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ARTICLE

Growth and Survival in Relation to Body Size of Juvenile Pink Salmon in the Northern Gulf of Alaska

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Abstract

The abundance of anadromous salmon is partially determined by size-selective mortality during the early marine life phase. Consequently, identifying the growth patterns of juvenile salmon during this life phase is important in understanding the dynamics of salmon populations. We examined patterns of early marine growth in juvenile pink salmon *Oncorhynchus gorbuscha* released by four hatcheries in Prince William Sound (PWS), Alaska, and explored how these patterns related to marine survival. Since larger individuals are thought to experience reduced mortality, we partitioned the data into weight-based quartiles and compared growth rates (% body weight/d) of all fish, the largest fish (top 25%), and the smallest fish (bottom 25%). Sampling occurred during summer 1997–2004 in PWS, the inshore Gulf of Alaska (GOA), and the offshore GOA. Growth rates varied significantly among years and sampling locations; however, the growth rate patterns were markedly similar among size-groups and hatcheries. Growth rates tended to be high in 1997, 2002, and 2004 and lower in 1998, 2001, and 2003. Fish sampled in the offshore GOA typically had faster growth rates than those sampled elsewhere, although this was less pronounced for the largest fish. For all size-groups, the relationship between survival and growth rate was strongest for fish captured in the offshore GOA and weakest for those captured in PWS, indicating that the likelihood of survival is greater for juveniles that migrate offshore earlier. The strength of the growth rate–survival relationship for pink salmon captured in the offshore GOA was similar among all size-groups, suggesting that once fish migrate offshore they are less vulnerable to size-selective predation.

It is widely recognized that mortality of Pacific salmon *Oncorhynchus* spp. during the marine life phase is inversely related to size (McGurk 1996). Consequently, faster growth of juvenile salmon during the marine period is expected to increase survival, as demonstrated for several salmon species (Koenings

et al. 1993; Willette et al. 1999; Ruggerone and Goetz 2004; Moss et al. 2005). The early marine phase is often designated as a critical period for juvenile salmon owing to high mortality rates during this period (Parker 1968; Bax 1983; Wertheimer and Thrower 2007). Significant mortality may also occur during

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the first marine winter if the juvenile salmon do not reach a critical size by the end of the first marine summer, indicating the importance of growth during the early marine period (Beamish and Mahnken 2001; Cross et al. 2009).

Growth rates of juvenile salmon are influenced by marine conditions during their first summer at sea (Holtby et al. 1990; Cross et al. 2008, 2009). Meso-scale variations in foraging conditions have been associated with differences in feeding intensity, condition, and growth of juvenile pink salmon *O. gorbuscha* in waters seaward of Vancouver Island, British Columbia (Perry et al. 1996). Finer-scale habitat variation can also be important in explaining the variation in size and condition of juvenile pink salmon in Prince William Sound (PWS), Alaska (Boldt and Haldorson 2004). In addition, physical conditions, such as increased water temperatures, have been associated with faster growth rates and thus higher marine survival of juvenile salmon (Mortensen et al. 2000).

Most of the research investigating the ocean growth of salmon has focused on mean growth of all captured fish. Because of size-selective mortality, however, the growth rate of an average fish may not best represent the growth rates of the fish that are most likely to survive. Consequently, the growth rate of the larger fish may provide better insight into how growth rate influences ocean survival. In this study, we investigated the variation in early marine growth rates of different-sized juvenile pink salmon and how this variation related to marine survival.

The pink salmon is the most abundant Pacific salmon in Alaska, typically comprising over half of the commercial harvest (ADFG 2009a). Pink salmon have an invariant 2-year life cycle, of which about 16 months are spent in marine waters. All maturing fish that return to natal freshwater spawning areas are of the same year-class; the short life cycle and nonoverlapping year-classes make the pink salmon attractive for research examining the effects of early marine growth on ocean survival. In PWS, four hatcheries (Figure 1) annually release about 600 million juvenile pink salmon during May to coincide with the spring zooplankton bloom (Cooney et al. 1995). All pink salmon produced by PWS hatcheries have thermally marked otoliths that identify release date and hatchery of origin. The numbers of returning adult pink salmon are estimated based on contributions to commercial catches and hatchery returns, resulting in hatchery-specific survival estimates that facilitate studies of marine mortality.

In the first summer after release, pink salmon from PWS hatcheries move through and inhabit three primary marine localities: PWS, the inshore Gulf of Alaska (GOA), and the offshore GOA (Figure 1). Prince William Sound is a large estuary (9,000 km²) with a surface mixed layer consisting of relatively fresh water in summer owing to large amounts of freshwater input from rain and snowmelt (Vaughan et al. 2001). The inshore GOA is characterized by the Alaska Coastal Current (ACC), a fast-flowing westerly coastal current that carries much of the

