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[Article]

Interannual Variability in Early Marine Growth, Size-Selective Mortality, and Marine Survival for Prince William Sound Pink Salmon

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Abstract.—The main objective of this study was to use scale patterns to compare the early marine growth of the average pink salmon *Oncorhynchus gorbuscha* with that of fish from the same year-class that survived to adulthood to gain insight on critical periods for growth and survival. During 2001–2004, pink salmon that survived to adulthood were larger and grew faster than the average juvenile throughout the first growing season, indicating that larger, faster-growing juveniles experienced higher survival. Growth rate declined from mid–late June to early–mid-July for both juveniles at-large and fish that survived to adulthood. The adult survivors then grew at a faster rate than the average juvenile through September. Both the juvenile pink salmon population at-large and all cohorts that survived to adulthood grew at a faster rate during high-survival years than low-survival years from mid–late June to mid–late August. Greater variability in the growth trajectories of surviving adults was observed during high-survival years, potentially a result of diversified feeding or distribution strategies. This study supports findings that significant size-selective mortality of juvenile pink salmon occurs after the first growing season. Investigating the timing and magnitude of size-selective mortality on juvenile pink salmon during their first growing season is an initial step toward understanding the processes regulating growth and survival.

Although early marine growth has repeatedly been correlated with overall marine survival in Pacific salmon *Oncorhynchus* spp. (Holtby et al. 1990; Henderson and Cass 1991; Murphy et al. 1998; Tovey 1999; Willette et al. 1999; Mortensen et al. 2000; Beamish et al. 2004), we currently lack a mechanistic understanding of the timing, magnitude, and source of stage-specific marine survival. The run size of adult pink salmon *O. gorbuscha* returning to Prince William Sound has varied widely in recent years: smolt-to-adult survival was lower than average for hatchery juveniles released in 2001 and 2003 (3% for each year) and high for pink salmon released in 2002 (9%) and 2004 (8%; ADFG 2005; PWSAC 2005; K. Morgan, Valdez Fisheries Development Association, personal communication).

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Prince William Sound hatcheries time their release of fry to coincide with the spring zooplankton bloom, which typically occurs in May (Cooney et al. 1995). Juvenile pink salmon migrate westward out of Prince William Sound to the coastal Gulf of Alaska by July or early August (Cooney 1993; Farley and Carlson 2000), move off the continental shelf by their first winter, and return to Prince William Sound the following summer as adults (Heard 1991). Although some juvenile pink salmon remain in Prince William Sound through October, the most common pattern is to migrate to the coastal Gulf of Alaska around July (Cross et al. 2008). On account of their 2-year life cycle, juvenile pink salmon that entered the ocean during 2001–2004 returned as adults during the following summers of 2002–2005.

Due to their small size at ocean entry, pink salmon are highly vulnerable to predation during their first months in marine waters (Hunter 1959), and consequent high juvenile mortality markedly affects year-class strength. The first weeks at sea are thus often referred to as a "critical period" for growth in salmon because significant mortality occurs during this time (Parker

1968; Beamish and Mahnken 2001). Pink salmon are hypothesized to undergo a second critical period after the first growing season, presumably during the winter (Beamish and Mahnken 1999, 2001; Moss et al. 2005). Under the "critical size/critical period" hypothesis, juvenile salmon that do not achieve a threshold size by the end of their first summer at sea will not survive the following winter (Beamish and Mahnken 2001). Therefore, high growth rates during the first summer of marine life could be important in determining recruitment of a year-class (Beamish and Mahnken 2001; Beamish et al. 2004; Moss et al. 2005). Cross et al. (2008) compared spatial and temporal patterns of pink salmon growth over the first 5 months of juvenile residence in Prince William Sound and in Gulf of Alaska coastal areas and showed that larger, faster-growing fish experienced higher overall survival.

Calcified structures in fish, such as scales, can be used to reconstruct the growth history of individual fish. Juvenile salmon produce circuli on their scales at regular intervals of approximately 4–8 d (Courtney et al. 2000; Cross et al. 2008), and the rate of circulus formation and the growth of the scale determine the spacing between rings (Fukuwaka and Kaeriyama 1997). Scale radius is proportional to fish length (Lee 1920; Ricker 1992); thus, the radius of the scale at previous circuli reflects size at a younger age, and the width of circulus increment spacing reflects growth during specific intervals (Fukuwaka and Kaeriyama 1997; Courtney et al. 2000; Beamish et al. 2004). During periods of faster growth, rings on scales and otoliths form at wider intervals; slower growth results in narrower spacing. Because of variability in the timing of ocean entry, using scales to study growth allows more accurate comparisons between cohorts at certain points in their life history than by tracking mean sizes of fish captured at sea.

Prince William Sound hatcheries thermally mark the otoliths of 100% of their pink salmon fry prior to release, providing a unique opportunity to trace each hatchery fish recovered to a specific entry date, location, and average size at release. Moss et al. (2005) used scales to compare the early marine growth of pink salmon entering Prince William Sound as juveniles in 2001 and returning in 2002 as adults. The authors showed that pink salmon that survived to adulthood grew faster than the average juvenile during the first summer at sea, and significant size-selective mortality occurred after the first growing season.

This study extends the analysis by Moss et al. (2005) to an interannual comparison of the timing and magnitude of differences in the growth and size of juveniles versus returning adults. Our main objective was to use scale patterns to compare the growth of juvenile pink salmon collected during July–September 2001–2004 and that of surviving adults from the same year-class. By comparing observed patterns over 4 years, we can gain insight into whether the processes regulating survival are similar among years.

Methods

Field sampling.—Juvenile pink salmon were collected during 2001–2004 at three stations in southwest Prince William Sound and stations 1–6 on the Global Ocean Ecosystem Dynamics Program (GLOBEC) Seward Line in the Gulf of Alaska (Table 1; Figure 1). Stations were sampled during 6–10-d cruises monthly from July to September (Table 1) with the following exception: no cruise occurred during September 2002. We sampled out to station 10 on the Seward Line in August 2002 and to station 7 in September 2003. In 2003 and 2004, we also sampled a transect extending south from Cape Fairfield, east of the Seward Line, during all months (Table 1; Figure 1). Two stations west of the Seward Line (not shown in Figure 1) were also sampled in August 2003. This sampling scheme encompassed the migration period from Prince William Sound to coastal areas of the Gulf of Alaska for juvenile pink salmon and allowed reasonably high spatial and temporal data resolution during the first growing season.

