The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood

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Abstract.–Juvenile pink salmon, *Oncorhynchus gorbuscha*, from four consecutive brood years were tagged as they emigrated to the estuarine waters of Auke Bay, and information was obtained on the relationships between early marine growth, environmental conditions, and survival to adulthood. Juveniles that emigrated from Auke Creek later in the spring spent significantly less time in the estuary. Individual growth rates of tagged fish recovered in Auke Bay ranged from 3.1% to 7.1% per day. In all study years, juvenile pink salmon grew more slowly in early April than in late April and early May. Water temperature and growth were significantly correlated in all years, but growth did not consistently correlate with the biomass of epibenthic prey or zooplankton available to the fish. Comparisons of expected and observed growth rates suggested that low prey availability, as well as low temperatures, may have limited growth for early spring emigrants. Although early emigrants encountered poorer growth conditions, survivors were larger at a given date than later emigrants, their larger size possibly protecting them from size-selective predation. Early marine growth was significantly related to intra-annual cohort survival to adults (r^2=0.65, P<0.05). Larger fish consistently survived better than their smaller cohorts for all years. Although early marine growth was an important determinate of survival within a cohort of pink salmon, other factors, such as predator abundance, contributed to the large interannual variability observed.

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Pink salmon, *Oncorhynchus gorbuscha*, are the most abundant Pacific salmon species native to the west coast of the United States and Canada (Morrow, 1980). In southeastern Alaska pink salmon typically mature after 15 to18 months at sea and return to their native streams to spawn in late summer and early fall. Pink salmon usually spawn in the lower portions of streams just above the intertidal zone and in intertidal areas at stream mouths (Bailey, 1969). Eggs hatch in January or February and the embryos (alevins) continue to develop within the gravel of the stream bed. In late March or early April juvenile pink salmon (fry) emerge from the gravel and emigrate downstream to salt water and begin feeding on epibenthic organisms and small zooplankton. They form schools and reside in the nearshore marine habitat for several weeks (Heard, 1991). This early marine residency is evidently a critical stage in the early life history of salmon and can significantly affect year-class strength (Parker, 1968; Walters et al., 1978; Bax, 1983; Nichelson, 1986). Rapid growth during this early marine period may be a mechanism by which size-selective mortality is reduced (Parker, 1971; Hargreaves and LeBrasseur, 1985).

Growth and mortality of juvenile fish is thought to be coupled with the magnitude and timing of primary and secondary production (Cushing, 1976; Pitcher and Hart, 1982; D’Amours, 1987). Slight variations in migration timing and the developmental rate of juvenile fish in relation to secondary production influence feeding success and may in turn affect growth and survival. Subarctic estuarine ecosystems are characterized by high levels of primary and secondary production in spring (Russell-Hunter, 1970; Larrance, 1971; Goering et al., 1973). Consequently, the timing of emigration of species such as juvenile pink and chum, *O. keta*, salmon may have evolved so that this highly productive period maximizes growth and survival (Murphy et al., 1988; Holtby et al., 1989). This concept is somewhat intuitive and there is little direct supportive evidence. To test this idea, we designed our study with the following objectives: 1) to examine emigration timing and growth of tagged individual juvenile pink salmon in relation to secondary production and water temperature and 2) to investigate the relation between timing of emigration, early marine growth, and intra- and interannual variability in marine survival.

Methods

This research focused on the Auke Creek pink salmon population. Auke Creek is a small, lake-fed stream that empties into Auke Bay in southeast Alaska (Fig. 1). The National Marine Fisheries Service maintains a permanent two-way counting weir (where both seaward-migrating and returning salmon are counted) at the confluence of Auke Creek with Auke Bay. The pink salmon run at Auke Creek is bimodal, that is it has a distinct early and late spawning component. Salmon in the early run begin spawning in late July through August and salmon in late run spawn from September through mid-October. The emigration of fry in the spring lasts from late March to mid-May and is relatively unimodal. The peak emigration usually occurs in late April (Taylor, 1980)

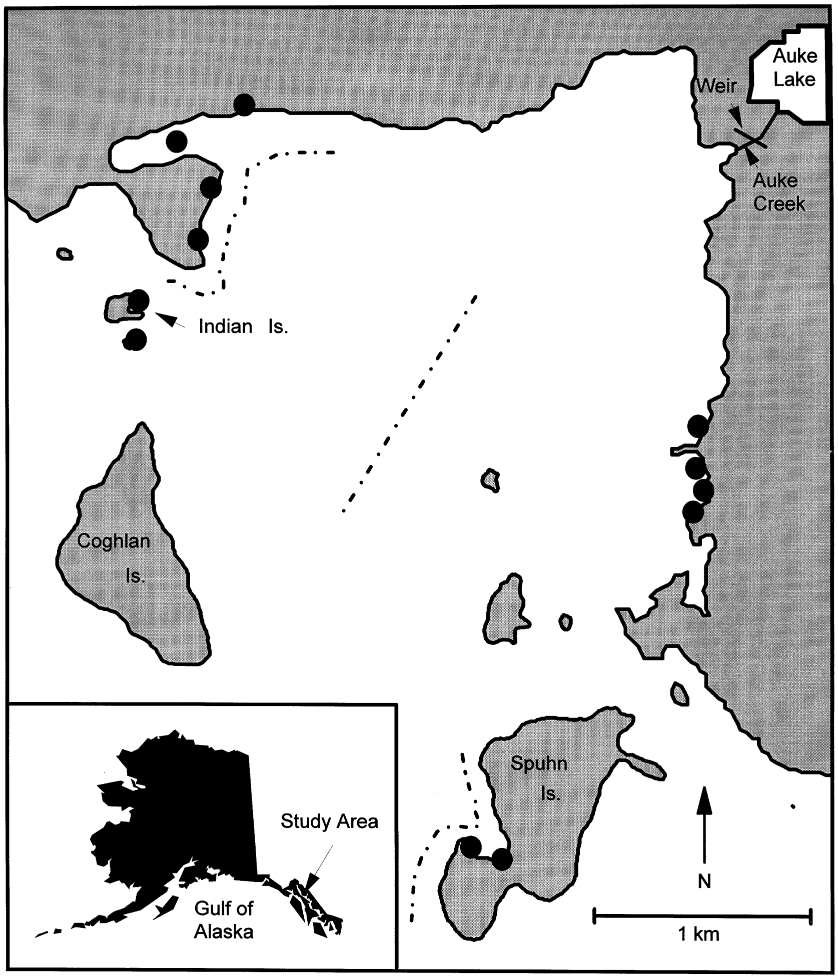

Figure 1

Map of Auke Bay, Alaska, showing beach seine sites (circles) and surface trawl transects (dashed lines).

The downstream emigration of wild pink salmon juveniles from Auke Creek into Auke Bay generally begins in early March, peaks between mid-April and early May, and ends by mid-May. From 1986 to 1989, 53,526, 17,249, 38,149, and 42,599 juvenile pink salmon emigrated from Auke Creek respectively. Each day all captured emigrants were counted and samples were measured to the nearest millimeter fork length.

Each year a portion of the emigrants was marked. Marking involved the excision of the entire adipose fin after a 0.5-mm binary coded wire was injected into the snout. Tag codes were assigned in lots of 10,000; therefore to use all the tags in a particular code-lot, tagging was conducted over several days each week. The 1985 brood was tagged in five-day emigration periods when sufficient numbers of fish were captured. The 1986 through 1988 broods were tagged in two to three-day emigration periods. After having been tagged, the fish were held for one day (1985 and 1986 broods) or three days (1987 and 1988 broods) to assess mortality and tag loss. Dead fish and those missing tags were deducted from the total tagged in each group. Release dates were similar each year.

Nearshore areas of Auke Bay were sampled for juvenile pink salmon from late March to early July with a 37-m long × 3-m deep beach seine. All captured juvenile salmon were identified to species, counted, and checked for evidence of tagging at the capture site; recaptured tagged fish were retained for tag recovery and size measurements. Random samples of up to 100 unmarked fish from each beach seine from sites on Spuhn and Indian Islands in Auke Bay were retained for length and weight measurements and stomach analysis. Other species (nonsalmonid) that were captured in the beach seines were enumerated and measured to the nearest millimeter (fork length

[FL] or total length [TL] depending upon the species). These fish have the potential to be either predators on or competitors with pink salmon juveniles.