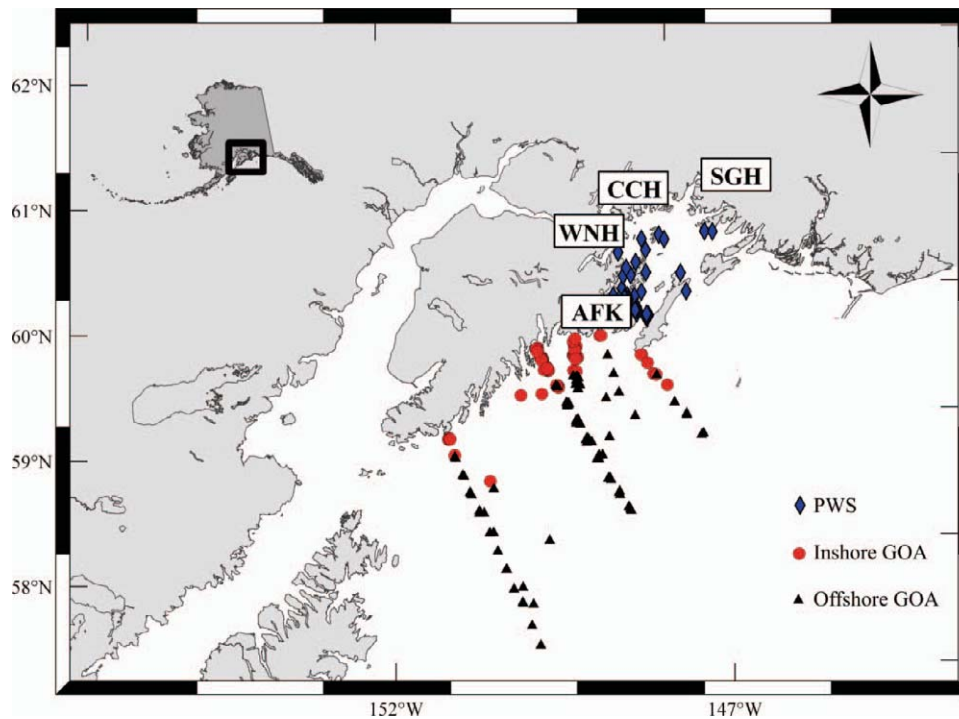


FIGURE 1. Sampling locations and the four hatcheries that release pink salmon into Prince William Sound (PWS), Alaska (GOA = Gulf of Alaska; AFK = Armin F. Koernig Hatchery; CCH = Cannery Creek Hatchery; SGH = Solomon Gulch Hatchery; WNH = Wally Noerenberg Hatchery). Inset shows the general location of the study area in Alaska.

TABLE 1. Dates of pink salmon sampling (across all sampling years) conducted by four projects (see Methods) at three locations (PWS = Prince William Sound, sampled in early summer or midsummer; GOA = Gulf of Alaska, sampled in midsummer only; ADFG = Alaska Department of Fish and Game; APEX = Alaska Predator Ecosystem Experiment; U.S. GLOBEC = U.S. Global Ocean Ecosystem Dynamics; NMFS = National Marine Fisheries Service).

Location	ADFG	APEX	U.S. GLOBEC	NMFS
Early summer PWS	17–27 Jun			
Midsummer PWS	1–23 Jul	15–18 Jul	11 Jul–4 Aug	
Inshore GOA			8 Jul–12 Aug	22 Jul–13 Aug
Offshore GOA			9 Jul–12 Aug	22 Jul–14 Aug

freshwater runoff entering the northeast Pacific Ocean from British Columbia, southeast Alaska, and the north coast of the GOA, including PWS (Weingartner et al. 2002). In the northern GOA, the ACC typically extends 30–40 km from shore. Seaward of the ACC front, offshore shelf water is marked by an increase in salinity in the surface mixed layer. In the offshore GOA, summer water column stratification is primarily due to heating, whereas in PWS and the inshore GOA salinity is more important for stratification (Stabeno et al. 2004).

Our principal objectives were to (1) investigate how marine growth rates vary among juvenile pink salmon captured in different sampling years and locations, (2) determine whether the growth rate patterns among sampling years and locations differ among pink salmon of different sizes and hatchery cohorts, and (3) determine whether the relationship between marine survival and growth rate varies among different-sized pink salmon captured at different locations.

METHODS

Field Sampling

Juvenile pink salmon were sampled during 31 cruises conducted in summer (June–August) 1997–2004 (Table 1) by four projects: (1) the National Marine Fisheries Service (NMFS) Auke Bay Laboratories, (2) the U.S. Global Ocean Ecosystem Dynamics (U.S. GLOBEC) program (University of Alaska Fairbanks), (3) the PWS monitoring program (Alaska Department of Fish and Game [ADFG]), and (4) the Alaska Predator Ecosystem Experiment (APEX; University of Alaska Fairbanks).

Samples were collected by purse seine (ADFG, APEX) and surface trawl (NMFS, U.S. GLOBEC) in all sampling years and by gill nets (U.S. GLOBEC) in 1998–2000. The purse seine for both the ADFG and APEX projects was 200 m long \times 20 m deep and was constructed of 22-mm stretch mesh. The NMFS study used a 198-m-long midwater rope trawl with a 1.2-cm-mesh liner in the cod end and a typical spread of 40 m horizontally and 15 m vertically. The NMFS trawl was towed at the surface and typically fished for 30 min at 6.5–9.3 km/h (3.5–5.0 knots). The U.S. GLOBEC project used a Nordic 264 surface rope trawl that was 198 m long, 25 m wide, and 35 m in vertical height and had a 1.2-cm-mesh liner in the cod end. The U.S. GLOBEC trawl fished a depth of approximately 11.4 m and a width of approximately 14.3 m for 30 min at 3.7–5.6 km/h (2–3 knots).

The U.S. GLOBEC gill nets were 200 m long and 3 m deep and were composed of four 50-m panels with 19-, 25-, 32-, and 38-mm stretch mesh. The gill nets were fished at the surface for approximately 2–4 h. Fish from all projects were frozen in seawater for further analysis.