At each station, two or more trawls were performed during daylight hours using a Nordic 264 surface rope trawl with 3-m doors and a 1.2-cm mesh liner in the cod end. The net fished a depth of approximately 11.4 m and a width of approximately 14.3 m (S. Patterson, Net Systems, personal communication) for 30 min at 2.8–5.7 km/h (1.5–3.0 knots). If juvenile pink salmon were present but fewer than 10 were caught in a single haul, the tow was repeated to increase sample size. Catches were sorted to species and counted (large catches were subsampled), and fork lengths (FLs) of up to 200 fish/species were measured. Up to 50 juvenile pink salmon from each tow were frozen in seawater for subsequent analysis.

Adult pink salmon were collected by the Alaska Department of Fish and Game in terminal cost-recovery fisheries in Prince William Sound upon return to Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH) during the summers of 2002–2005 (Table 1). Adult fish were captured by purse seine at hatchery-specific terminal fishery sites located directly in front of each hatchery (Figure 1).

Laboratory and scale growth analyses.—Personnel at the University of Alaska Fairbanks–Juneau recorded lengths and weights of all juvenile pink salmon

TABLE 1.—Sampling dates and trawling locations in Prince William Sound (PWS), Gulf of Alaska (GAK) coastal areas, Cape Fairfield (CF), and West Fairfield (WF) during July–September 2001–2004 and the total number of scales measured from pink salmon released by Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH). Pink salmon were collected as juveniles during their first summer and also upon hatchery return the following year. Because no adult scales were collected from PWS hatcheries in 2003, scales from adults collected by the Ocean Carrying Capacity (OCC) program of the National Marine Fisheries Service were used as surrogate scales.

		Hatchery scale source					
Sampling period	Sampling locations	AFK	CCH	SGH	WNH	OCC	Total
8–14 Jul 2001	PWS 1–3; GAK 1-6	5	4	13	13	0	35
11–19 Aug 2001	PWS 1–3; GAK1, li-6	20	13	25	18	0	76
18–22 Sep 2001	PWS 1–3; GAK 1-6	12	8	2	2	0	24
Summer 2002	AFK, CCH, SGH, WNH	32	14	25	23	0	94
20–26 Jul 2002	PWS 1–3; GAK li-6	0	2	14	4	0	20
20–24 Aug 2002	PWS 1–3; GAK li-10	0	9	5	3	0	17
24 Jul–1 Aug 2003	GAK; CF; Gore Point; Blying Sound; Cape Aialik; Cape Cleare	0	0	0	0	87	87
13–19 Jul 2003	PWS 1–3; GAK li-6; CF 1, 5, 10	1	3	6	2	0	12
1–7 Aug 2003	PWS 1, 3; GAK li-6; CF 0, 9, 12, 13; WF 1, 2	4	10	9	4	0	27
9–15 Sep 2003	PWS 1–3; GAK li-6; CF 5, 6, 12, 13	1	0	0	0	0	1
1–15 Aug 2004	AFK, CCH	43	38	0	0	0	81
18–24 Jul 2004	PWS 1–3; GAK li-5; CF 3, 6, 10, 11	5	18	14	15	0	52
17–23 Aug 2004	PWS 1–3; GAK li-6; CF 3, 4, 5, 10, 11	3	0	0	0	0	3
12–17 Sep 2004	PWS 1–3; GAK li, 2, 6, 7; CF 1, 2, 4, 6, 8	1	0	0	2	0	3
5 Jul–9 Aug 2005	AFK, CCH, SGH, WNH	98	98	55	97	0	348

collected and read otoliths for thermal markings that designated hatchery of origin (L. Haldorson, J. Boldt, and J. Piccolo, University of Alaska Fairbanks–Juneau, personal communication). Marine survival was computed as the hatchery-origin adult run size divided by the number of hatchery juveniles released. Survival rates were computed both for each hatchery separately and for all hatchery pink salmon in Prince William Sound collectively. A known number of otolith-marked juveniles was released from each hatchery, and the adult run size was computed as the hatchery returns plus terminal harvest.

Several scales were collected from the preferred area (Davis et al. 1990) of both the juvenile and adult pink salmon. Preferred scales were located in a rectangular area one to four scale rows above the lateral line and between two vertical lines drawn from the posterior edge of the dorsal fin and halfway between the posterior edge of the dorsal fin and the anterior edge of the adipose fin (Scarnecchia 1979). We analyzed scales from up to 15 randomly selected juvenile pink salmon from each station × cruise × year combination. Scales were collected from 50 adult pink salmon at each hatchery in 2002, from 50 pink salmon at AFK and CCH in 2004, and from 250 pink salmon at each hatchery in 2005.

Because no adult scales were collected by Prince William Sound hatcheries in 2003, scales from adult pink salmon collected during the summer of 2003 by the Ocean Carrying Capacity (OCC) program of the National Marine Fisheries Service were used as surrogate scales for adults returning to Prince William Sound during this year (Table 1). Scales collected by the OCC program and used in this analysis were obtained from fish captured just west of Prince William Sound during late July and early August. Thermal otolith markings were not read to determine the origins of these fish; however, due to their location at capture and the large number of pink salmon released by Prince William Sound hatcheries, many of these fish were presumably returning to Prince William Sound. Studies show that environmental processes during the early marine period are related to juvenile salmon survival and affect survival at regional (up to 1,000 km) rather than ocean basin-wide scales (Pyper et al. 2001, 2005; Mueter et al. 2002). This suggests that even if fish from the OCC program were not bound for Prince William Sound, they likely experienced similar marine conditions as juveniles.