Beginning in 1987, offshore areas of Auke Bay (>100 m from shore) were sampled weekly, at night, with a 6.1-m wide × 3.0-m deep surface trawl (Bax et al.[1]). All tagged salmon and a sample of up to 100 untagged juvenile pink salmon from each tow were retained for length and weight measurements and stomach analysis. All other fish captured in each tow were identified, enumerated, and measured.

Water temperature at 1-m depth was recorded daily in Auke Bay. Spuhn Island was sampled weekly for littoral epibenthic crustaceans in 1987–1989, with an epibenthic pump (1987) (Simenstad et al.[2]) or an epibenthic sled (1988 and 1989) (Celewycz and Wertheimer, 1996b). Zooplankton data for the upper 5-m and upper 40-m water column in Auke Bay were collected concurrently with our study by University of Alaska researchers (Coyle and Paul, 1990).

Stomachs of a subsample of untagged juvenile pink salmon retained from beach seine and trawl catches were examined to determine feeding habits. Stomach contents were weighed, and prey items were identified, measured, and counted. A mean volume and dry weight were calculated for each prey category, and the index of relative importance (IRI; Pinkas et al., 1971) was then computed by using the formula

$$IRI = (N + V)\,F,$$

where N = the numerical percentage;
V = the volumetric percentage of each prey item in the diet; and
F = the percent frequency of occurrence of the prey item.

The importance of individual prey groups were compared as a percentage of the total *IRI* for all prey.

The maximum residence of tagged fish from each weekly release group in Auke Bay was calculated by subtracting the actual release date for a particular lot of tagged fish from the last recovery date of a tagged juvenile from the same lot of tagged fish, yielding the number of days from release to recapture. The weighted mean residence time for each tag release group ($\overline{D}_{res_i}$) was calculated by subtracting the weighted mean release date for each weekly release group from the weighted mean recovery date for each release group. The weighted mean release date ($\overline{D}_{rel_i}$) for weekly release group i was calculated from the formula

$$\overline{D}_{rel_i} = \frac{\sum_{d=1}^{d=n} d_{rel} N_{d_{rel}}}{\sum_{d=1}^{d=n} N_{d_{rel}}},$$

where n = the number of release days per week;
d_{rel} = the actual release day (Julian date); and
$N_{d_{rel_i}}$ = the number of tagged fish from that day that were released. The weighted mean residence for each weekly group was then calculated by subtracting the weighted mean release date of a juvenile for a given week from the weighted mean recovery date. The weighted mean recovery date ($\overline{D}_{rec_i}$), for a particular release group was calculated as

$$\overline{D}_{rec_i} = \frac{\sum_{d=1}^{d=n} d_{rec} N_{d_{rec}}}{\sum_{d=1}^{d=n} N_{d_{rec}}},$$

where n = the number of recovery days per week;
d_{rec} = the actual recovery day (Julian date) of a tagged juvenile; and
$N_{d_{rec_i}}$ = the number of tagged fish recovered on day d.

The weighted mean residence time ($\overline{D}_{res_i}$) was regressed against release date for each year. Analysis of covariance (ANCOVA) was used to determine whether significant differences existed among years, followed by the Newman-Keuls multiple comparison test to determine if significant differences (α=0.05) existed within years.

The instantaneous growth rate, g, for individual tagged pink salmon juvenile was calculated as

$$W_2 = W_1 \exp^{gt},$$

where t = the period in days from the mean release date, over which the growth rate was calculated; and
W_1 and W_2 = the fish weight at the beginning and end of the period, respectively.

In addition the natural log of the weight of tagged fish at capture was regressed against days from

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[1] Bax, N. J., E. O. Salo, B. P. Snyder, C. A. Simenstad, and W. J. Kinney. 1978. Salmonid outmigration studies in Hood Canal. Final Report FRI-UW-7819, Phase III, January to July 1977, University of Washington, College of Fisheries, Fisheries Research Institute, Seattl, WA.

[2] Simenstad, C. A., C. D. Tanner, and R. M. Thom. 1989. Estuarine wetland restoration and monitoring protocol. Report FRI-UW-8918, University of Washington, College of Fisheries, Fisheries Research Institute, Seattle, WA.

release to recovery to provide the growth rate (the slope of the regression line) for each release group. Using g we then calculated the relative growth, h, as the percentage of body weight per day (%bwd) for each fish and for each group was calculated from the formula

$$h = (\exp^{g} - 1)\ 100.$$

Tagged juveniles that were recaptured within a week of the mean release date from the Auke Creek weir were not used in growth rate calculations. It was assumed that after a week the fish had acclimated to the marine environment and were recovered from prerelease tagging stress. In addition to the above calculations, the weights of tagged and untagged juveniles at successive capture dates were logarithmically transformed and regressed against days from the mean release day to the day of capture.

To determine how water temperature and food abundance relate to growth in the estuary, individual growth rates of tagged fish were correlated with average surface water temperature and prey biomass over the period between release and recapture. The average daily biomass of prey organisms was calculated for three habitats: the upper 5-m of the water column, the upper 40-m of the water column, and the littoral zone (harpacticoid copepods only). Correlation analysis and stepwise regression (Zar, 1974) were employed to determine significant correlations and provide partial correlation coefficients for each of the above parameters.

To test the possibility that estuarine growth of juvenile pink salmon could be limited by prey availability, the residual (difference) between expected and actual growth of individual juvenile pink salmon at given water temperatures was calculated and plotted against average water temperature. Expected maximum growth rates for given temperatures were obtained from (Mortensen and Savikko, 1993).

Growth of the tagged juvenile pink salmon was also computed for two periods or stanzas. Each year, the early period was that before and including 5 May, and the late period was that after 5 May. These dates were chosen because of the distinct change in size of juveniles between the two periods and the distribution of tag recoveries. Each year a dramatic increase in length was noted in the tagged fish at the beginning of May. Growth for each tagged group within a year was calculated for the early period; this rate was then used to estimate the initial weight for each tag group for computation of growth in the late period. Differences in growth between periods and years were tested by using analysis of covariance (ANCOVA) and the Newman-Keuls multiple comparison or Dunnet's tests (Zar, 1974). Significance levels were set at $\alpha = 0.05$.

Survival of fish from each release group for each emigrant year, 1986–1989 (brood years 1985–1988) was determined from the number of adult salmon returning to the Auke Creek weir. Each pink salmon adult passing through the weir was examined for a coded wire tag (cwt) on the adipose fin. Clipped fish were killed and their heads removed. Fish with adipose fins were returned to the creek to spawn. Coded-wire tags were removed from heads of the clipped fish later at the laboratory. Fish that showed a clip mark but were missing cwts were assigned to an emigration group that was based upon the proportion of all tag codes recovered each return week. Therefore, the return of each emigration group was the number of known tagged fish plus an expansion for clipped fish that had lost their tags. The total return of pink salmon adults to Auke Creek was the product of weir recoveries and a fishery correction factor. The fishery correction factor for each brood year was determined as

$$1/(1 - h),$$

where h = harvest rate determined as the proportion of the total return that is caught in the commercial fishery according to estimates by Alaska Department of Fish and Game (ADF&G) commercial fisheries management personnel.

Fishery correction factors obtained from the commercial fisheries branch of ADF&G for the 1985–1988 broods at Auke Creek were 1.45, 1.03, 1.53, and 1.43, respectively.[3] Growth and survival of the individual release groups within each year were standardized as a proportion of the highest rates observed. The proportional growth rate for each release group was regressed against proportional survival to determine the degree to which growth rate was a predictor of intra-annual survival. Survival rates were regressed against growth rates to determine the relation between growth and interannual survival.

