.051	NS	0.106	0.046	0.167	0.118
	hatchery abundance	Positive P=0.018	NS	0.127	0.017	0.005	0.961
	SST	NS	NS	0.096	0.071	0.219	0.039
	salinity	NS	NS	−0.012	0.825	−0.178	0.095
2005	date	Positive P<0.01	Positive P<0.01	0.350	<0.01	0.642	<0.01
	wild abundance	NS	NS	−0.129	0.034	−0.414	<0.01
	hatchery abundance	NS	Positive P<0.01	0.005	0.933	0.083	0.130
	SST	NS	NS	0.309	<0.01	0.576	<0.01
	salinity	NS	NS	−0.011	0.859	−0.318	<0.01

Table 3

Results of analyses relating wild chum salmon (*Oncorhynchus keta*) fry condition factor to environmental factors and to hatchery chum salmon fry abundance from beach-seine collections in littoral habitat by inner and outer location in Taku Inlet, Alaska, during the out-migration period for wild fry (late May to mid-June), 2004–05, determined with stepwise multiple regressions and correlation analyses (Eq. 3). SST = sea surface temperature; NS = not significant.

| | | Significance of regression parameters | | Bivariate correlations with wild fry abundance | | | |
| | | | | Inner | | Outer | |
		Inner	Outer	r	P	r	P
2004	date	NS	Positive P < 0.01	0.098	0.064	0.465	<0.01
	wild abundance	Positive P < 0.01	Positive P < 0.01	−0.036	0.503	0.481	<0.01
	hatchery abundance	NS	NS	−0.086	0.106	0.108	0.312
	SST	Negative P <0.01	Negative P = 0.015	−0.162	0.002	0.308	0.003
	salinity	NS	NS	−0.106	0.045	−0.164	0.124
2005	date	Positive P<0.01	NS	0.044	0.473	0.069	0.212
	wild abundance	Positive P<0.01	Negative P=0.045	0.254	<0.01	−0.088	0.110
	hatchery abundance	NS	Positive P<0.01	−0.079	0.198	0.278	<0.01
	SST	NS	NS	−0.060	0.396	0.162	0.101
	salinity	NS	NS	0.144	0.018	−0.166	0.234

fry during their early marine life history (Kaeriyama and Ueda, 1998; Wertheimer and Thrower, 2007).

To date, it is unclear how changes in fry abundance due to hatchery releases may affect predation risk and survival probability for wild chum salmon during their early life history. Changes in juvenile salmon abundance caused by hatchery releases can significantly change the dynamics of predator-prey interactions for wild fish (Einum and Fleming, 2001; Brannon et al., 2004). For example, the presence of hatchery fry could diminish predation on wild fry in the early marine phase by buffering wild fry from predators (Willette et al., 2001; Briscoe et al., 2005), could increase predation on wild fish by attracting predators and increasing predator-prey interactions (Holling, 1959; Beamish et al., 1992; Ruggerone and Rogers, 1984), or could lead to direct competition for food or space (Levings et al., 1986; Olla et al., 1998; Ruggerone and Nielsen, 2004). Size-selective mortality is not necessarily tied to hatchery practices or density-dependent interactions, but size-selective mortality would inflate our estimates of growth and condition. If such a bias did occur, it was probably not large enough to eliminate the apparent growth rates that we observed. Diminished growth and survival of wild fry may occur if the number of predators in relation to the number of salmon prey increases in response to increased hatchery releases (Ruggerone and Rogers, 1984; Beamish et al., 1992; Scheel and Hough, 1997), or if such an increase in fry abundance results in predators consuming wild chum salmon fry at a faster rate than they consume hatchery-produced fish (Holling, 1959).

The estuarine phase of the chum salmon life cycle in Taku Inlet provides ample time for interactions to occur that may influence survival of chum salmon fry, although this phase lasts less than a month. This short estuarine phase, however, is a critical period of rapid growth (Duffy et al., 2005; Simenstad et al., 1982; Wertheimer and Thrower, 2007), when fry must feed frequently to gain the energy to smolt, grow, avoid predators, migrate, and compete with other members of their cohort (Healey, 1982; Fukuwaka and Suzuki, 2002; Duffy and Beauchamp, 2008). In several studies on the daily mortality of chum salmon fry in estuaries, it was concluded that a large proportion of each cohort dies in the first 21 days at sea (Parker, 1962; Bax, 1983; Fukuwaka and Suzuki, 2002; Wertheimer and Thrower, 2007). Estuarine survivors often more than double in weight (Duffy et al., 2005) and larger fry are subsequently less susceptible to predation (Parker, 1971; Hargreaves and LeBrasseur, 1986; Wertheimer and Thrower, 2007). Similarly, survival of hatchery-reared chum salmon fry is influenced by body size at the time of release (Kaeriyama, 1999; Wertheimer and Thrower, 2007). Widespread conditions favorable to growth can increase survival of chum salmon cohorts from many stocks simultaneously (Pyper et al., 2002; Mueter et al., 2005; Duffy and Beauchamp, 2008), but interannual differences in environmental conditions are also reflected in size and survival rates (Wertheimer

et al., 2004; Seo et al., 2006; Armstrong et al., 2008; Sturdevant et al., 2009).