The scales from each fish were placed on gummed cards (sculptured surface up) and impressed in transparent acetate at a pressure of 351.53 kg/cm^2 (5,000 lb/in^2) for 3 min. We read acetate impressions using a computerized video digitizing system (Optical Pattern Recognition System Model OPR-512). For each fish, the first scale showing clear, unbroken circulus bands, an unbroken scale edge, and no signs of regeneration was measured. Scale circuli were measured along the anterior–posterior axis from the back of the focus to the scale edge, as this is the most commonly used measurement (Martinson et al. 2000). Each circulus that crossed the measurement axis was

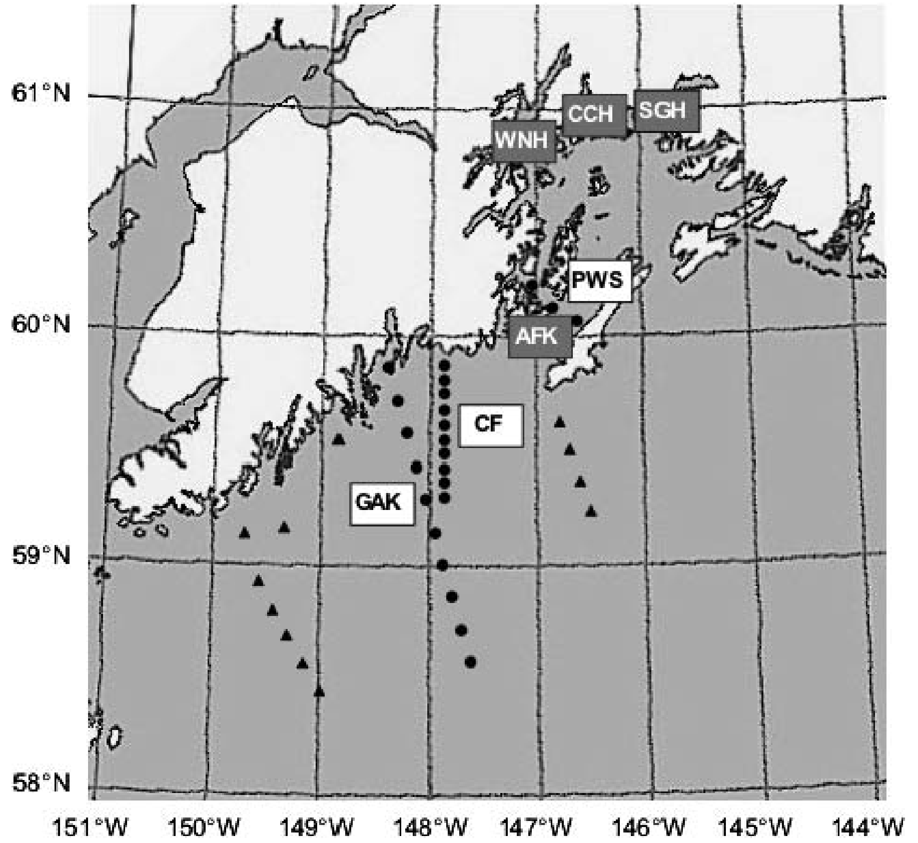

FIGURE 1.—Locations of sampling stations for juvenile pink salmon (black circles) in Prince William Sound (PWS) and on the Seward (Gulf of Alaska [GAK]) and Cape Fairfield (CF) lines. Station 1 is the station closest to shore on all lines. Returning adults were captured during 2002, 2004, and 2005 at Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH) in PWS (gray rectangles). During 2003, adult pink salmon were captured by the Ocean Carrying Capacity program at GAK and CF stations as well as at Gore Point, Cape Aialik, Blying Sound, and Cape Cleare (black triangles).

automatically marked by the digitizing system, and marks were added or deleted to correct for errors.

Total scale radius equaled the distance from the midpoint of the focus (focus/2) to the scale edge. To remove outliers, measurements from fish with a FL : scale radius ratio greater than 0.45:1.00 or with a focus exceeding 250 μm were deleted. Between 3–15% of juvenile scales from each year-class were removed as outliers, while between 3% and 43% of adult scales from each year-class were removed. Scales were analyzed from a total of 135 hatchery pink salmon juveniles caught during July–September 2001, from 37 hatchery juveniles caught during July–August 2002, from 40 hatchery juveniles caught during July–September 2003, and from 58 hatchery juveniles caught during July–September 2004. Scales were analyzed from 94, 87, 81, and 348 returning adult pink salmon captured during 2002, 2003, 2004, and 2005, respectively.

A linear scale radius–body length relationship most closely characterized the growth of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska during 2001–2004 (Cross et al. 2008). Because of the linear relationship between scale size and fish length and between circulus spacing and fish growth rate, fish length could be inferred directly from scale radius and growth rate from scale circulus spacing. Because growth trajectories did not differ significantly among juvenile pink salmon from different hatcheries during May–October 2001–2004 (Cross et al. 2008), we pooled all hatchery juveniles within each year for growth analyses.

We estimated the frequency distribution of scale radius measurements at circuli 3, 6, 9, 12, and 15 from pink salmon within each year-class caught as juveniles and as adults to track size modes during May–September, and we also compared mean sizes at circuli. A comparison of incremental scale growth between specific circuli revealed the timing and magnitude of differential growth between juveniles that survived to adulthood and the general population of juveniles at-large. Because of the linear relationship between FL and scale size for juvenile pink salmon, a decrease in average scale growth rate over time indicates a decrease in growth rate of the fish.

Differences in distributions of scale size at circuli for juveniles and adults were compared using Kolmogorov–Smirnov statistical tests ($\alpha = 0.05$). We used analysis of variance and Tukey's multiple comparison tests with Bonferroni-adjusted alpha levels to determine differences in mean scale size at circuli and circulus spacing between juvenile and adult fish from the same year-class, among adult cohorts (AFK, CCH, SGH, WNH, and OCC) from the same year-class, and among adult cohorts caught during different years. The mean daily growth rate of juvenile and adult scales was determined by dividing the mean scale growth increment over groups of three circuli by the number of days between circuli: 6.1 d in 2001, 5.8 d in 2002, 5.5 d in 2003, and 4.4 d in 2004 (Cross et al. 2008). The dates on which circuli formed were estimated using the relationships between day of year and number of full circuli presented in Cross et al. (2008).