Results

Catch and residency times

Juvenile pink salmon use Auke Bay as a nursery area throughout the spring and early summer and reside nearshore from late March until mid-June. Pink salmon

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[3] Ingledue, D. 1987–90. Alaska Department of Fish and Game, Division of Commercial Fisheries, Southeast Regional Office, 802 Third Street, Douglas, Alaska 99609. Personal commun.

were most abundant in late April and early May; 70–80% of the catch occurred between 5 May and 1 June. Most pink salmon left the nearshore area by late May. Salmon catch offshore tended to increase coincidentally with the decline in catch near shore; offshore catches peaked between May and mid-June, depending on the year (Fig. 2). Most tagged juveniles were recaptured near shore; only 11 and 2 fish were recaptured offshore in 1987 and 1988, respectively (no fish were recaptured in 1989, and no offshore sampling occurred in 1986). By mid-July of each year, juveniles were not present in nearshore or offshore catches.

Estuarine residence time (based on recaptures of tagged fish) generally decreased with progressive release dates. The exception was 1988, when residence time was similar between all release groups. Mean residence time ranged from a high of 30 d for the early release in 1986 and 1987 to about 7 d for the late release in 1989. The mean residence was also significantly longer in the first two weeks of 1986 and 1987 than in 1988 and 1989 (Table 1). Mean residence times did not differ significantly by release week between 1986 and 1987 or between 1988 and 1989, but were significantly different between 1987 and 1988. Based on recaptured tagged fish, maximum residence times in Auke Bay ranged from 19 d for juveniles from the 3 May release in 1988 to 72 d for the juveniles from the 13 April release in 1987 (Table 1).

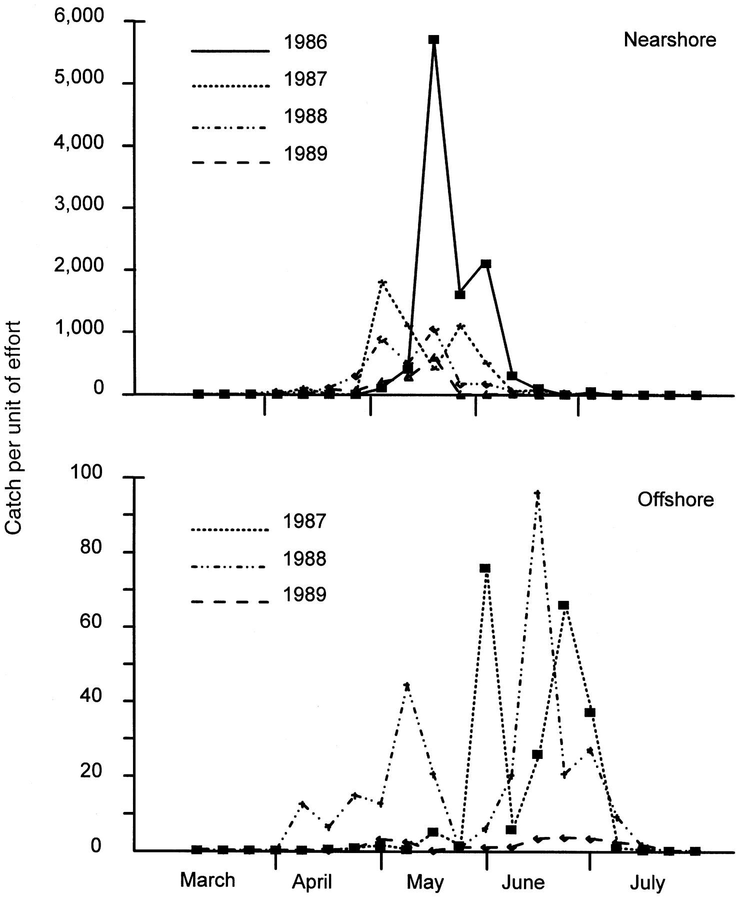

Figure 2

Catch per unit of effort (CPUE) of juvenile pink salmon at nearshore and offshore transects in Auke Bay, Alaska.

Nearshore catches consisted primarily of juvenile pink and chum salmon (Fig. 3). In even years, pink salmon juveniles were more abundant than chum salmon juveniles; pink salmon juveniles made up 83% and 65% of the catch in 1986 and 1988, versus 16% and 17% for chum salmon juveniles. In contrast, the ratios of pink and chum salmon in odd years were nearly equal (52–43%, 1987, and 52–44%, 1989). Coho (*O. kisutch*) and sockeye (*O. nerka*) salmon smolts and juvenile and adult Dolly Varden (*Salvelinus malma*) were also captured each year. Other nonsalmonid fishes captured included juvenile Pacific herring (*Clupea pallasi*) sculpins (Cottidae,) juvenile flatfish (Pleuronectidae), and juvenile walleye pollock (*Theragra chalcogramma*). Juvenile Pacific herring made up a significant proportion of the nearshore catch (14%) only in 1988.

Offshore catch composition for 1987 through 1989 consisted primarily of Pacific herring and capelin (*Mallotus villosus*). Pink salmon were the most abundant salmonid captured in offshore sampling. In 1987 and 1988, pink salmon made up 10% and 13% of the offshore catch respectively. Juvenile herring and capelin accounted for 76% and 74% of the offshore catch in 1987 and 1988, respectively. In 1989, pink salmon accounted for only 0.1% of the offshore catches, whereas juvenile Pacific herring were abundant and accounted for 97% of the total fish numbers. Fewer chum salmon juveniles and sockeye, coho, and chinook (*O. tshawytscha*) smolts were caught offshore than inshore. Other fish caught included juvenile and adult walleye pollock, sculpins, Pacific sandfish (*Trichodon trichodon*) and starry flounder (*Platichthys stellatus*).

Predators

Coho salmon smolts, medium (fork length $15 \geq x \geq 30$ mm) and large (fork length >30 cm) Dolly Varden, and three sculpin species (great sculpin, *Myoxoceph-*

Table 1

Release dates, number released, maximum and weighted mean residence (days), growth rate (percent body weight per day), and adult survival of coded-wire-tagged Auke Creek pink salmon for each release year followed by brood year in parentheses. Standard deviations for mean residence and growth are given in parentheses.

	Release week						
	1 April	7 April	15 April	22 April	29 April	6 May	13 May
1986 (1985)							
Number released	4322	8697	7416	10,136	11,446	10,866	643
Number recaptured	1	32	11	27	22	9	0
Maximum residence	29	47	35	65	31		—
Mean residence	29 (0)	30.5 (10.6)	17.6 (10.1)	18.3 (14.7)	12.8 (9.6)	10.6 (8.7)	—
Growth rate	—	3.6 (0.01)	4.0 (0.06)	4.0 (0.07)	3.7 (0.06)	3.4 (0.10)	—
Survival rate	1.14	1.44	2.62	2.17	3.14	1.18	0
1987 (1986)							
Number released	3442	4646	7684	1477	—	—	—
Number recaptured	17	54	53	8	—	—	—
Maximum residence	62	71	72	28	—	—	—
Mean residence	27.5 (16.3)	23.2 (8.7)	20.2 (12.2)	14.9 (9.3)	—	—	—
Growth rate	3.8 (0.08)	4.3 (0.07)	4.6 (0.09)	4.6 (0.05)	—	—	—
Survival rate	1.97	3.10	3.41	3.76	—	—	—
1988 (1987)							
Number released	5207	6031	8548	10,513	7880	—	—
Number recaptured	25	33	27	47	34	—	—
Maximum residence	26	34	33	41	19	—	—
Mean residence	15.5 (5.4)	12.0 (11.3)	16.8 (10.9)	15.4 (8.3)	13.5 (7.6)	—	—
Growth rate	3.5 (0.08)	4.3 (0.08)	5.6 (0.14)	5.8 (0.06)	6.4 (0.08	—	—
Survival rate	0.48	0.69	1.03	1.44	1.83	—	—
1989 (1988)							
Number released	—	3670	5113	8819	10,160	11,467	3370
Number recaptured	—	5	2	27	56	120	21
Maximum residenc	—	33	27	31	34	27	22
Mean residence	—	14.0 (15.1)	21.7 (5.2)	10.0 (8.7)	12.5 (10.6)	9.4 (12.3)	6.9 (11.1)
Growth rate	—	4.5 (0.05)	5.6 (0.02)	5.3 (0.06)	6.1 (0.07)	5.9 (0.06)	4.2 (0.09)
Survival rate	—	2.58	4.33	5.34	5.88	4.86	3.30

alus polyacanthocephalus, Pacific staghorn sculpin, *Leptocottus armatus*, and buffalo sculpin, *Enophrys bison*) were captured in beach seines and surface trawls along with juvenile salmon. We also observed these fish striking at schools of juvenile pink salmon in nearshore areas. Examination of the stomachs of a few of these predators showed that pink salmon juveniles were indeed a dietary item. The abundance of potential predators captured in beach seines and tow net trawls was similar for all study years. Temporally, the number of predators initially increased slowly in April, then rose sharply in late April, peaked by late May, and declined sharply in June (Fig. 4). The period of rapid increase and decline each year was due primarily to the pulse of coho salmon smolts entering Auke Bay in May and leaving in June. Dolly Varden and sculpin numbers increased more gradually in the spring and remained steady throughout late spring and early summer.