New recruits to the inner inlet could create a negative bias in our estimates of apparent growth of wild fry because newly emigrated fry coming from the river would likely be smaller. In contrast, new recruits to the outer inlet come from the inner inlet and therefore the fact that wild fry were larger in the outer inlet than the inner inlet supports the conclusion that wild fry increased in fork length. Future research should include sampling near the mouth of the river itself for the benefit of comparing the size and outmigration timing of wild fry in the inner inlet with that of wild fry from the lower river. This bias did not exist for hatchery fry because there were no new recruits of hatchery fry after release. Although we do not have data on the length of time wild fry reside in the inner inlet, the fact that average length did not change substantially through the season indicates the catch could have been heavily influenced by new recruits. Our data indicated that at least some of the increase in length of wild fry in the outer inlet was due to actual growth. Fork length of early hatchery fry increased throughout the season in the outer inlet and wild fry also appeared to increase in size as they moved from the inner to the outer inlet. Early hatchery fry spent up to a month in the outer inlet and our catch data indicated that wild and early hatchery fry use habitat similarly. Consistent with other research (Healey, 1982; Mortensen et al., 2000; Duffy et al., 2005), both groups tended to be smaller in littoral than in neritic habitat, indicating that they exhibited the behavioral pattern of moving from shallow to deeper water with growth. Both size and predation risk can accelerate hatchery fry dispersal from nearshore habitats (Willette, 2001), which could also buffer the smaller wild fish from a different predator suite that coincides with this transition to offshore zones (Willette, 2001; Moss et al., 2005; Sturdevant et al., 2009).

Food availability for chum salmon fry may directly affect their survival, albeit to a lesser degree than predation risk (Mortensen et al., 2000; Willette, 2001; Willette et al., 2001). Based on a study of the bioenergetics of juvenile chum salmon in Icy Strait, Southeast Alaska, it was concluded that prey availability does not generally limit their growth (Orsi et al., 2004). However, compared to our early estuarine research, the study of Orsi et al. was conducted in epipelagic habitat and focused on larger hatchery and wild fish that had been in the marine environment for a minimum of 45 days; consequently, any competitive interactions may have occurred earlier. On the other hand, in studies of other estuaries of Southeast Alaska, spring carrying capacity far exceeded the estimated abundance of wild pink and chum salmon fry (Bailey et al., 1975), and fry rapidly outgrew predation vulnerability (Murphy et al., 1988). If estuarine conditions were equally favorable in Taku Inlet, hatchery fish may not directly compete with wild fish for food even when their densities are relatively high and the fish co-occur; instead, prey could be partitioned among size and stock groups of chum

salmon or according to foraging behavior and abilities, with little negative effect (Levings et al., 1986; Murphy et al., 1988; Sturdevant et al., 1996; Landingham et al., 1998). However, the timing of food resource availability in relation to estuarine entry of wild salmon or hatchery releases could affect residency time, diet, growth rate, predation, and survival (Hargreaves and LeBrasseur, 1986; Mortensen et al., 2000; Willette et al., 2001; Duffy and Beauchamp, 2008), and thus the extent and duration of potential interactions. The difference in environmental conditions that we observed in Taku Inlet in 2004 compared to 2005 indicates that this was a likely scenario. A companion study of diet and energy density of wild and hatchery chum salmon fry in Taku Inlet and Icy Strait is currently underway and should shed light on prey utilization, foraging behavior, and the extent to which hatchery and wild stocks partition food.