Results

Differences in the distribution of scale measurements and mean size at circuli were not significant among adult pink salmon returning to different Prince William Sound hatcheries in 2002 (circuli 1–41, except adults from AFK were smaller at circuli 4–5 than adults from CCH) and 2004 (circuli 1–30) or among adults captured at different locations by the OCC program during summer 2003 (circuli 1–44, except differences between two of six locations at circuli 5–6). Adult pink salmon captured at hatcheries in 2002 and 2004 (2001 and 2003 juveniles) and adults captured during summer OCC cruises in 2003 (2002 juveniles) were therefore pooled into a single group within each year. For fish returning to hatcheries during 2005, mean size differed based on hatchery of origin at circuli 1–41, so adults returning to different hatcheries in 2005 (2004 juveniles) were analyzed as discrete cohorts.

Frequency distributions of scale measurements at every third circulus showed that surviving adults were significantly larger than the average juvenile throughout the first growing season during 2001 and 2002 ($P < 0.003$ for circuli 1–13), indicating that larger, faster-growing juveniles were more likely to survive than smaller juveniles (Figure 2). Although juveniles at-large also tended to be smaller than survivors during 2003, the differences were only significant at circuli 1–2 (Figure 2). Similarly, juveniles in 2004 tended to be smaller than surviving hatchery adults based on size distributions but were only consistently significantly smaller than adults from SGH (based on circuli 1–18, $P < 0.001$; Figure 3). During all years, scale size distributions of the juveniles and surviving adults had not yet converged by circulus 15 (Figures 2, 3), suggesting that significant size-selective mortality occurred after the juveniles were sampled in September.

Comparing mean size at circuli, the juvenile cohort at-large during 2001 was significantly smaller than surviving adults (circuli 1–16, $P < 0.001$; Figure 4). Juveniles at-large during 2002 and 2003 were significantly smaller than surviving adults from the same year-class at circuli 1–2 ($P < 0.001$; Figure 4). During 2004, juveniles were significantly smaller than survivors from the SGH cohort (circuli 1–18, $P < 0.001$) but rarely differed significantly from the sizes of survivors from AFK, CCH, or WNH.

Both the juvenile pink salmon population at-large and adult hatchery cohorts grew faster during high-survival years (2002 and 2004) than during low-survival years (2001 and 2003) from mid–late June to mid–late August (circuli 2–13; Figure 5). During all years, growth rates for juveniles at-large and the population that survived to adulthood were similar from mid–late June to early–mid-July (circuli 2–4, 5–7; Figure 5). In early to mid-July, growth rates for both juveniles and adults declined during all years and began to diverge thereafter.

Surviving fish began growing at a faster rate than the average juvenile by late July or early August (circuli 8–10) during all years (Figure 5). Growth diverged at an even earlier point during some years: the 2002 pooled adult cohort (juveniles during 2001) and the 2005 SGH cohort (juveniles during 2004) began growing significantly faster than the average juvenile in early to mid-July (circuli 5–7). The 2005 AFK cohort grew significantly faster than the average juvenile during late June (circuli 2–4).

Juvenile growth rate increased after late July or early August during 2001 and 2003, low-survival years for juvenile rearing (Figure 5). During the 2002 and 2004 high-survival years, growth rate for the average juvenile decreased steadily from approximately mid–late June to late September (circuli 2–19). The growth rate of adult survivors increased from late July to late September (circuli 8–19) during all years, although this trend was not as pronounced during high-survival years.

Similar trends in growth and survival were observed when comparing juveniles and adults from specific