Water temperature and prey

Water temperature generally increased rapidly during April, May, and early June (Wing and Pella, 1998). Temperatures ranged from 3° to 5°C in late March to 10–14°C in June (Fig. 5). Temperature in 1986 and 1987 remained below 8%C for at least a week longer in April compared with temperature in 1988 and 1989.

Prey organisms of the juvenile salmon consisted primarily of zooplankton and littoral harpacticoid copepods. The seasonal dynamics of the biomass of zooplankton prey in the upper 40 m and upper 5 m of the Auke Bay water column have been discussed

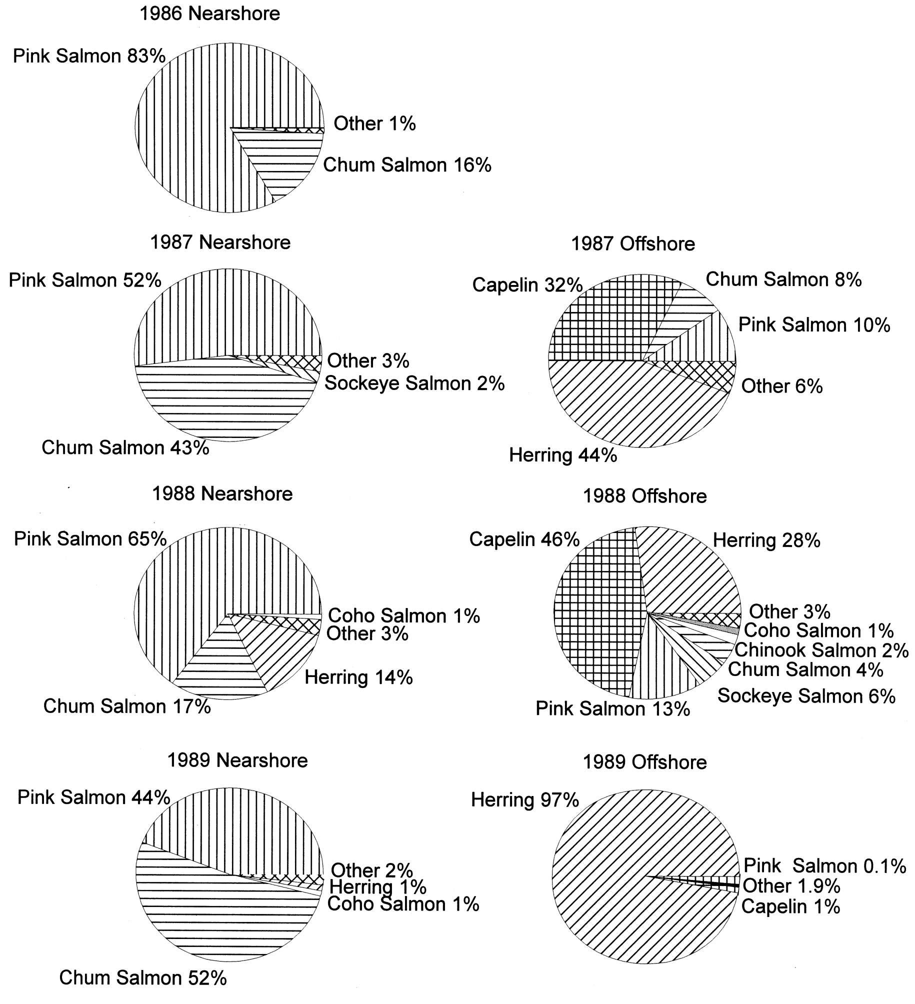

Figure 3

Species composition of nearshore and offshore catches from Auke Bay, Alaska, 1986–89.

by Coyle and Paul (1990), and we used their data to develop these profiles. Generally the biomass of zooplankton prey in the upper 40 and the upper 5 m of the water column began rising in mid-April and peaked in mid-June. However, in 1986 the biomass of prey in the upper 5 m remained low throughout the spring (Fig. 5).

Littoral harpacticoids were sampled at Spuhn Island in 1987, 1988, and 1989. Although the sampling method changed between 1987 and 1988, an indication of the dynamics of the harpacticoid population is achieved by presenting indices of biomass as a proportion of the highest value within each year. In 1987, harpacticoid copepod biomass was characterized by rapid fluctuations but remained low, except for a peak in mid-May. The biomass in 1988 again fluctuated rapidly, with peaks in late April and early May. In 1989, the biomass peaked in early April and again in early May.

Diet

Harpacticoid copepods and zooplankton (principally calanoid copepods, euphausid larvae, *Oikopleura* sp., and fish eggs and larvae) were eaten by the pink salmon juveniles captured near shore (Fig. 6). Between April and May, pink salmon consumed epibenthic prey more than pelagic prey; by mid-May they switched to a predominately pelagic diet.

Pink salmon juveniles captured offshore in Auke Bay exhibited a predominately pelagic diet, but some epibenthic organisms were still present. This finding may indicate that at times epibenthic prey are transported to offshore areas by water currents, or that the juvenile salmon optimize feeding by moving between pelagic and epibenthic areas in Auke Bay.

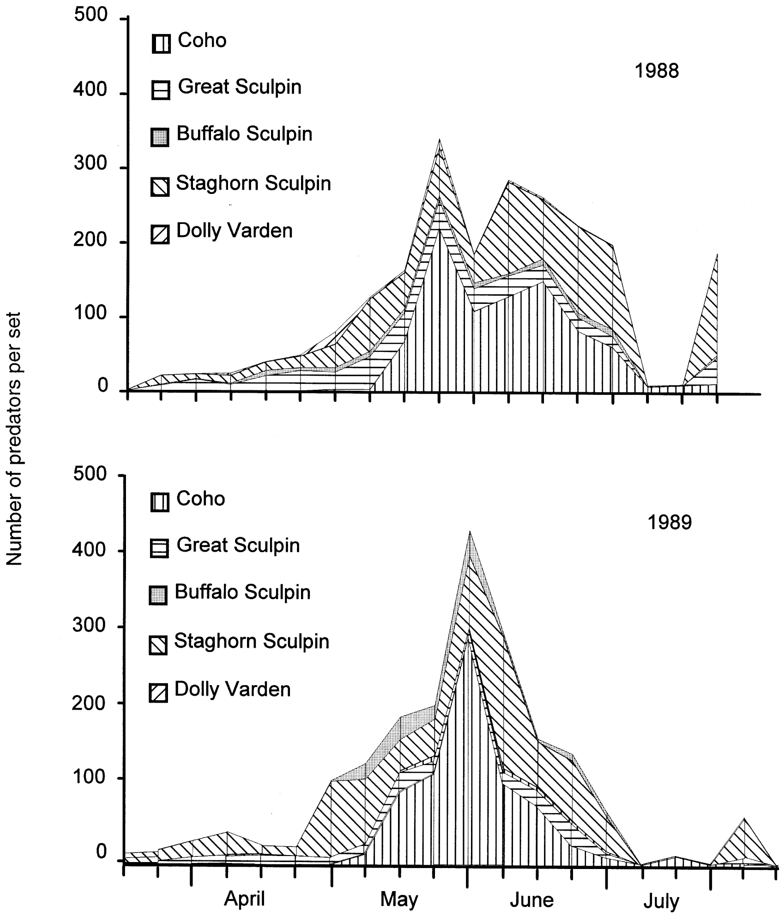

Figure 4

Mean catch per set of potential predators of juvenile pink salmon in the nearshore areas of Auke Bay, Alaska, 1988 and 1989.