All sampling stations were assigned to one of three areas (Table 2). Sampling stations within the geographic bounds of PWS were all designated as PWS (Figure 1). Outside PWS, salinity profiles were used to classify stations as inshore GOA or offshore GOA. Inshore stations were those with salinity less than 30 at 2-m depth; offshore stations were those with salinity greater than 31.5 at 2-m depth. Stations with near-surface salinities that were intermediate to the inshore and offshore categories occurred in the vicinity of the ACC front and were not included in these analyses. Prince William Sound sampling was further separated into early summer (June) or midsummer (July–August) periods, as there are seasonal differences in oceanographic conditions (Vaughan et al. 2001) and zooplankton assemblages (Cooney et al. 2001b; Coyle and Pinchuk 2003).

Laboratory Analysis

Juvenile pink salmon from all projects were thawed, weighed, and measured for fork length. All hatchery-released pink salmon in PWS are given a unique thermal otolith mark by one of the four PWS hatcheries: Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery, and

TABLE 2. Total number of pink salmon juveniles described by growth rate data across all sampling years and locations (PWS = Prince William Sound, sampled in early summer or midsummer; GOA = Gulf of Alaska, sampled in midsummer only).

Year	Early summer PWS	Midsummer PWS	Inshore GOA	Offshore GOA
1997	403	299	37	66
1998	201	53	38	6
1999	193	424		
2000	561	55	27	214
2001	534	422	196	191
2002	505	599	96	575
2003	583	85	215	189
2004	439	131	110	95

Wally Noerenberg Hatchery (WNH). Information on hatchery of origin, release date, and release weight was obtained by examining the otoliths of all captured juvenile pink salmon for thermal marks. Fish without a thermally marked otolith were presumed to be of wild origin and were removed from the analyses.

Data Analysis

Growth rate.—An instantaneous growth rate was estimated for each individual fish with a weight-based exponential growth model:

$$W_c = W_r e^{gt},$$

where W_c is weight at the time of capture, which is unique for each fish; W_r is weight at the time of release, which is an average for all fish released in a particular cohort; t is the number of days between release and capture; and g is the instantaneous growth rate expressed as percent body weight per day. The rate g has the implicit assumption that the fish's growth is exponential between ocean entry and capture. Therefore, it is important to note that we did not assign habitat- or time-specific growth rates to individual fish.

Marine survival.—Marine survival time series for each PWS hatchery were available for the release years 1997–2004 (S. Moffitt, ADFG, Cordova, personal communication). The marine survival rates were calculated for all hatcheries by dividing total returns by the total number of fry released. Total returns included commercial common-property harvests, hatchery cost-recovery harvests, broodstock escapement, and miscellaneous harvests that included donated or discarded fish (Joyce and Evans 2000).

Statistical Analysis

Size-group classifications.—Data were stratified by cruise, capture location, and hatchery; within each stratum, fish were assigned a weight-based quartile rank. Analyses were conducted on the entire data set (all fish) and on two subsets of the data: the largest fish (top 25%) and the smallest fish (bottom 25%). Two hatcheries (AFK and WNH) release several individually marked cohorts at different times in May. These releases were grouped into a single hatchery cohort for our statistical analyses; however, specific hatchery release data were used in calculating the growth rates of the individual fish (Cross et al. 2008).

Differences among years and capture locations.—Two-way fixed-effect analysis of variance (ANOVA) models were used to test for growth rate differences among years and locations in the midsummer period. Separate models were fitted for each hatchery and size-group; each model included year, location, and an interaction term. Prince William Sound was the only location sampled during the early summer period; therefore, one-way fixed-effect ANOVA models were used to test for interannual differences in growth rates of each hatchery cohort and size-group for fish captured in PWS during that period.

To investigate patterns of interannual growth rate among fish captured in different locations, we compared growth rate time series among locations by using Pearson's product-moment correlation coefficients. Owing to low sample sizes, all hatchery time series were combined when assessing the covariation among locations. Because the growth rate variable differed in scale among hatcheries, growth rates for each hatchery were standardized by subtracting the hatchery-specific mean and dividing by the hatchery-specific SD. The correlation analyses used standardized growth rate values averaged for each year, sampling location, and hatchery.

Marine survival analyses.—Linear regression models were used to investigate the relationships between growth rate and marine survival for each of the size-groups. Each linear regression model was fitted with standardized growth rate values averaged by year, location, and hatchery. Separate models were fitted for each size-group and location, and each model included all hatcheries.

RESULTS

Differences among Capture Locations

The variation in growth rates among sampling locations for the largest and smallest fish was similar to the variation observed when all fish were combined (Figure 2). For all hatchery groups and size-groups, growth rates were generally higher in fish captured offshore, although this was less pronounced for the largest fish and for fish released from AFK. The AFK fish had lower variation in growth rates among sampling locations than fish from the other hatcheries and did not display the same midsummer growth rate pattern observed in fish from the other hatcheries (i.e., PWS < inshore GOA < offshore GOA; Figure 2). The ANOVA models indicated that variation in growth rates among fish captured in different locations was significant ($P < 0.05$) for all hatcheries and for all fish (Table 3), the largest fish, and the smallest fish. Similarly, the year \times location interaction term in the ANOVA models was significant for all hatcheries and size-groups except the small fish from AFK ($F = 1.26$; $df = 9, 230$; $P = 0.26$).

Comparison of growth rate time series among the locations indicated that growth rates tended to be more similar among locations for the average-size and largest fish compared with the smallest fish. The strongest correlations occurred between the early summer and midsummer PWS time series and between the inshore GOA and offshore GOA (Table 4).