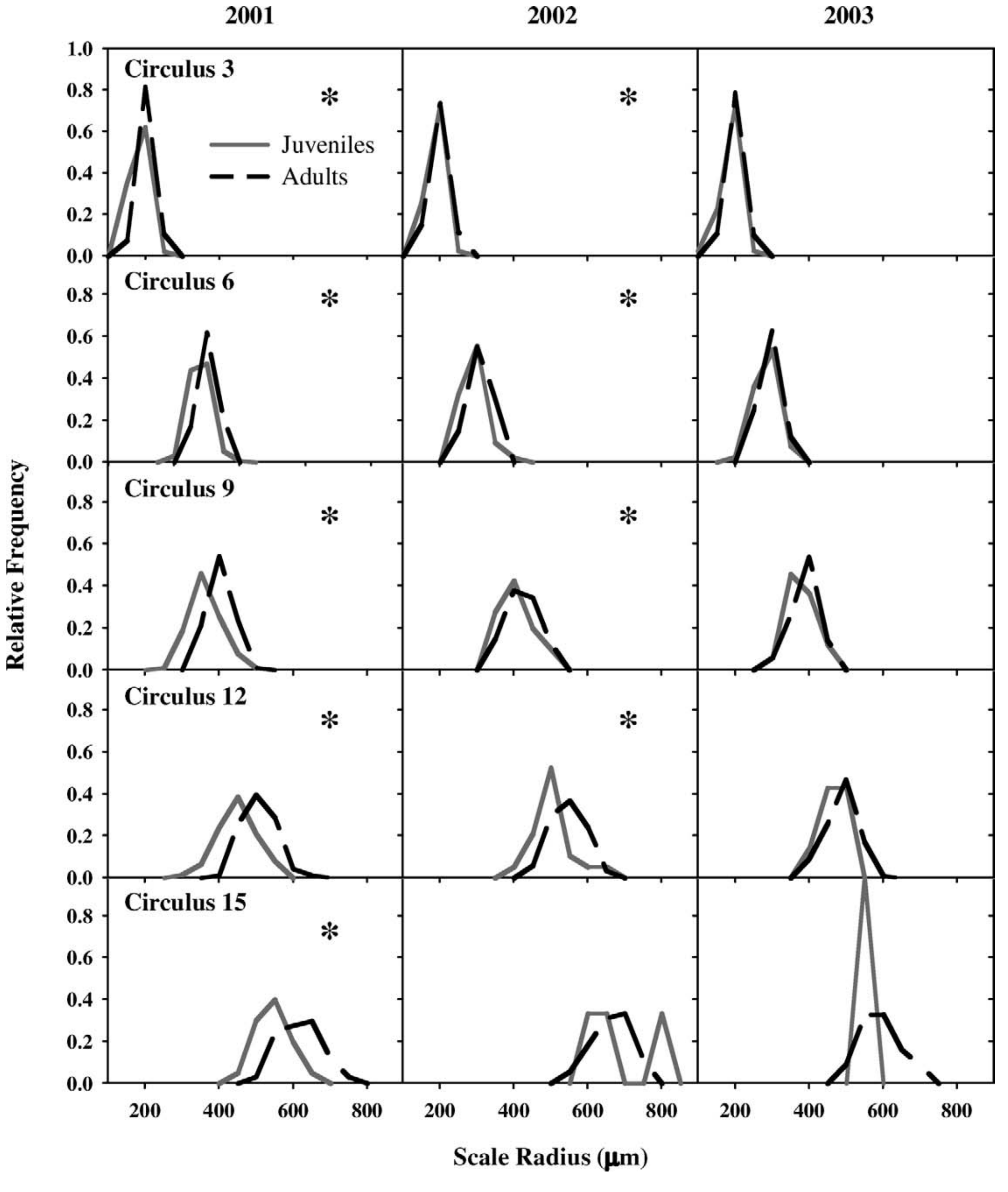

FIGURE 2.—Relative frequency distribution of scale radii (μm, in 50-μm bins) at every third circulus (between circuli 3 and 15) during the first growing season for juvenile pink salmon collected by trawling in Prince William Sound and the coastal Gulf of Alaska during July–September 2001–2003 and for pink salmon from the same year-class that survived to adulthood. In 2002 and 2004, adults were collected at terminal fisheries in front of four hatcheries in Prince William Sound. In 2003, adults were captured in the Gulf of Alaska by the Ocean Carrying Capacity program of the National Marine Fisheries Service. An asterisk indicates statistically significant differences (Kolmogorov–Smirnov test, $P < 0.05$) at a particular circulus between juveniles at-large and those that survived to adulthood.

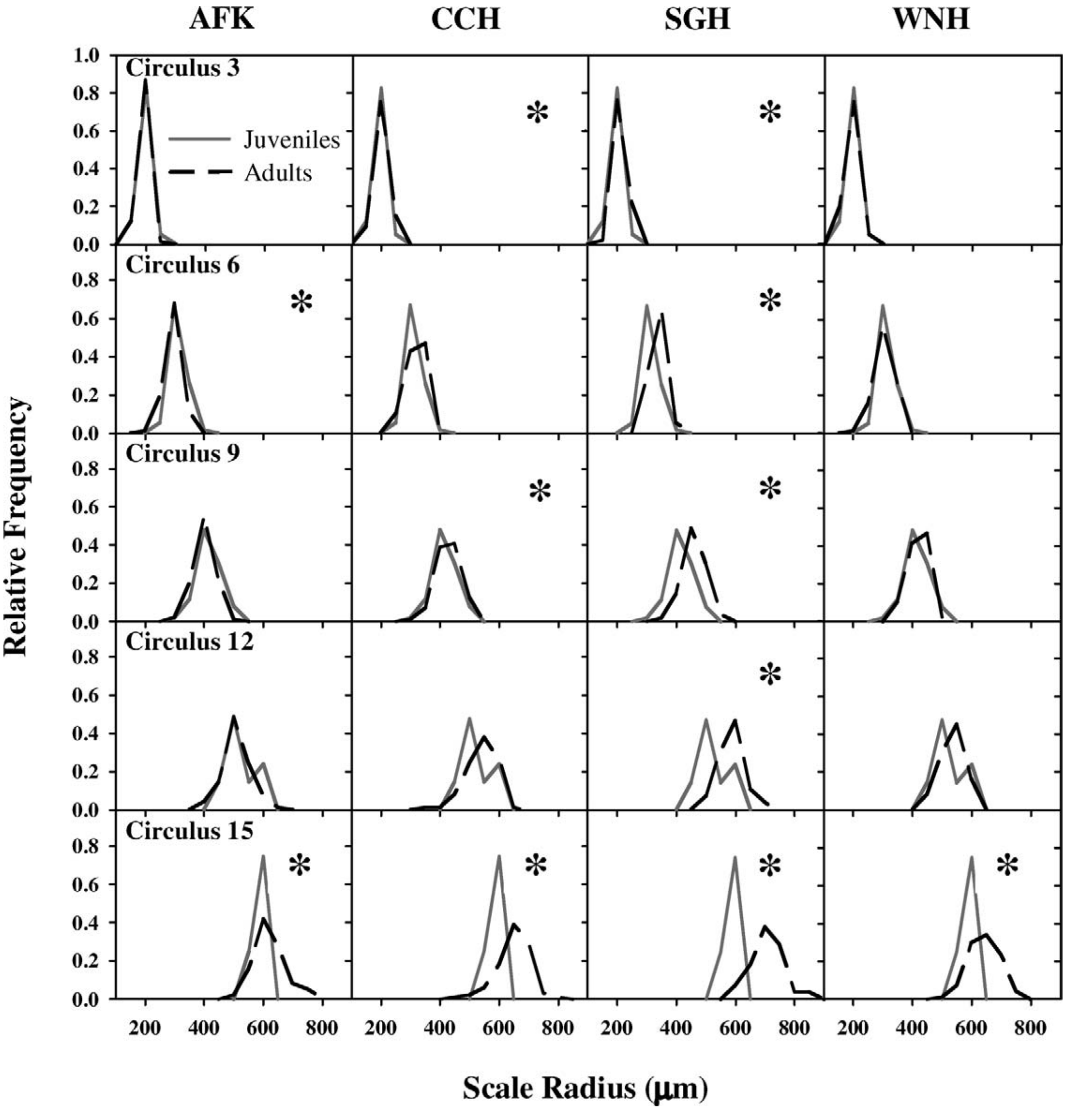

FIGURE 3.—Relative frequency distribution of scale radii (μm, in 50-μm bins) at every third circulus (between circuli 3 and 15) during the first growing season for juvenile pink salmon collected by trawling in Prince William Sound and the coastal Gulf of Alaska during July–September 2004 and for pink salmon from the same year-class that survived to adulthood. During 2005, adults were collected at terminal fisheries in front of Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH) in Prince William Sound. An asterisk indicates statistically significant differences (Kolmogorov–Smirnov test, $P < 0.05$) between juveniles at-large and those that survived to adulthood.

hatcheries during each year. During May–September 2001 and 2003, juvenile pink salmon from each hatchery were significantly smaller than adult survivors returning to the same hatchery. During 2004, the average juvenile from AFK, CCH, and WNH was not significantly different in size from the average adult survivor from the same hatchery, but the average juvenile from SGH was significantly smaller in size than those that survived to adulthood.

