

Inter-Annual Patterns in Stage-Specific Feeding, Growth, and Survival of Juvenile Pink Salmon in the Gulf of Alaska

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Evidence is mounting for the positive relationship between marine survival of salmon and larger juvenile size or higher growth rates, but little is known about the precise timing of critical life stages or the mechanisms underlying size-selective marine mortality. The temporal dynamics and variety of factors that potentially affect distribution, growth, and survival can confound determinations of the processes that most influence performance during critical life stages in the ocean. Hatcheries in Prince William Sound (PWS) release approximately 600 million otolith-marked juvenile pink salmon annually, and these hatchery fish represent the largest biomass of juvenile salmon in the eastern coastal Gulf of Alaska (GOA). Pink salmon are considered the primary zooplankton consumers in this region. Juvenile pink salmon in PWS and the coastal GOA exhibited a three-fold difference in marine survival during the GLOBEC sampling program in 2001–2004. For otolith-marked hatchery pink salmon released in PWS Sound during 2001–2004, we investigated the relationship of growth and size-selective mortality during and after the first growing season. Using a bioenergetics model, we examined monthly and inter-annual patterns in spatial distribution, thermal experience, growth, and diet composition to relate feeding and growth performance to inter-annual variability in stage-specific mortality and total ocean survival.

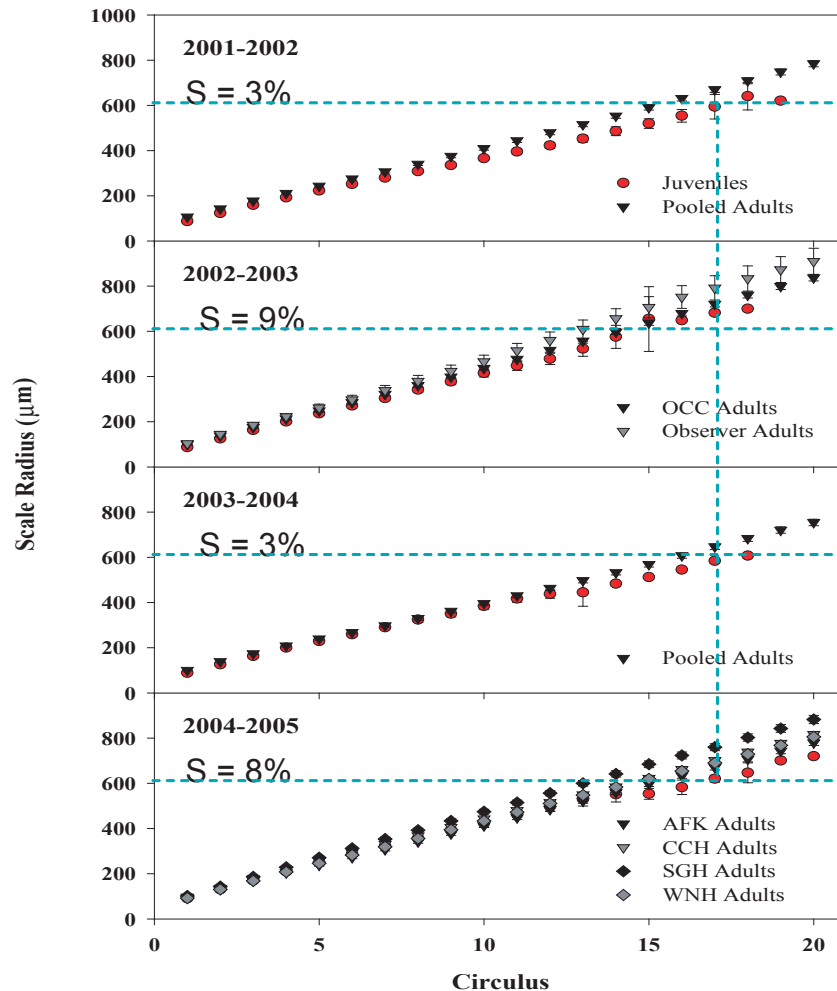
During 2001–2004, monthly sampling cruises were conducted from July through September or October at three sites in PWS and six or more sites along the Seward Line (GAK 1-6) in the coastal Gulf of Alaska (GOA). At each station, fish were sampled with a surface trawl and zooplankton were collected with a 500 micron Tucker trawl towed at the surface or 0–10 m vertical tows with a 333 micron bongo net; vertical temperature and salinity profiles were recorded with CTD casts. Fish were identified, counted, measured, weighed, and frozen for additional processing. In the lab, fish were thawed, reweighed and measured, and scales, otoliths, and stomach contents were removed. Energy densities were measured for a subset of fish and some zooplankton using a bomb calorimeter. Energy densities for the remainder of the prey were taken from literature values.