Growth rates

Growth (as a percentage [bwd]), of tagged and untagged juvenile pink salmon was examined in two periods, 1 April to 6 May (early) and 7 May to 16 June (late) in all study years (Table 2). Growth of tagged fish in the early period ranged from 2.93% bwd in 1986 to 4.88% in 1989 and of untagged fish from 1.21% bwd in 1987 to 2.10% in 1989. In the late period, growth of tagged fish ranged from 4.82% bwd in 1986 to 6.66% in 1988, and of untagged fish from 2.87% bwd in 1989 to 4.86% in 1988. Tagged and untagged juvenile pink salmon grew significantly slower in the early period than in the late period in all years.

Growth rates calculated for tagged juvenile pink salmon in any given period in a year were consistently higher than the apparent growth rates calculated from the mean weights of samples of untagged pink salmon (Table 2). Continuous recruitment of newly emigrated juveniles (fork length <33 mm) into the untagged population caused this pattern. The number of untagged juvenile pink salmon shorter than 33 mm that were captured by beach seine ranged from highs between 59% and 100% in late March each year to below 10% by 20 May of each year except 1989, when they remained at 11% until 12 June. Such variations in the number of new recruits and the number of larger fish leaving the nearshore juvenile pink salmon population resulted in a bias for growth rate calculations from untagged populations. Tagged fish provided a more realistic assessment of growth in relation to the environment.

Factors limiting growth

Fish growth can be limited by low water temperatures (Weatherley and Gill, 1995) and low prey abundance (Brant et al., 1992). To determine when growth

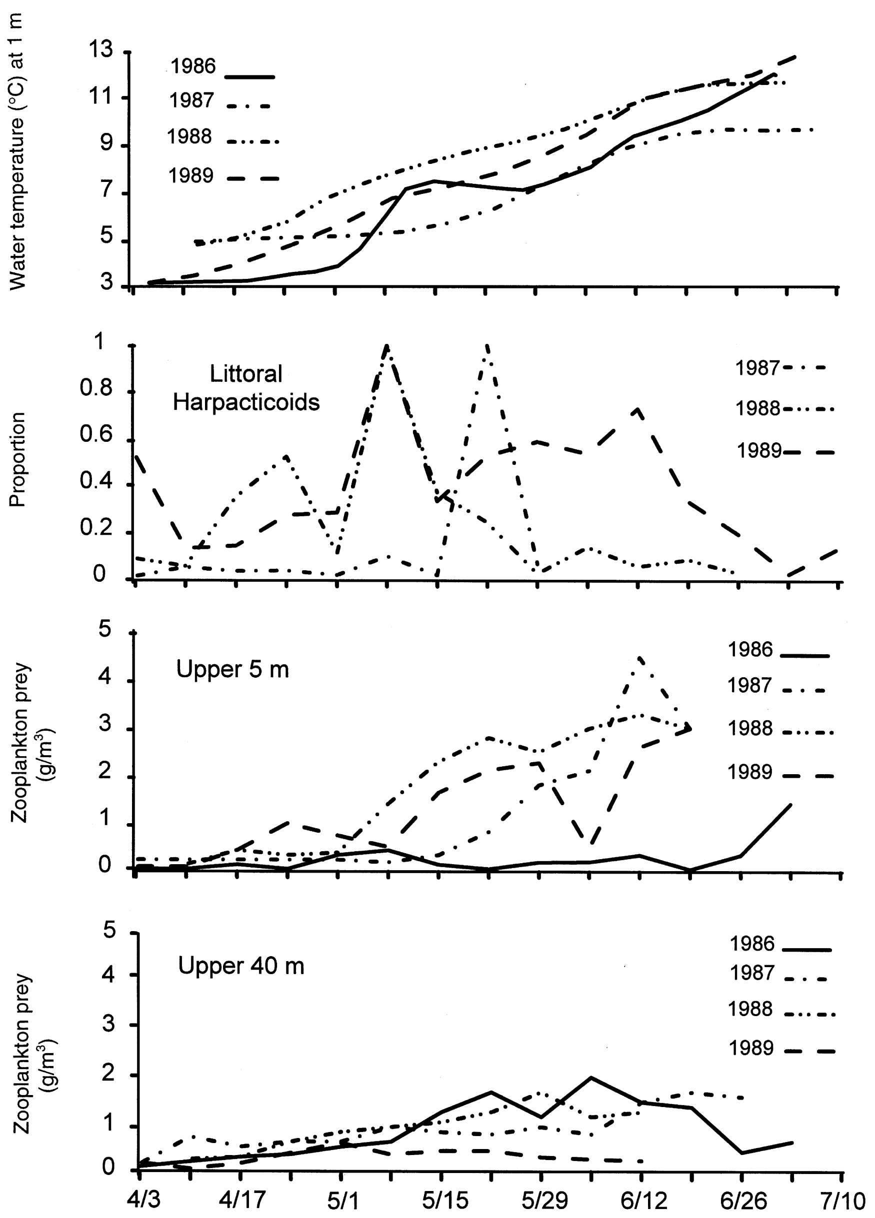

Figure 5

Water temperature, biomass of zooplankton and harpacticoid copepod prey of juvenile pink salmon from the epibenthos, upper 5 m, and 40 m of Auke Bay, Alaska. Owing to differences in collection technique between years, the values depicted for littoral harpacticoids are expressed as a proportion of the highest biomass within each year. Littoral harpacticoids were not collected in 1986. Zooplankton data for the upper 5 m and 40 m were taken from Coyle and Paul (1990).

of juvenile pink salmon might be restrained by prey abundance, the observed growth of each tagged fish was compared to maximum expected growth at similar water temperatures. In all years, the residuals between observed and expected growth (observed–expected) had significant positive slopes (Fig. 7), indicating that a higher proportion of early emigrants (rearing in relatively cool water) were below expected growth rates compared with fish at higher water temperatures (later emigrants). If abundance of prey is not growth-limiting, the growth rate of juvenile pink salmon at 5°C water temperature in

Table 2

Growth rate (as percent body weight per day [% bwd]), of tagged and untagged juvenile pink salmon caught in Auke Bay in early and late growth periods (1 April–6 May and 7 May–16 June). Growth of tagged juveniles was calculated between release and recapture within the early period and the number of days from the end of the early period to recapture within the late period. To calculate the rate of growth of tagged fish, the average weight of the fish from release to recapture within the early period was used, whereas in the late period the estimated weight of fish at the end of the early period and at the date of recapture within the late period was used. The growth of untagged fish was calculated similarly, except that the number of days from the beginning to the end of a specific growth period was used. The standard deviation (SD), coefficient of determination (r^2), and sample size (n) are also shown.

Growth period	Tagged	Growth rate (% bwd)	SD	r^2	n	Growth period	Tagged	Growth rate (% bwd)	SD	r^2	n
1986						1988					
Early	tagged	2.93	0.237	0.84	76	Early	tagged	2.95	0.208	0.62	134
	untagged	1.41	0.213	0.71	422		untagged	1.51	0.398	0.50	2019
Late	tagged	4.82	0.221	0.83	23	Late	tagged	6.66	0.274	0.60	32
	untagged	3.21	0.391	0.65	955		untagged	4.86	0.341	0.42	2535
1987						1989					
Early	tagged	3.14	0.203	0.78	101	Early	tagged	4.88	0.287	0.44	173
	untagged	1.21	0.333	0.62	569		untagged	2.10	0.335	0.36	462
Late	tagged	5.40	0.173	0.94	31	Late	tagged	5.40	0.202	0.82	58
	untagged	4.34	0.433	0.77	1658		untagged	2.87	0.387	0.36	1030

early April should be about 2.0% or more (Mortensen and Savikko, 1993). Examination of growth residuals from tagged juveniles in relation to those at “maximum” feeding levels, indicates that fish in early April tended to have lower than expected growth rates, up to 2% lower depending upon the year. The slope of the residuals was lowest in 1988, when a higher proportion of the observations fell below the zero line throughout the temperature range observed.