There were, in fact, more differences in scale size for the 2004 year-class among surviving adults from different hatcheries than between the survivors and juveniles from the same hatchery. Pink salmon from AFK that survived to adulthood were significantly

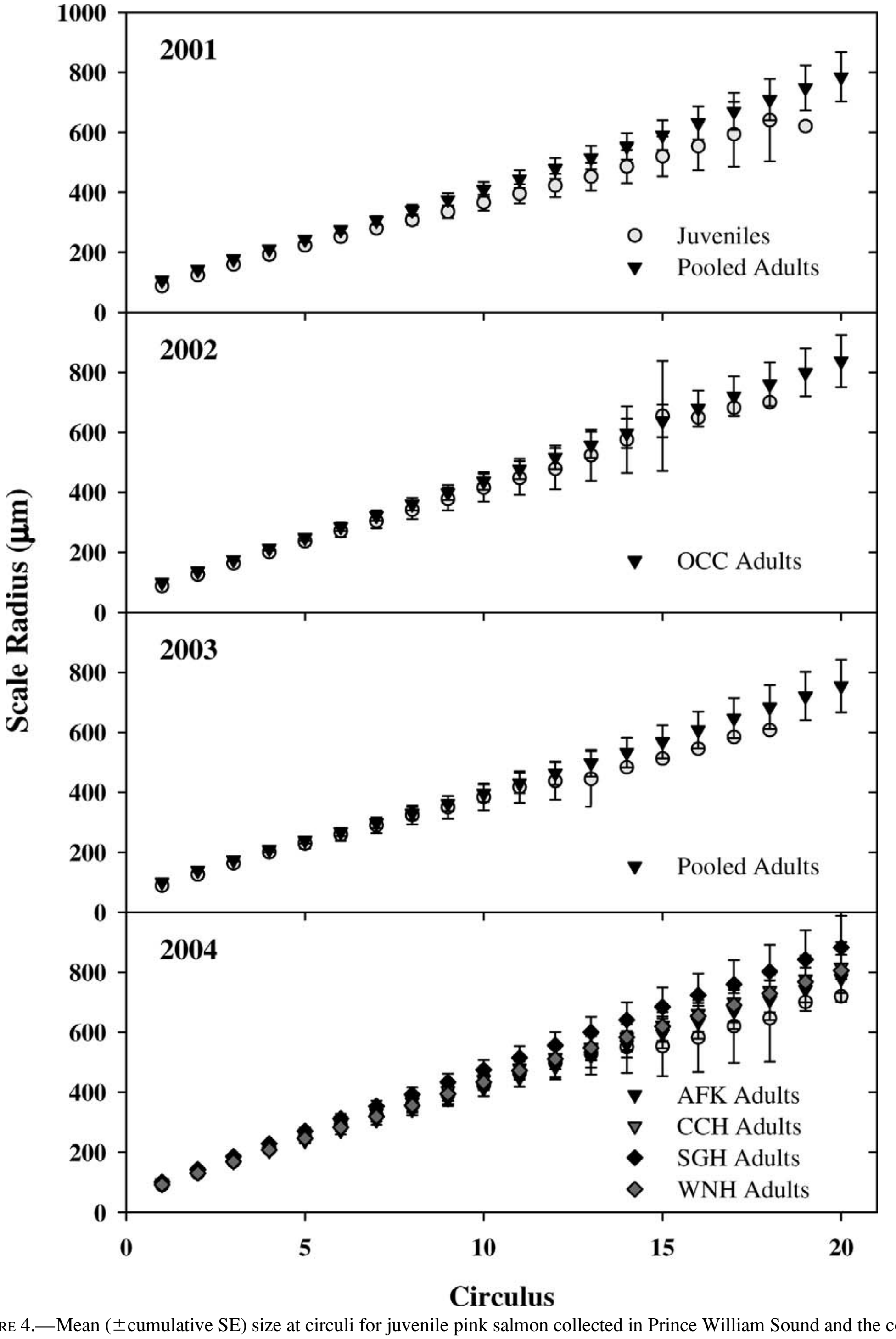

FIGURE 4.—Mean (±cumulative SE) size at circuli for juvenile pink salmon collected in Prince William Sound and the coastal Gulf of Alaska during July–September 2001–2004 and for pink salmon from the same year-class that survived to adulthood. Adults that were juveniles during 2001, 2003, and 2004 were collected in 2002, 2004, and 2005, respectively, at terminal fisheries in front of Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH) in Prince William Sound. Adults that were juveniles during 2002 were captured in 2003 in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) program of the National Marine Fisheries Service.