Stage-specific, size-selective mortality was examined following Moss et al. (2005) by comparing back-calculated size and growth (based on the radius of specific circuli on scales) at the same life stages for both juveniles sampled during the first summer in PWS and GOA, and for surviving adults from the same hatchery groups that were harvested in cost recovery fisheries close to each hatchery.

A bioenergetics model simulated monthly consumption rates and growth efficiency for hatchery cohorts of juvenile pink salmon, from the time of their release into PWS in May, through September each year during 2001–2004. Inputs for these simulations tracked the modal distribution, diet composition, and thermal experience of identifiable hatchery cohorts within and among different specific water masses (PWS; the Alaska Coastal Current-ACC; and the shelf transition zone-TRANS). Monthly spatial distribution patterns were assigned to the water mass(es) with CPUE \geq 30% of the monthly total catch rate. For these water masses, back-calculated lengths were converted to weights and were combined with monthly diet composition and thermal experience to estimate feeding rates using a bioenergetics model (Beauchamp et al. in press). Feeding rates were reported both as the biomass of prey consumed over prescribed periods and as proportions of the maximum consumption rate expected for a given size of consumer and thermal regime. Feeding rates and growth efficiency were used to infer inter-annual differences in prey availability.

As indicated by larger average scale radius at the same circuli, juvenile pink salmon were generally smaller during years when the ocean survival was low (3% smolt-adult) for cohorts entering the ocean in 2001 and 2003, and were larger when the ocean survival was higher (8–9%) in 2002 and 2004 (Fig. 1). Juveniles that survived to adulthood were significantly larger than the average juveniles from the same hatchery group *in situ* at the same life stage, and the size of the survivors tended to diverge from average juveniles around August (circuli 8-13; Fig. 1). Since the average size of the juveniles at large in GOA had not converged with the size of the surviving adults by the