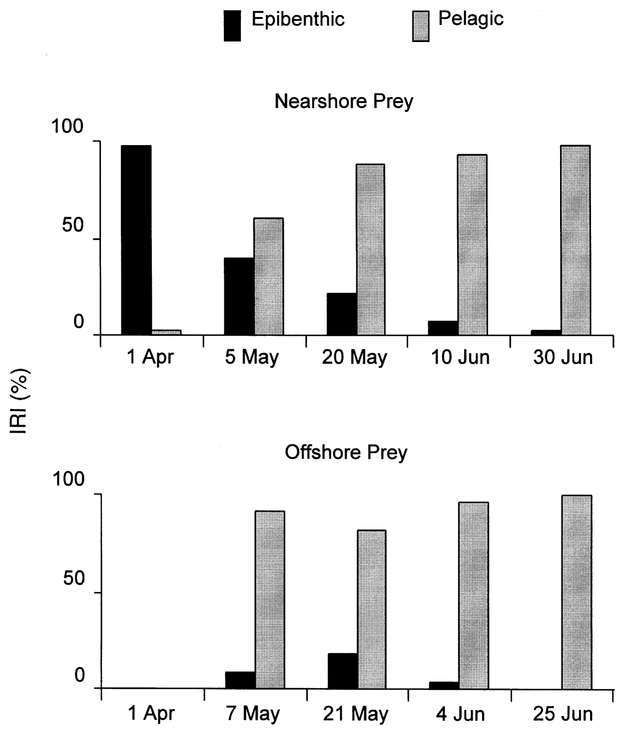

Figure 6

Index of relative importance (IRI) of pink salmon prey during residence in the nearshore and offshore areas of Auke Bay, Alaska.

Intra-annual growth of tagged pink salmon

Growth of tagged juvenile pink salmon generally increased each year with successive release dates, reaching a maximum in late April, and then declining for later emigrants (Table 1). Recovery year is specified in the following sections, and brood year (BY) is given in parentheses. In our study, brood year corresponded to the spawning year of the parental generation and was always the year prior to the year when the sample was taken. Growth of weekly release groups varied from a low of 3.38% bwd in 1986 (1985 BY) to a high of 6.39% in 1988 (1987 BY). The decline in growth of emigrants from late releases was not observed in 1987 (1986 BY) and 1988 (1987 BY), when emigration ended before the end of April. In 1986 (1985 BY), the lowest growth rates were observed for the latest fish emigrating in the first week of May. In 1989 (1988 BY), the lowest growth rates were also observed for the last emigrants. However, these fish emigrated in the second week in May; fish emigrating in the first week in May in 1989 (1988 BY) had growth rates similar to those at the midpoint of the emigration timing.

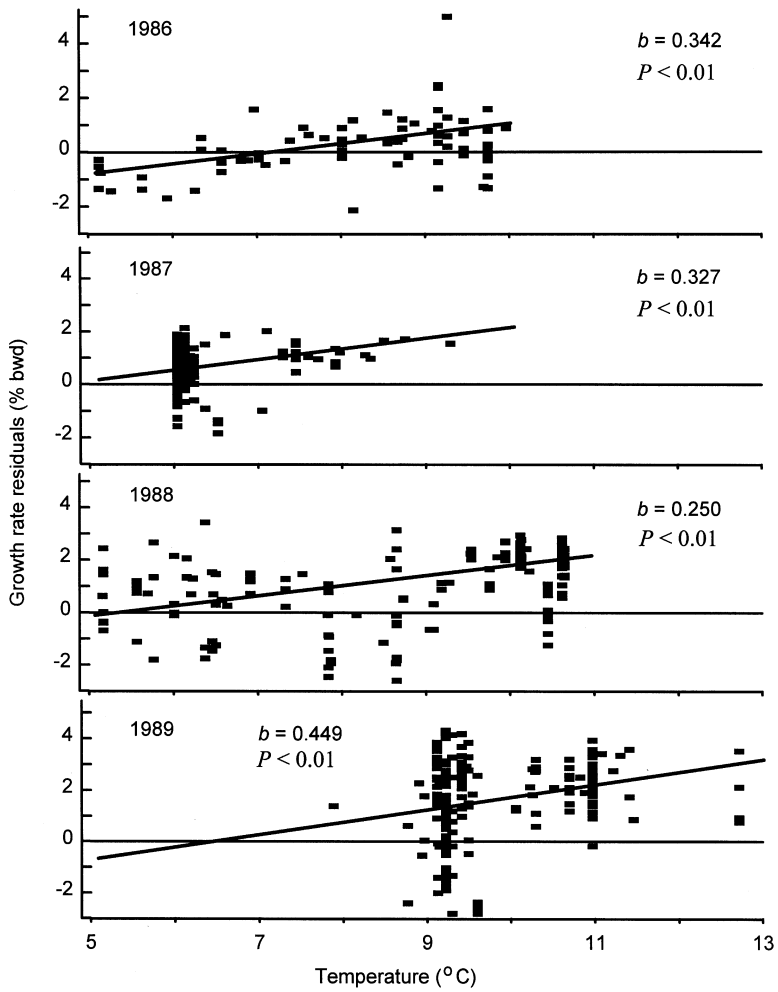

Figure 7

Residuals between the observed growth rate of tagged juvenile pink salmon and expected growth rate of juvenile pink salmon fed excess ration. Year shown refers to recovery year.

Interannual growth of tagged pink salmon

The growth rates of juvenile pink salmon from individual release groups varied substantially between years (Table 1). All release groups of juvenile pink salmon in recovery year 1986 (1985 BY) grew significantly slower than those of juveniles in subsequent years. In 1987 (1986 BY) and 1988 (1987 BY), the only years when tagged juveniles from the 1 April group were recovered, growth was not significantly different. Similarly the growth of juveniles from the 7 April groups were not significantly different between years. Juvenile pink salmon from the 15 April and 22 April releases grew significantly slower in 1987(1986 BY) than in 1988 (1987 BY) or 1989 (1988 BY), by nearly 1%. Growth was significantly slower (about 0.5% bwd) for the 22 April release group in 1989 (1988 BY) than in 1988 (1987 BY). The juveniles from the 29 April release grew significantly faster (0.3% bwd) in 1988 (1987 BY) than in 1989 (1988 BY).

Growth in relation to water temperature and prey biomass

Water temperature was the only environmental parameter measured that was significantly correlated with growth rate over all years (Table 3). Both simple and partial correlations were significant (<0.05) in each year for water temperature, and in every year except 1988, temperature explained the most variation in the parameters tested.

Table 3

Simple and partial (S/P) correlation coefficients between the instantaneous growth rate of juvenile pink salmon and average water temperature; average harpacticoid biomass; average biomass of prey integrated from 40 m to surface; average biomass of prey in the upper 5 m; and average biomass of harpacticoids + prey from the integrated water column. An * indicates a significant ($P<0.05$) correlation. NA = not available.

Year	Average water temperature	Average harpacticoid biomass	Average integrated column biomass	Average biomass in upper 5 m
1986	0.696*/0.696*	NA	0.630*/0.187*	–0.187/-0.046
1987	0.312*/0.312*	–0.201*/-0.017*	0.193/0.248	0.228/0.046
1988	0.423*/0.047*	0.337/0.000	0.505*/0.505*	0.472/0.228
1989	0.354*/0.354*	–0.226*/-0.118*	0.057/0.003	0.254/0.128*

The 5-m depth zooplankton biomass was not significantly related to growth in any year, whereas biomass from the 40-m integrated water column was significantly correlated in two of the four years. In 1988, the biomass from the 40-m integrated water column was the parameter most correlated with growth.

The biomass of littoral harpacticoids was significantly correlated with juvenile pink salmon growth for two of the three years for which data were available. In both cases, the relationship was negative (Table 3). Because feeding habits showed that the pink salmon were switching between epibenthic and zooplankton resources during the nearshore phase, growth rate was also correlated with a combined index of the biomass of littoral harpacticoids and the 40-m depth zooplankton. This combined index did not fit the growth data as well as either water temperature or zooplankton biomass considered independently (Table 3).