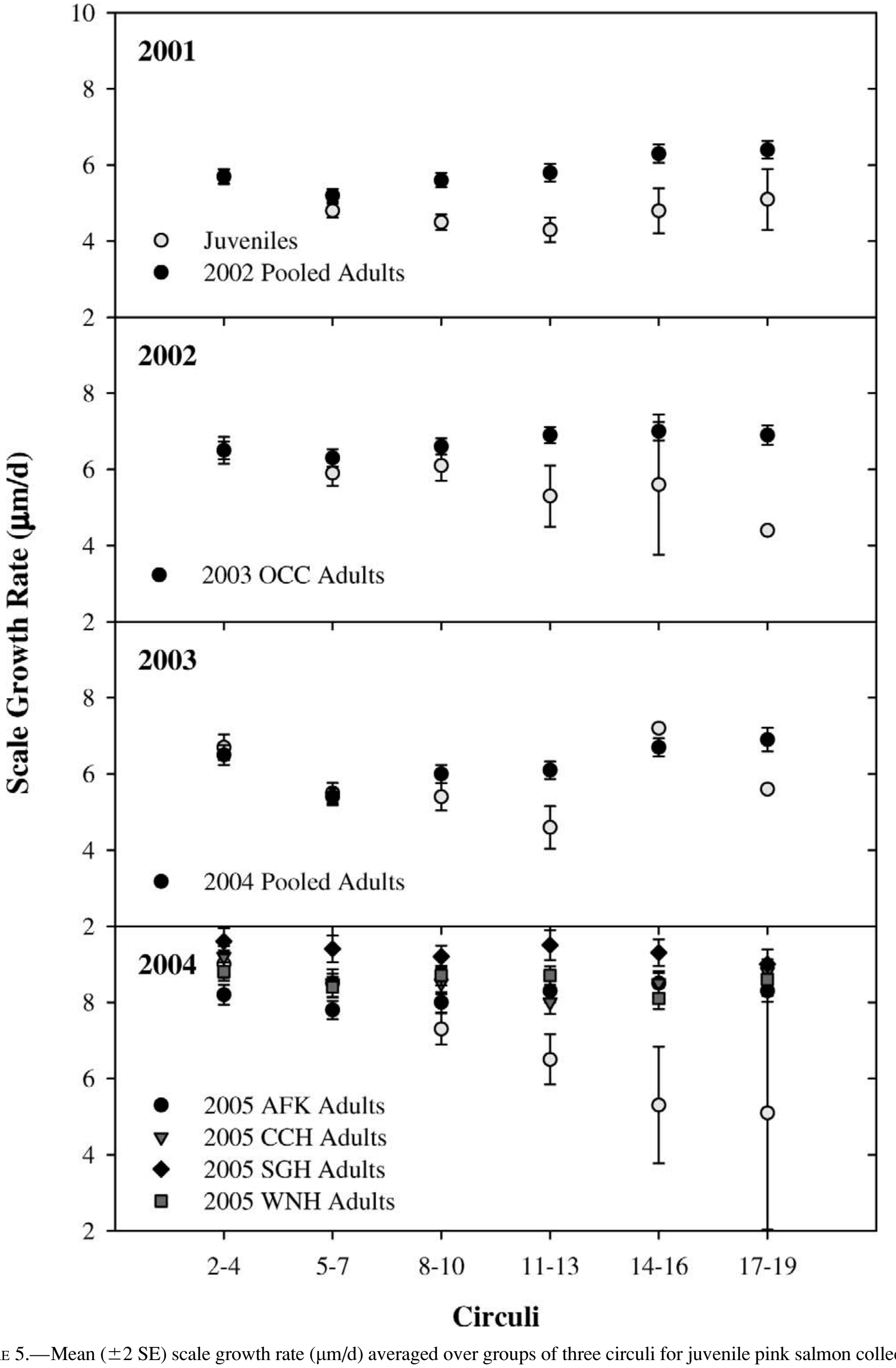

FIGURE 5.—Mean (±2 SE) scale growth rate (µm/d) averaged over groups of three circuli for juvenile pink salmon collected in Prince William Sound and the coastal Gulf of Alaska during July–September 2001–2004 and for pink salmon from the same year-class that survived to adulthood. Adults that were juveniles during 2001, 2003, and 2004 were collected in 2002, 2004, and 2005, respectively, at terminal fisheries in front of Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH) in Prince William Sound. Adults that were juveniles during 2002 were captured in 2003 in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) program of the National Marine Fisheries Service.

smaller as juveniles during 2004 than CCH survivors (circuli 3–18), SGH survivors (circuli 7–16, 18), and WNH survivors (circuli 3–18). Surviving fish from CCH were significantly smaller as juveniles than survivors from SGH (circuli 4–18) and smaller than WNH survivors at circuli 1, 3, and 4. Interestingly, CCH fry were released at a much smaller average size in 2004 than fry from all other hatcheries (0.37 g compared to 0.62–0.69 g) but had higher survival than AFK and WNH fish, were larger at return than WNH adults, and were similar in size at return to AFK adults.

For individual hatchery cohorts within each year, the relationship between size and survival was not always consistent. Pink salmon returning to CCH in 2002 were larger as juveniles than survivors from AFK, SGH, and WNH yet experienced lower survival (1.1% compared to 5.2, 4.4, and 2.6%, respectively; McNair 2002). During 2004, adults returning to AFK (3.6% survival) were larger than the CCH cohort (2.0% survival), though not significantly so. During 2005, surviving fish from SGH (10.3% survival) were larger than survivors from CCH (8.6%), WNH (7.3%), and AFK (6.1%; Figure 4); surviving fish from CCH were larger than survivors from WNH and AFK; and surviving fish from WNH were larger than survivors from AFK.

Total scale size at return was largest for the 2002 and 2004 year-classes, which experienced high survival, and smallest for the 2001 and 2003 year-classes, which experienced low survival. However, no consistent relationship was observed between final FL and survival. Adult pink salmon returning to Prince William Sound hatcheries were on average largest during 2004 (2003 year-class), a low-survival year, and smallest during 2005 (2004 year-class), a high-survival year. Adults returning to Prince William Sound in 2003 (2002 year-class), a high-survival year, were larger than adults returning in 2002 (2001 year-class), a low-survival year.

Discussion

The increased abundance of juveniles from hatchery production has elicited concerns that we are reaching or exceeding the carrying capacity for juvenile pink salmon, which could be potentially food-limited at one or more stages in their life cycle and in one or more regions. Growth declines have been reported in relation to reduced zooplankton biomass (Orsi et al. 2000). Recent studies present evidence for the competitive dominance of pink salmon over other salmon species (Ruggerone et al. 2003; Ruggerone and Nielsen 2004), and it is not unreasonable to think that intraspecific competition exists as well. Wertheimer et al. (2004a, 2004b) contended that although density-independent ocean conditions primarily drive pink salmon spawner abundance and productivity, large-scale supplemental stocking from hatcheries in Prince William Sound has contributed to reduced body size due to density-dependent growth in the Gulf of Alaska. Farley and Carlson (2000) suggested that coastal waters of the Gulf of Alaska could be food limiting for juvenile pink salmon, and Beauchamp et al. (2007) determined that the average juvenile fed at 90% or more of their theoretical maximum consumption rate during the first summer of growth in 2002, compared with 79–83% during 2001, when marine survival was threefold lower. These patterns suggest that strong selection pressure can act on seemingly small changes in feeding and growth rates by juvenile salmon in the ocean.