Interactions between hatchery and wild salmonids are complex and competition may occur only at critical periods during the life history of a cohort when resources are limited (Orsi et al., 2004; Ruggerone and Nielsen, 2004). Mixed schools of wild and hatchery fry formed in outer Taku Inlet, which may indicate that there is a potential for interactions as long as the schools persist. Both hatchery and wild juvenile chum salmon must learn to integrate many factors related to habitat, prey, and potential competitors and predators as they enter marine ecosystems (Willette et al., 2001; Warburton 2003; Armstrong et al., 2008; Duffy and Beauchamp, 2008). Hatchery salmon may rapidly learn to feed on natural prey after their release, yet these naïve fish also lack predator-recognition and -avoidance skills and may lag behind wild individuals in such abilities (Olla et al., 1998). Laboratory studies conducted with chum salmon indicate a potential for growth of wild fry to be affected by the presence of hatchery fry if there is a significant difference in body size, as we observed in Taku Inlet. This research indicates that larger individuals aggressively defend food when food is patchy but school with smaller fish when food is distributed evenly (Olla et al., 1998). On the other hand, we observed chum salmon fry in Taku Inlet before hatchery releases, and other studies concluded that despite smaller size, prior residence gives wild salmon a competitive advantage because the hatchery fish have to develop foraging behavior and search images for wild prey instead of hatchery pellets (Huntingford and Garcia de Leaniz, 1997; O'Connor et al., 2000). Later wild outmigrants in Taku Inlet also have the opportunity to develop foraging and predator-avoidance behavior in the inner inlet while few hatchery fish are present.

Although the focus of this article has been the potential for intraspecific interactions, the probability for interspecific interactions in Taku Inlet should not be overlooked, because these interspecific interactions may also occur in Taku Inlet. We captured considerable numbers of pink salmon fry that often co-occurred in similar habitats with chum salmon fry. Several studies have noted diet and habitat overlap between pink and chum salmon in their early marine life (Bailey et al., 1975; Sturdevant et al., 1996; Moulton, 1997; Duffy et al., 2005) or later (Landingham et al., 1998; Ruggerone and Nielsen, 2004). Commercial catches of pink salmon in Taku Inlet have been substantial, but variable, over the past 30 years and abundant populations of pink and chum salmon have co-existed in the Taku River. No data on historical abundance of pink salmon fry exist and there is no evidence that pink salmon returns have declined in the Taku River during the years since hatchery production of chum salmon began. The investigation of interspecific interactions, especially between pink and chum salmon, would be an important focus for future research.

Marine survival of most other chum salmon populations in Southeast Alaska has been stable (Orsi et al., 2004), and therefore poor ocean conditions are not the likely cause of the decline of wild chum salmon in the Taku River. Local evidence from the early ocean phase in epipelagic habitat has indicated that juvenile chum salmon consumed only a small portion of the available zooplankton (Orsi et al., 2004), and feeding indices have remained high throughout the diel cycle and summer season, indicating that growth of the fish was not food limited at this time. During the late ocean phase, run timing and harvest of adult wild and hatchery stocks are segregated in Taku Inlet; wild stocks return in the fall, whereas hatchery stocks (derived from broodstocks of summer-run chum salmon from coastal streams near Juneau) return in the summer. Although it is not known how many hatchery fish stray into the Taku River, this difference in run timing of adults presumably prevents large numbers of summer-run hatchery strays from interbreeding with the wild fall-run (Bachen and Linley, 1995; Heard et al., 1995). No directed fishery on wild Taku River chum salmon has operated since the early 1990s when the decline began. Wild fall-run chum salmon are intercepted in an annual coho salmon fishery in Taku Inlet and the catch of fall-run chum salmon in this fishery has averaged 4100 fish per year since 1992.

In summary, our results indicate that interactions in Taku Inlet between hatchery and wild chum salmon from the Taku River are possible because of the co-occurrence of these fish, particularly in the littoral habitat of the outer inlet, and the large proportion of early-released hatchery fry with larger body size. However, direct indications of competitive effects on wild fry, such as poor condition or reduced apparent growth rates in the presence of abundant hatchery fry, were not observed in this study. Because our understanding of the migration patterns of wild Taku chum salmon fry after leaving the inlet is inferred from data collected from hatchery fish, research to better define the degree of interaction should include a program to mark wild fry as they leave the river. Marking wild fry in the river would also allow a comparison of results of interactions such as growth, condition, feeding, and residence duration between wild and hatchery fry not only in the inlet but along their migratory corridor.

Our results also demonstrate that it is possible for hatcheries to successfully employ strategies that could reduce overlap between wild and hatchery fry and these strategies could apply to other salmonid hatcheries. DIPAC released fry near the outer inlet; because few hatchery fry entered the inner inlet, this release strategy reduced the potential for interactions with freshly emigrated small wild fish that are potentially more vulnerable. Potential negative interactions between early hatchery chum salmon and wild fish were also minimized by timing the release around periods of increased food resources and favorable temperatures for growth to reduce competition (Mortensen et al., 2000; Willette et al., 2001; Seo et al., 2006) and to minimize agonistic, size-related behavior (Olla et al. 1998); later releases of chum salmon fry may provide the best chance for the fish to avoid predation (Olla et al., 1998; Hawkins et al., 2008), and our data demonstrate that these later release fry will likely emigrate to sea more quickly, a strategy that could be useful to fishery managers seeking to reduce the potential for interactions between wild and hatchery fry during the critical life stage of estuarine and early marine residence.

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