Differences among Years

In the midsummer period, there was a large amount of interannual variation in growth rates; however, the growth rate patterns were similar for all hatchery groups and size-groups. The magnitude of interannual variation was reflected in the significance of the year term in the ANOVA models for all hatchery cohorts (Table 3). Growth rates for all hatchery groups and size-groups tended to be high in 1997 and 2002 and low in 1998

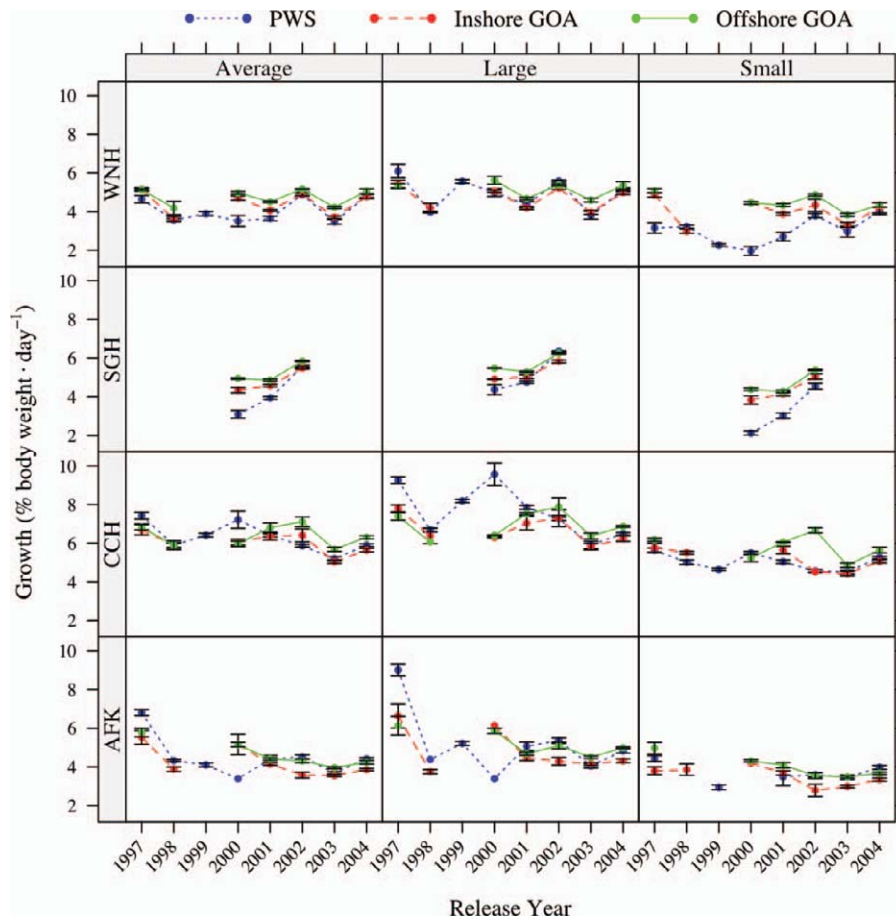


FIGURE 2. Mean (\pm SE) growth rates of average-sized juvenile pink salmon and the largest (top 25% based on weight) and smallest (bottom 25%) juveniles sampled during midsummer (abbreviations are defined in Figure 1).

and 2003 (Figure 2). From 2000 to 2004, only fish from WNH displayed a distinct even–odd year pattern (high growth rate in even years), although in general, 2002 and 2004 were years of relatively high growth rates. Fish from CCH tended to have the highest growth rates in all years and at all locations.

Within PWS during early summer, CCH fish again had the highest overall growth rates (Figure 3). The growth rate for AFK fish in 1997 was markedly higher than the growth rates of fish from the other hatcheries and most other years, while the growth rate of CCH fish in 2000 was the highest observed in the early summer period (Figure 3). The growth rate patterns among size-groups sampled in PWS were notably similar in the early summer period. There were significant interannual differences in early summer growth rate for fish from all hatcheries and size-groups.

Marine Survival

Marine survival varied greatly among fish from the four PWS hatcheries (Figure 4). Fish from WNH tended to have the highest marine survival rates, while those from CCH tended to have the lowest survival rates. Beginning in 2000, there was a pattern

of higher survival in even years of release; AFK fish were the exception to this pattern, as they exhibited a decline in survival from 2001 to 2002.

All relationships between survival and growth rate were positive except the relationship observed for small fish captured in PWS during the early summer period (Table 5). The estimated effect of growth rate on survival was weakest for fish captured in PWS during early summer and increased for all size-groups as the sampling moved offshore. Similarly, for the entire data set and for the two subsets (large fish and small fish), the best-fitting models were those based on fish captured in the offshore GOA: the model for average-sized fish explained 31% of the variation in marine survival of the entire pink salmon cohort, the model for large fish explained 27% of the variation, and the model for small fish explained 35% of the variation.

DISCUSSION

We investigated size-based patterns of marine growth rates among juvenile pink salmon across years and sampling locations and related these patterns to interannual variations in

TABLE 3. Summary of ANOVA models describing the growth rate (% body weight/d) of juvenile pink salmon from four Prince William Sound hatcheries (AFK = Armin F. Koernig Hatchery; CCH = Cannery Creek Hatchery; SGH = Solomon Gulch Hatchery; WNH = Wally Noerenberg Hatchery; SS = sum of squares).