Growth and survival

Mid- to late April emigrants had significantly higher survival than the earliest emigrants within a year (Table 1). Brood year is specified in the following paragraphs unless otherwise noted. When emigration extended into May (1985 and 1988 brood years), survival decreased by as much as 2% from the groups released from mid- to late April. The last emigrants from both the 1985 and 1988 broods, which had the lowest growth rates of those years, also had significantly lower survival than emigrants from mid- to late April.

The intra-annual survival of cwt juvenile pink salmon exhibited a pattern similar to that for growth rates. Regression of growth rate against survival (as proportions within each year) indicated a highly significant relationship ($r^2=0.65$, $P<0.003$; Fig. 8). Within-year survival generally increased with growth rate.

To examine the relation between growth and survival interannually, growth rate (%bwd) was regressed against survival rate of each release group. Although survival appears to increase with increasing growth rate, there was no relationship when all years were considered ($r^2=0.02$, $P>0.397$). Fish from the 1987 brood year (1988 emigrants, 1989 adults) had a distinctly different growth versus survival trajectory than fish for other years (Fig. 9). Data from brood years 1985, 1986, and 1988 fitted well ($r^2=0.88$, slope=1.82, $P=0.001$). Survivals of the 1987 brood were also significantly related to growth when considered separately from the other years ($r^2=0.93$, slope=0.40, $P=0.001$).

Discussion

Pink salmon juveniles were abundant in the nearshore areas of Auke Bay in April and May; by the end of May or early June, the fish had moved farther offshore. This pattern is typical for juvenile pink salmon, which generally follow shorelines during their first weeks in the marine environment, then migrate offshore as they grow (Heard, 1991; Celewycz and Wertheimer, 1996a).We found water temperature to be the main factor that determined the growth rate of juvenile pink salmon during their early marine existence. The metabolism and growth of fish are influenced extensively by water temperature and prey density (Brett et al., 1969; Weatherley and Gill, 1995). To attain maximum growth at a particular temperature, prey concentrations must be adequate (Bailey et al., 1975; Cooney et al., 1981). In our study there were indications in early spring of each year that the growth of juvenile pink salmon was limited by abundance of prey. These early fish enter the Auke Bay estuary before the spring zooplankton bloom and rely on overwintering epibenthic prey organisms such as harpacticoid copepods.

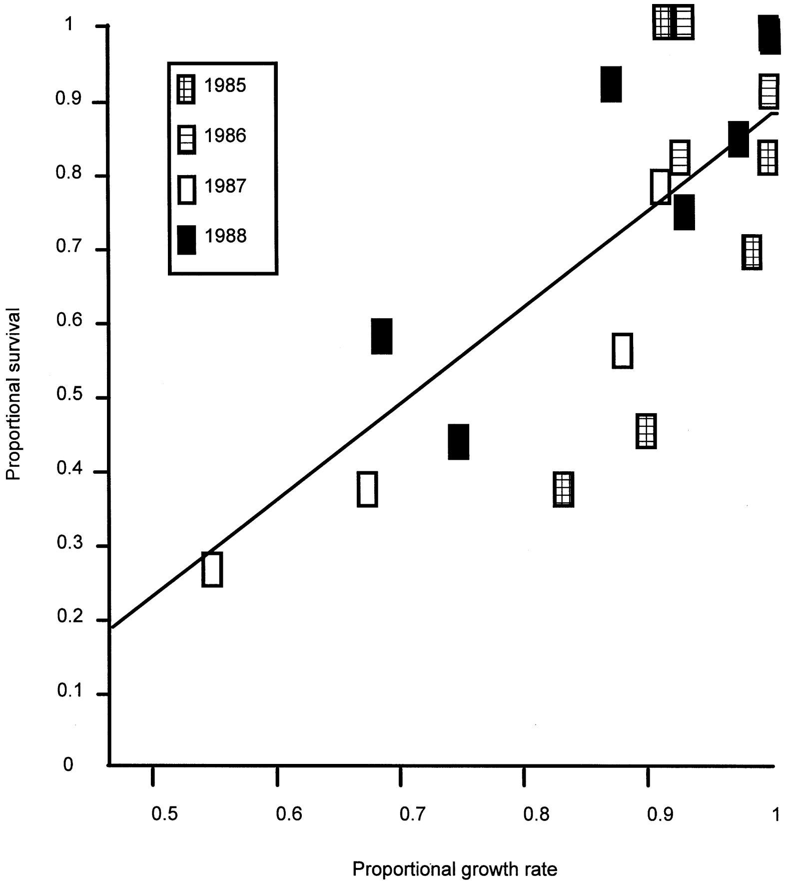

Figure 8

Intra-annual survival depicted as a regression of proportional survival on proportional growth rate of tagged Auke Creek pink salmon (r^2=0.65, P=0.003). Years represent brood year.

The relatively sparse population of potential predators in early spring allow a portion of the juveniles to survive the period of low growth. Growth was strongly related to adult survival within each of the study years; however, this relationship did not hold true between years.

Growth of fish in the tag groups over all recovery years ranged from 3.4% (8 May 1986 release) to 6.4% (29 April 1988 release). These rates are within the 1.5–7.6% range of growth rates previously reported for pink salmon during their initial marine residency (LeBrasseur and Parker, 1964; Healey, 1980). Willette (1996) also observed growth rates of 3.5–5.2% for cwt pink salmon in Prince William Sound.

Variations in the feeding activity of salmonids is characteristic of opportunistic and broad-spectrum predators, which optimize their food consumption in response to prey density (Parker and Vanstone, 1966; Parker, 1969; Ware, 1972; Hunter and Thomas, 1974; Godin, 1981). Both epibenthic crustaceans and zooplankton were important components of the prey of juvenile pink salmon during their nearshore residence in Auke Bay. In previous studies, harpacticoid copepods, among other epibenthic organisms, have been reported as the primary prey of pink salmon juveniles in nearshore marine habitats (Healey, 1980; Godin, 1981; Landingham, 1982; Webb, 1991). In Alaska waters, however, planktonic prey often predominate in the early diet of pink salmon (Bailey et al., 1975; Cooney et al., 1981; Sturdevant et al., 1996; Willette, 1996). Some of these differences are due to the types of beaches where juvenile pink salmon are sampled. In studies where harpacticoid copepods are the primary dietary component, the fish are sampled at low-gradient beaches with substantial epibenthic production (e.g. Kaczynski et al., 1973; Godin, 1981; Webb, 1991). Sturdevant et al. (1996) also found that a higher proportion of epibenthic prey was consumed by juvenile pink salmon captured on lower-gradient than on steep-gradient beaches. In Auke

Bay, pink salmon samples for diet analysis were taken from low-gradient beaches where there is a high production of epibenthic harpacticoid copepods (Landingham, 1982; Cordell, 1986). However, even at this habitat type, pelagic zooplankton was an important dietary component. Similarly, Sturdevant et al. (1996) found zooplankton to be the dominant dietary component of pink salmon juveniles from all nearshore habitat types sampled in Prince William Sound, Alaska.

From a bioenergetics standpoint, prey density and water temperature are critical factors affecting fish growth by influencing consumption rate, metabolic rate, and gastric evacuation rate (Willette, 1996). Temperature was significantly correlated with observed growth of juvenile pink salmon, but indices of prey abundance were not consistently correlated with growth and were even inversely related in the case of harpacticoid copepods. This lack of correlation may be due to the typically high and variable productivity of zooplankton and littoral epibenthos found in subarctic ecosystems such as Auke Bay (Cordell, 1986; Coyle and Paul, 1990). Assuming there is some threshold level of prey density required to sustain maximum growth of juveniles, then the pronounced spikes in biomass of prey populations associated with the spring bloom would mean that much of the variability in prey occurs above the density threshold, thereby masking a relationship between prey biomass and juvenile pink salmon growth. Any such relationship should occur primarily before or after the prey population peaks. Analysis of residuals between expected growth of pink salmon and observed initial growth indicated that food abundance did limit growth at low water temperatures, (i.e. growth rates observed in the early period of nearshore residency were possibly constrained by food availability as well as lower temperatures (Fig. 7).