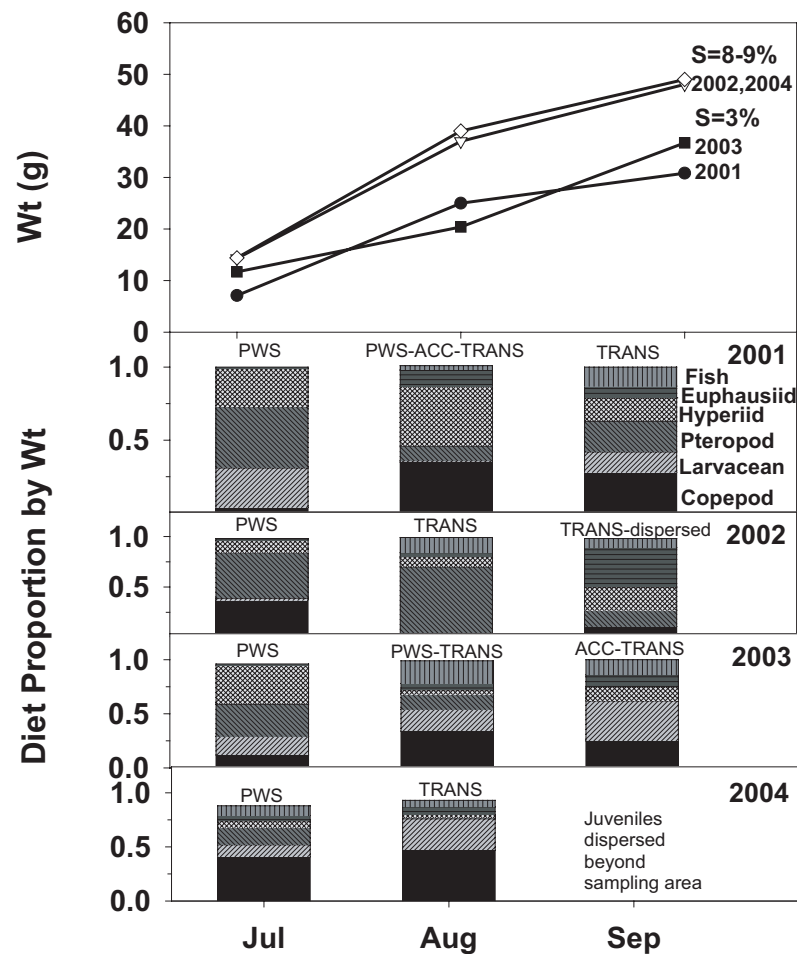
Fig. 1. Size-at-circuli for juvenile pink salmon sampled in PWS and GOA during the first summer in the ocean (circles), and for surviving adults from the same PWS hatchery groups released in 2001, 2002, 2003, and 2004 (diamonds and triangles). Adults were intercepted the following summer in cost-recovery fisheries outside the hatcheries in 2002, 2004 and 2005, and from adult samples provided by foreign vessel observers and the NOAA Ocean Carrying Capacity cruises from regions and times when PWS hatcheries were the highest probability source of the adults (Cross 2006). In all years, the average juveniles are noticeably smaller than survivors in August at around circuli 8–13. Dashed reference lines demonstrate that juvenile pink salmon were larger in years with high ocean survival (2002, 2004) than during low survival years (2001, 2003).



end of the summer, significant size-selective mortality must have occurred after the first summer.

High survival was associated with broader spatial distribution, greater feeding rates, faster growth and larger size during the first summer of ocean feeding (Fig. 2). Back-calculated stage-specific lengths were converted to body mass. There was no consistent pattern between thermal regime and inter-annual growth or survival. Modal sea surface temperatures during July–September were 11.5–14.0°C in 2001 (low survival), 12–13.0°C in 2002 (high survival), 12.5–14.0°C in 2003 (low survival), and 13.0–15.5°C in 2004 (high survival). Bioenergetic simulations indicated that growth and consumption rates were insensitive to the inter-annual differences in summer temperatures. From marine entry in May through August, feeding rates were considerably higher during years of high survival (80–100% of the maximum consumption rate C_{max} in 2002 and 2004) compared to 2001 and 2003 (65–80% of C_{max}). The biomass of prey consumed from May through August was also higher during high survival years: 145–154 g in 2002 and 2004 compared to 64–95 g in 2001 and 2003. Moreover, the incremental increase in consumption required for the average juveniles to attain the mean size of the survivors was only 12–15% in 2002 and 2004 compared to 20–22% higher consumption during 2001 and 2003. During the high survival years in the apparently critical August growth period, pteropods contributed most to the energy budget of juveniles in 2002, and larvaceans and large copepods were most important in 2004. In lower survival years hyperiid amphipods and large copepods were the primary prey during August 2001 and a mix of crustacean zooplankton and fish were the predominant prey in 2003.

Fig. 2. Inter-annual variability in mean monthly body mass and ocean survival of pink salmon (top panel) and associated distribution and diet patterns (lower panels) of juvenile pink salmon in Prince William Sound (PWS) and the coastal Gulf of Alaska during the first summer of marine growth in 2001–2004. Abbreviations above the bars for diet composition indicate the modal spatial distribution of juveniles: ACC = Alaska Coastal Current, and TRANS = Slope transition zone in the Gulf of Alaska. Juveniles were mostly dispersed beyond the Seward Line in September 2002 and 2004.



These analyses suggest that growth trajectories between average juveniles and survivors diverge in August, and that factors like broader dispersal, higher feeding rates, and higher prey availability (especially gelatinous zooplankton like pteropods and larvaceans) were more important than the direct thermal effects for higher growth and survival.

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