Hatchery	Term	df	SS	F	P
AFK	Year	6	68.5	25.8	<0.001
	Habitat	2	23.9	27.0	<0.001
	Year × habitat	9	11.2	2.8	0.003
	Error	772	341.7		
CCH	Year	7	288.1	36.4	<0.001
	Habitat	2	17.6	7.8	<0.001
	Year × habitat	12	45.2	3.3	<0.001
	Error	1,097	1,239.2		
SGH	Year	2	391.3	583.2	<0.001
	Habitat	2	76.8	114.4	<0.001
	Year × habitat	4	46.1	34.3	<0.001
	Error	893	299.6		
WNH	Year	7	277.2	65.1	<0.001
	Habitat	2	50.5	41.5	<0.001
	Year × habitat	12	24.2	3.3	<0.001
	Error	1,065	647.9		

marine survival. We found that (1) growth rates of pink salmon varied greatly among sampling years and locations but that the patterns of variation were similar among hatchery cohorts and size-groups; (2) growth rates were generally higher for fish sampled in the offshore GOA than for fish sampled in PWS; and (3) variation in marine survival was best explained by the growth rates of fish captured in the offshore GOA, but the strength of these relationships did not differ greatly among different-sized fish.

Pink salmon that were sampled in the GOA tended to exhibit faster growth rates than those sampled in PWS. This probably reflects a tendency for larger, faster-growing juveniles to move

TABLE 4. Summary of pairwise correlations (Pearson's product-moment correlation coefficients) of growth rates between sampling locations for each size-group (large = top 25% based on weight; small = bottom 25%) of juvenile pink salmon (PWS = Prince William Sound, sampled in early summer or midsummer; GOA = Gulf of Alaska, sampled in midsummer only). Values in bold italics are significant at the 0.05 level.

Comparison	All fish	Large fish	Small fish
Early summer PWS vs. midsummer PWS	0.65	0.66	0.64
Early summer PWS vs. inshore GOA	0.41	0.43	0.19
Early summer PWS vs. offshore GOA	0.19	0.21	-0.02
Midsummer PWS vs. inshore GOA	0.64	0.81	0.08
Midsummer PWS vs. offshore GOA	0.48	0.56	0.15
Inshore GOA vs. offshore GOA	0.92	0.82	0.84

offshore earlier than smaller, slower-growing fish. This corresponds with previous research by Cross et al. (2008), who found that juvenile pink salmon tended to migrate out of PWS earlier in years of faster growth than in years of slower growth. The faster-growing pink salmon may move offshore earlier to take advantage of more energy-rich prey resources. It is also possible that growth rates are higher in the offshore GOA than at other sampling locations. The exponential growth model used to calculate growth rates averages fish growth from hatchery release to capture, inhibiting the quantification of differential growth among the sampling locations. However, Cross et al. (2009) found that growth rates of PWS pink salmon juveniles declined in early to mid-July during 2001–2004. Since the majority of our offshore GOA samples were collected during this period of slow growth, it is possible that the larger fish attained a majority of their size while they inhabited PWS.

The three sampling regions—PWS, inshore GOA, and offshore GOA—each have unique oceanographic characteristics (Weingartner et al. 2002). In this study, growth rates covaried positively and strongly between fish captured in PWS during the early summer and midsummer periods and between fish captured at the GOA locations. However, we found weaker relationships for growth rates in the comparisons between PWS and the GOA locations. This pattern is probably caused by differences in oceanographic and biological conditions between PWS and the GOA; for example, zooplankton abundances and distributions have been shown to differ significantly between these areas. During 1997–2001, large mesopelagic copepods, amphipods, and shrimp dominated PWS, while the GOA was dominated by a mixture of small and large copepods and contained high abundances of pteropods in the nearshore areas (Coyle and Pinchuk 2003, 2005). Similarly, previous work indicated that the quality of food ingested by juvenile pink salmon differed between fish captured in PWS and those captured in the GOA (Armstrong et al. 2005, 2008).

Interannual variation in growth rates tended to be similar among hatchery cohorts, suggesting that fish from all hatcheries experience some degree of concordance in the marine environment. Some of the interannual patterns were stronger for particular hatcheries, as evident in the strong even–odd growth rate pattern observed for fish released from WNH. Based on measurements of fish scales, Cross et al. (2008) also observed an even–odd growth rate pattern during 2001–2004 for pink salmon originating from PWS. However, the even–odd growth pattern was not observed from 1997 to 2000, indicating that the pattern was not a consequence of the obligate 2-year life cycle of pink salmon.

Higher average growth rates were observed in 1997, 2002, and 2004 for all areas and in 2000 for the GOA. Mean monthly sea surface temperature (SST) data (International Comprehensive Ocean-Atmosphere Data Set) indicate that 1997 and 2004 were warm years, 2002 was a relatively cool year, and 2000 had average SST values. Similarly, the diets of juvenile pink salmon in the northern GOA during August differed between