In this study, growth rates for juvenile pink salmon declined for both the average and surviving fish in early to mid-July during all years, suggesting a potential bottleneck in growth. As zooplankton production in Prince William Sound and the coastal Gulf of Alaska declined beginning in early June and large copepods migrated to diapause depths (Cooney et al. 2001; Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), the overall amount of zooplankton in the surface layer was usually reduced (Eslinger et al. 2001). Juvenile pink salmon therefore might have experienced a bottleneck in growth at this time due to reduced prey availability. Fish that survived this growth bottleneck were the larger individuals of each year-class and grew at a faster rate than the average juvenile throughout the rest of the summer.

Ocean conditions and abundance likely regulate the strength of density dependence and carrying capacity for juvenile salmon, although it is difficult to separate the effects of each on growth and survival. The large influx of juvenile pink salmon into the Gulf of Alaska, in conjunction with the seasonal dynamics of zooplankton prey, could create localized prey depletions and density-dependent growth. Both the juvenile pink salmon population at-large and all cohorts that survived to adulthood grew at a faster rate from approximately mid–late June to mid–late August during the higher-survival years of 2002 and 2004 than during the low-survival years of 2001 and 2003. If density-dependent growth occurred, it might have been less intense during the summers of high-survival years than during low-survival years. Also, more differences in size at all circuli existed among adult hatchery cohorts during high-survival years than during low-survival years. Diversified feeding or distribution strategies could produce greater variability in growth trajectories during high-survival years, while growth might have been more limited during low-survival years.

Early marine growth and mortality are undoubtedly affected by size-selective predation as well. The abundance and size of predators that feed on juvenile pink salmon (e.g., walleye pollock *Theragra chalcogramma*, Pacific herring *Clupea pallasii*, and other salmonids) and the abundance of alternative prey for these fish will influence the extent of early mortality during each year (Willette et al. 2001).

Temperature can also affect pink salmon metabolism, growth, and survival (Brett et al. 1969; Weatherly and Gill 1995; Mueter et al. 2005). However, Beauchamp et al. (2007) found that because juvenile pink salmon in the Gulf of Alaska experienced near-optimal growth temperatures, feeding rate and prey quality affected growth much more than a several-degree shift in temperature.

Beamish and Mahnken (2001) hypothesize that while growth-based mortalities are continuous throughout the summer months, mortality predominantly occurs in two major stages: immediately after ocean entry and during the late fall and winter of the first year. This study supports the findings of Beamish and Mahnken (2001) and Moss et al. (2005) that additional size-selective mortality occurs after the first growing season and significantly influences smolt-to-adult survival for pink salmon. The discrepancy in body size between the juvenile population at-large and those that survived to adulthood through circulus 15 suggests that significant size-selective mortality occurred after late summer. The probability of reaching a critical size in order to survive winter could be exacerbated by bottlenecks in prey supply. Also, the size threshold for pink salmon success could vary among years in response to conditions experienced during later life stages. Aydin et al. (2005) hypothesized that mixed-layer depth influences zooplankton availability and thus final body weight for pink salmon, and size achieved by the end of the first growing season could potentially determine the ability to exploit high-energy squid and impact overall survival.

The relative importance and magnitude of early and late size-selective mortality thus likely vary among years because of different initial conditions (e.g., juvenile size at entry) and different environmental conditions (e.g., temperature, prey availability) that influence distribution and growth during the first growing season; moreover, the results of the earlier phase might alter the severity of the later phase. Mortality may also be more of a continuous process rather than occurring in distinct stages, but this study was not designed to gain insight on overall mortality throughout the summer.

To allay concerns that the trawls could be catching a disproportionate number of smaller or larger fish, we examined the potential for size-selective sampling by our trawl gear. The size composition of our catches indicated that the trawls did not impose a size-selective sampling bias over the range of juvenile sizes pertinent to our analysis. Although juvenile pink salmon are thought to reside in the top approximately 10 m during the first summer growing season and the net sampled to a depth of 11.4 m, larger fish residing below the depth of the net might not have been sampled, imposing a subtle bias on these results. Moss et al. (2005) examined this question explicitly by comparing size frequencies of fish in our net with those in a much larger net and concluded that no size-selective bias was associated with our sampling methodology.

Some of the adult pink salmon caught in terminal fisheries might have been released from a hatchery other than the one to which they returned or might have been stray members of the wild cohort. The possibility of straying adds uncertainty to the origin of returning adults and could affect estimates of stock-specific survival as well as comparisons of the growth performance of adults from different hatcheries; however, given the relatively large number of adult scales measured we do not believe that strays would significantly affect our results.

A major assumption of using scales to study growth history is that the relationship between scale radius and fish growth is linear and does not change with the growth rate of the fish. However, linear models of fish growth are preferred over other methods by many scientists (Ricker 1992; Klumb et al. 2001) and continue to be the most widely used, especially when looking at short growth intervals. A linear model best captured the relationship between FL and scale size for juvenile pink salmon in Prince William Sound and the Gulf of Alaska during 2001–2004 (Cross et al. 2008).

Investigating the importance of early marine growth to smolt-to-adult survival, as well as the timing and magnitude of mortality periods, is an initial step toward understanding the processes that regulate growth and survival for juvenile pink salmon. Related research will compare the consumption demand of juvenile pink salmon to the biomass of exploitable prey in localized areas in an attempt to identify and quantify ecological bottlenecks, such as periods of prey depletion. Scale-based growth estimates from juvenile pink salmon collected during or shortly after the first winter could help fill in part of the temporal gap between ocean entry and return and give insight on the rate and importance of ocean growth after the first growing season. The integration of scale data from juvenile, mature, and returning pink salmon would provide insight into the timing of one or more "critical periods" in their life history, the magnitude of size-selective mortality, and the importance of juvenile growth to adult survival and run strength. Understanding the timing and causes of mortality will lead to more effective management practices and provide insight into mechanisms regulating growth and survival for pink salmon.

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