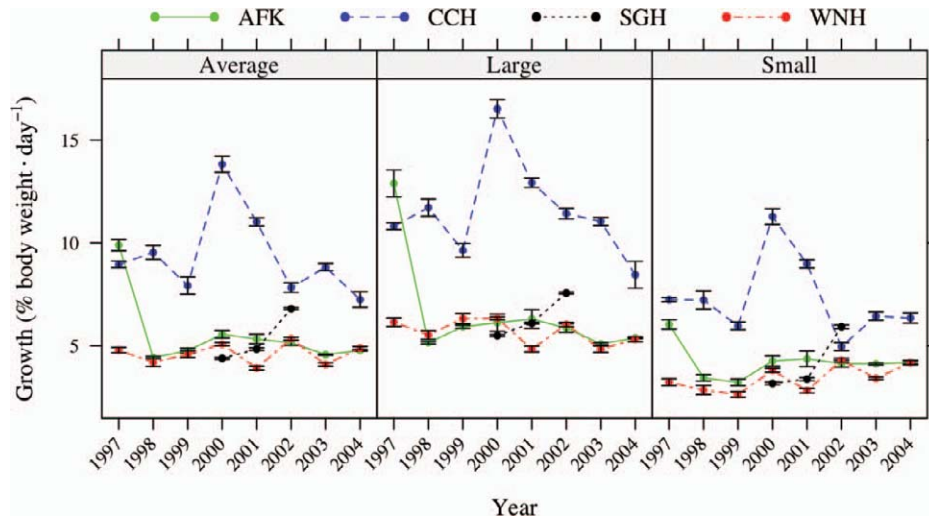


FIGURE 3. Mean (\pm SE) growth rates of average-sized juvenile pink salmon and the largest (top 25% based on weight) and smallest (bottom 25%) juveniles sampled in Prince William Sound during the early summer period (abbreviations are defined in Figure 1).

2002 and 2004; diets in 2002 were dominated by pteropods, while diets in 2004 were dominated by large copepods and larvaceans (Armstrong et al. 2008). Such differences suggest that different mechanisms are responsible for the faster growth rates of juvenile pink salmon in the northern GOA during those years. In contrast, growth rates were lower on average in 1998, 2001, and 2003. The SST data indicate that 1998 and 2001 were cool years, whereas 2003 was a moderately warm year. This supports previous research indicating that temperature is a factor

with only marginal control of salmonid early marine growth rates in the northern GOA (Beauchamp et al. 2007).

The growth rate differences between 1997 and 1998 may be explained by a major shift in oceanographic conditions. Fish that were released in 1997 experienced El Niño conditions for their first year in the ocean, whereas fish that were released in 1998 experienced rapidly changing conditions that led to La Niña conditions in 1999 (Wolter and Timlin 1998). The El Niño and La Niña events can influence nitrate and silicate levels in the GOA, which may have a strong effect on the food supply for juvenile salmon (Whitney and Welch 2002). Although these events do not appear to have influenced zooplankton community composition in the northern GOA (Coyle and Pinchuk 2003), the timing and strength of the phytoplankton (Henson 2007) and zooplankton (Mackas et al. 1998) blooms may have been strongly affected by differences in nutrient supply (Whitney and Welch 2002) and water column stability (Childers et al. 2005). The timing and duration of the spring zooplankton bloom have been linked to various factors influencing mortality of juvenile pink salmon in PWS (Willette et al. 1999; Cooney et al. 2001a), and other research has highlighted the importance of the link between early marine growth of salmon and the timing of the spring phytoplankton bloom (Mathews and Ishida 1989; Aydin et al. 2005).

Fish from AFK tended to deviate from the general patterns shown by the other hatchery cohorts. The AFK fish had less variation in growth rates among sampling locations, growth rates were not markedly faster for fish captured offshore, and the growth rate differences between the largest and smallest fish did not significantly differ across sampling locations. The differing patterns for AFK fish relative to fish from other hatcheries may be related to the geographic location of AFK within PWS. Out-migrating salmon in PWS are thought to move in a southerly

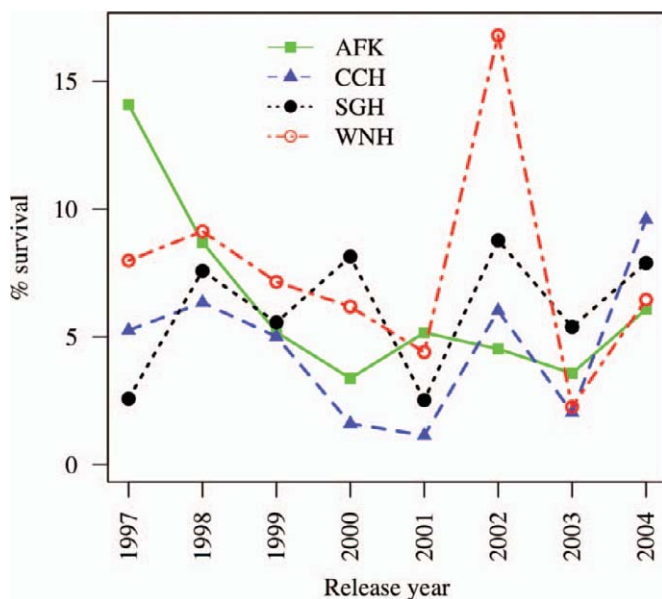


FIGURE 4. Marine survival time series for the four hatchery stocks of pink salmon released into Prince William Sound (abbreviations are defined in Figure 1).

TABLE 5. Summary of results for regression models of marine survival versus growth rate of juvenile pink salmon (large fish = top 25% based on weight; small fish = bottom 25%; PWS = Prince William Sound, sampled in early summer or midsummer; GOA = Gulf of Alaska, sampled in midsummer only).

Data set	Location	Intercept	Slope	R ²	P
All fish	Early summer PWS	6.18	0.06	0.00	0.937
	Midsummer PWS	7.18	2.34	0.13	0.060
	Inshore GOA	7.50	3.88	0.18	0.038
	Offshore GOA	6.60	5.74	0.31	0.006
Large fish	Early summer PWS	6.06	0.25	0.00	0.744
	Midsummer PWS	6.89	1.70	0.12	0.076
	Inshore GOA	8.32	3.35	0.16	0.049
	Offshore GOA	7.86	5.26	0.27	0.013
Small fish	Early summer PWS	6.29	-0.28	0.01	0.662
	Midsummer PWS	7.05	1.67	0.07	0.189
	Inshore GOA	6.62	1.77	0.08	0.194
	Offshore GOA	4.61	4.24	0.35	0.005

and southwesterly direction (Willette 1996). Once they have left PWS and entered the coastal GOA waters, juvenile pink salmon are believed to migrate westward and disperse offshore during their first ocean summer (Farley and Munk 1997; Armstrong et al. 2005). The water circulation patterns in PWS are characterized by the influx of ACC water through Hinchinbrook Entrance that transits PWS from east to west before exiting via Montague Strait (Niebauer et al. 1994). The AFK is located on Evans Island in Montague Strait at the southwest corner of PWS. Since AFK is much closer to an exit point of PWS than the other hatcheries, the AFK fish may exit PWS earlier than fish from other hatcheries, as these other groups must travel a longer distance to reach the coastal GOA. Therefore, AFK fish may reach the inshore GOA much earlier in the summer than the other hatchery fish, resulting in the divergence in growth rate between AFK fish and fish from the other hatcheries.

Fish from CCH tended to have the fastest growth rates across most sampling years and locations. The CCH fry are released at a smaller size and later in the year than fish from the other three hatcheries (ADFG 2009b); because the releases are later, CCH fish are typically released into warmer marine waters than the other hatchery groups. Data from a National Oceanic and Atmospheric Administration buoy in the center of PWS indicated that during 1997–2004, average SST was 8.1°C for May and 11.8°C for June. These temperature differences may result in significantly higher growth rates for the CCH fish (Mortensen and Savikko 1993). Mortensen et al. (2000) showed that differences between early and late-spring growth rates of juvenile pink salmon in southeast Alaska were significantly influenced by water temperature.

Marine mortality of juvenile pink salmon during the first month of ocean residency is important in setting marine survival rates (Parker 1968; Bax 1983; Wertheimer and Thrower 2007). Recent evidence also suggests that significant size-selective mortality of juvenile pink salmon occurs after the first growing season (Moss et al. 2005; Cross et al. 2009). In the present

study, marine survival was consistently and positively related to the growth rates of juvenile pink salmon. In addition, the estimated effect of growth rate on marine survival was much stronger for juvenile pink salmon sampled in the offshore GOA than for fish sampled in PWS, which indicates that juveniles migrating out of PWS earlier are more likely to survive than fish that remain within PWS. Similar results based on scale analysis have also indicated a positive relationship between early marine growth rates and marine survival (Moss et al. 2005; Cross et al. 2008). In contrast, Cross et al. (2009) found inconsistent relationships between juvenile pink salmon size and marine survival rates, which they attributed to size-selective mortality occurring after the first growing season. Although we cannot clearly identify the habitats or processes that were critical to enhancing growth, the postrelease growth of juvenile pink salmon is certainly affected by conditions experienced after the initial month at sea. Clearly, the conditions for fish growth vary among years and habitats, and marine survival is closely linked to this temporal and spatial variability.

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REFERENCES

- ADFG (Alaska Department of Fish and Game). 2009a. ADFG bluesheet. Available: www.cf.adfg.state.ak.us/geninfo/finfish/salmon/catchval/blusheet/05sexvesl.php. (July 2009).
- ADFG (Alaska Department of Fish and Game). 2009b. ADFG coded wire tag laboratory. Available: tagotoweb.adfg.state.ak.us/CWT/reports/. (July 2009).

- Armstrong, J. L., J. L. Boldt, A. D. Cross, J. H. Moss, N. D. Davis, K. W. Myers, R. V. Walker, D. A. Beauchamp, and L. J. Haldorson. 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. Deep-Sea Research II Topical Studies in Oceanography 52:247–265.
- Armstrong, J. L., K. W. Myers, D. A. Beauchamp, N. D. Davis, R. V. Walker, J. L. Boldt, J. J. Piccolo, L. J. Haldorson, and J. H. Moss. 2008. Interannual and spatial feeding patterns of hatchery and wild juvenile pink salmon in the Gulf of Alaska in years of low and high survival. Transactions of the American Fisheries Society 137:1299–1316.
- Aydin, K. Y., G. A. McFarlane, J. R. King, B. A. Megrey, and K. W. Myers. 2005. Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. Deep-Sea Research II Topical Studies in Oceanography 52:757–780.
- Bax, N. J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Canadian Journal of Fisheries and Aquatic Sciences 40:426–435.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.
- Beauchamp, D. A., A. D. Cross, J. L. Armstrong, K. W. Myers, J. H. Moss, J. L. Boldt, and L. Haldorson. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. North Pacific Anadromous Fish Commission Bulletin 4:257–269.
- Boldt, J. L., and L. J. Haldorson. 2004. Size and condition of wild and hatchery pink salmon juveniles in Prince William Sound, Alaska. Transactions of the American Fisheries Society 133:173–184.
- Childers, A. R., T. E. Whitley, and D. A. Stockwell. 2005. Seasonal and interannual variability in the distribution of nutrients and chlorophyll a across the Gulf of Alaska shelf: 1998–2000. Deep-Sea Research II Topical Studies in Oceanography 52:193–216.
- Cooney, R. T., J. R. Allen, M. A. Bishop, D. L. Eslinger, T. Kline, B. L. Norcross, C. P. McRoy, J. Milton, J. Olsen, and V. Patrick. 2001a. Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasii*) populations in Prince William Sound, Alaska. Fisheries Oceanography 10(Supplement 1):1–13.
- Cooney, R. T., K. O. Coyle, E. Stockmar, and C. Stark. 2001b. Seasonality in surface-layer net zooplankton communities in Prince William Sound, AK. Fisheries Oceanography 10(Supplement 1):97–109.
- Cooney, R. T., T. M. Willette, S. Sharr, D. Sharp, and J. Olsen. 1995. The effect of climate on North Pacific pink salmon (*Oncorhynchus gorbuscha*) production: examining some details of a natural experiment. Canadian Special Publications in Fisheries and Aquatic Sciences 121:475–482.
- Coyle, K. O., and A. I. Pinchuk. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fisheries Oceanography 12:327–338.
- Coyle, K. O., and A. I. Pinchuk. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep Sea Research Part II Topical Studies in Oceanography 52:217–245.
- Cross, A. D., D. A. Beauchamp, J. H. Moss, and K. W. Myers. 2009. Interannual variability in early marine growth, size selective mortality, and marine survival for Prince William Sound pink salmon. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 1:57–70.
- Cross, A. D., D. A. Beauchamp, K. W. Myers, and J. H. Moss. 2008. Early marine growth of pink salmon in Prince William Sound and the coastal Gulf of Alaska during years of low and high survival. Transactions of the American Fisheries Society 137:927–939.
- Farley, E. V. J., and K. Munk. 1997. Incidence of thermally marked pink and chum salmon in the coastal waters of the Gulf of Alaska. Alaska Fishery Research Bulletin 4:181–187.
- Henson, S. 2007. Water column stability and spring bloom dynamics in the Gulf of Alaska. Journal of Marine Research 65:715–736.
- Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181–2194.
- Joyce, T., and D. Evans. 2000. Otolith marking of pink salmon in Prince William Sound salmon hatcheries. Alaska Department of Fish and Game, Restoration Project Report 99188, Anchorage.
- Koenings, J., H. J. Geiger, and J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50:600–611.
- Mackas, D. L., R. Goldblatt, and A. Lewis. 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. Canadian Journal of Fisheries and Aquatic Sciences 55:1878–1893.
- Mathews, S. B., and Y. Ishida. 1989. Survival, ocean growth, and ocean distribution of differentially timed releases of hatchery coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1216–1226.
- McGurk, M. D. 1996. Allometry of marine mortality of Pacific salmon. U.S. National Marine Fisheries Service Fishery Bulletin 94:77–88.
- Mortensen, D., A. Wertheimer, S. Taylor, and J. Landingham. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. U.S. National Marine Fisheries Service Fishery Bulletin 98:319–335.
- Mortensen, D., and H. Savikko. 1993. Effects of water temperature of juvenile pink salmon (*Oncorhynchus gorbuscha*). NOAA Technical Memorandum NMFS-AFSC-28.
- Moss, J. H., D. A. Beauchamp, A. D. Cross, K. W. Myers, E. V. Farley, J. M. Murphy, and J. H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Transactions of the American Fisheries Society 134:1313–1322.
- Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99:14113–14126.
- Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. Journal of the Fisheries Research Board of Canada 25:757–794.
- Perry, R. I., N. B. Hargreaves, B. J. Waddell, and D. L. Mackas. 1996. Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. Fisheries Oceanography 5:73–88.
- Ruggerone, G. T., and F. Goetz. 2004. Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). Canadian Journal of Fisheries and Aquatic Sciences 61:1756–1770.
- Stabeno, P. J., N. A. Bond, A. J. Hermann, N. B. Kachel, C. W. Mordy, and J. E. Overland. 2004. Meteorology and oceanography of the northern Gulf of Alaska. Continental Shelf Research 24:859–897.
- Vaughan, S., C. Mooers, and S. M. Gay. 2001. Physical variability in Prince William Sound during the SEA study (1994–98). Fisheries Oceanography 10(Supplement 1):58–80.
- Weingartner, T., K. Coyle, B. Finney, R. Hopcroft, T. Whitley, R. Brodeur, M. Dagg, E. Farley, D. Haidvogel, L. Haldorson, A. Hermann, S. Hinckley, J. Napp, P. Stabeno, T. Kline, C. Lee, E. Lessard, T. Royer, and S. Strom. 2002. The northeast Pacific GLOBEC program: coastal Gulf of Alaska. Oceanography 2:48–63.
- Wertheimer, A. C., and F. P. Thrower. 2007. Mortality rates of chum salmon during their early marine residency. Pages 233–247 in C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. Mckinnell, editors. Ecology of juvenile

- salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.
- Whitney, F., and D. Welch. 2002. Impact of the 1997–1998 El Niño and 1999 La Niña on nutrient supply in the Gulf of Alaska. *Progress in Oceanography* 54:405–421.
- Willette, T. M. 1996. Impacts of the *Exxon Valdez* oil spill on the migration, growth and survival of juvenile pink salmon in Prince William Sound. Pages 533–550 in S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright, editors. Proceedings of the *Exxon Valdez* Oil Spill Symposium. American Fisheries Society, Symposium 18, Bethesda, Maryland.
- Willette, T. M., R. T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences* 56:364–376.
- Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO events: how does 1997/98 rank? *Weather* 53:315–324.