The emigration of Auke Creek pink salmon extended from late March to mid-May; most of the fish emigrated within 2–3 weeks in mid- to late April. Holtby et al. (1989) proposed that the synchronous timing of emigration of chum salmon may be an adaptive feature based upon advantageous growth conditions in the estuarine environments, with synchrony acting as a mechanism to saturate predators and enhance survival. By this premise, it would be beneficial for all Auke Creek juveniles to emigrate together, later in the spring, within a narrow time window, so as to ensure optimum growth conditions. Each year, however, a portion of the Auke Creek pink salmon juveniles emigrate in early spring and they consistently encounter poor growth conditions. Water temperatures are usually 4°C, and zooplankton abundance is very low. These juveniles take longer to reach a particular size than do later emigrants and generally reside longer in estuarine nursery areas than the later, faster-growing emigrants (Table 1). Even though predator populations are relatively low in early spring, the early emigrants are exposed to predation over a longer period than are later

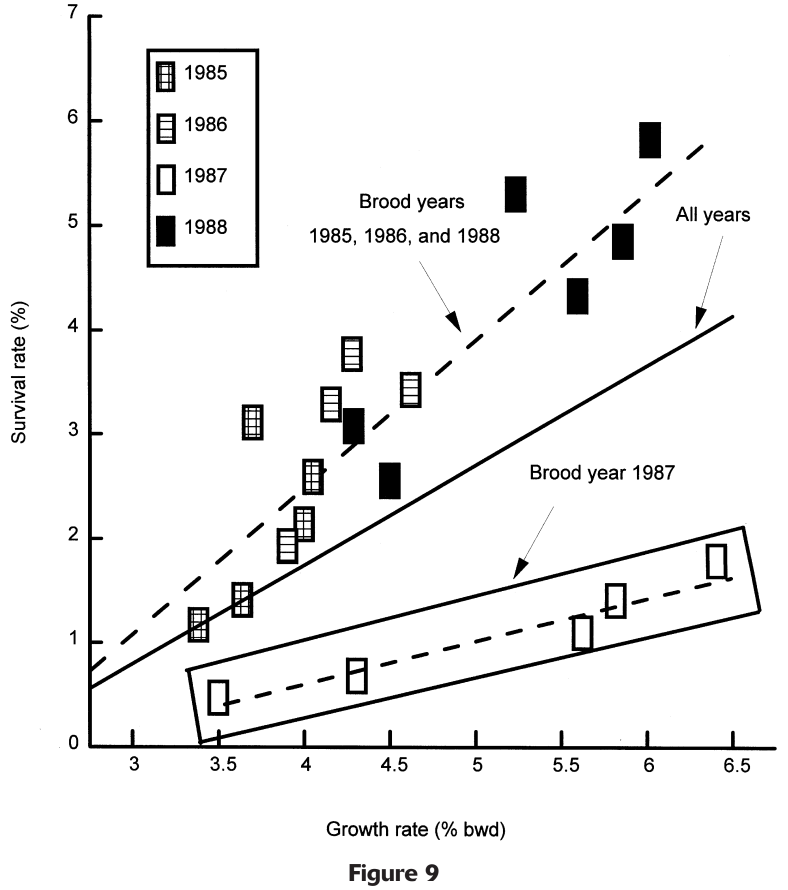

Figure 9

Interannual survival depicted as the regression of survival (adjusted for catch rate) versus growth rate of tagged Auke Creek pink salmon. When all four brood years are included in the regression, a poor relationship results (r^2=0.02, P>0.397). However, when brood year 1987 is excluded from the regression, the relationship between survival and growth rate improves (r^2=0.88, P=0.001). This relationship is also very good when based on data from just brood year 1987 (r^2=0.93, P=0.001).

emigrants. Despite spending more time in low-growth conditions, they will have the advantage of being larger at a given date than subsequent, faster-growing emigrants (Fig. 10). Thus, there is an adaptive advantage in lessening size-selective predation by being on the "leading edge" of the synchronous emigration to marine waters. However, this advantage is constrained by poorer growth early in the spring and poorer survival to adulthood.

The abundance of potential predators (coho salmon, Dolly Varden, and sculpins) near shore increases rapidly in May, emphasizing the importance of larger size and larger numbers for pink salmon to avoid predation. Late emigrants, although encountering what appear to be good conditions for growth, may not be able to effectively outgrow increasing predation pressure or may not be abundant enough to saturate the predator population. Other factors may combine to affect the growth and ultimately the survival of the late emigrants. The abundance of competitors such as young-of-the-year and juvenile herring and capelin may affect the availability of prey at critical times and could explain the lower growth rates observed for late-emerging pink salmon.

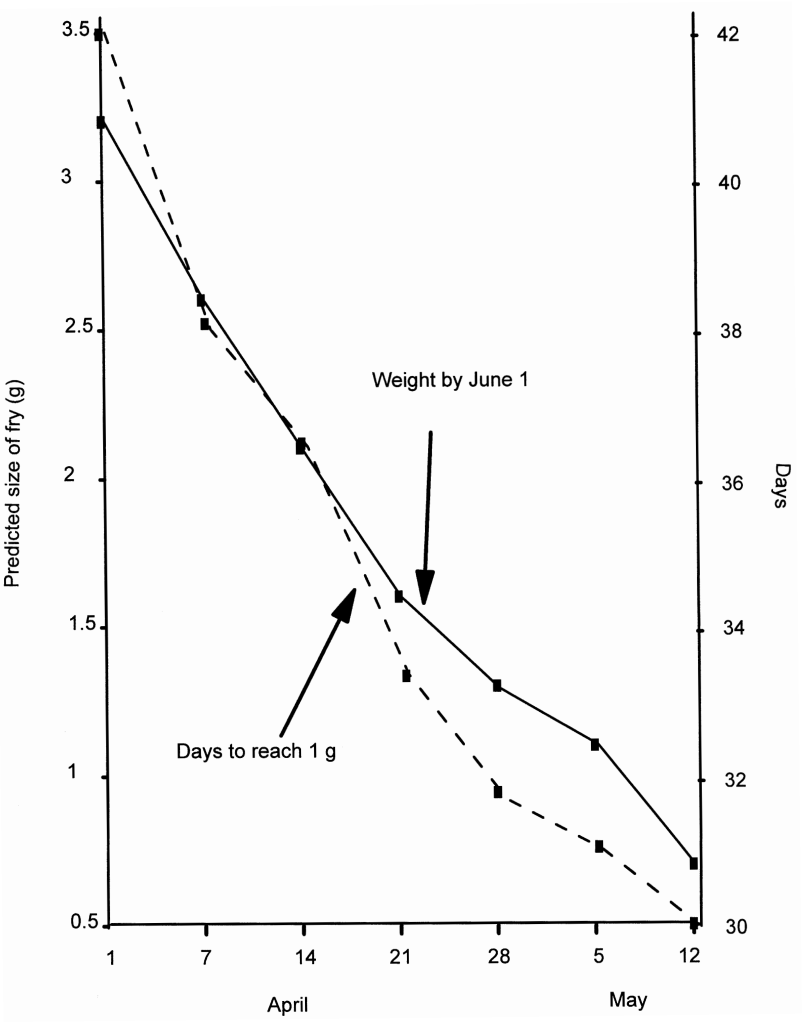

Figure 10

The predicted size of pink salmon fry by 1 June and the number of days to reach 1 g for emigration dates between 1 April and 12 May.

Growth rate of pink salmon juveniles in Auke Bay was consistently related to survival within a given year. This finding is consistent with the concept that high growth rates during early marine residency give a survival advantage by minimizing the intensity of predation (Parker, 1971; Heard, 1991). Following the *Exxon Valdez* oil spill in Prince William Sound in 1989, Willette (1996) found a direct relationship between growth and survival of pink salmon juveniles. However, he did not observe this association for juveniles captured in 1990 or 1991 and speculated that changes in the feeding habits of predators due to the absence of alternate prey obscured the relationship between growth and survival. Correlations of parameters for scale growth rates with run size of pink salmon in northern southeastern Alaska indicated that nearshore growth conditions are a significant contributor to the interannual variation in marine survival. Early scale growth (Jaenicke et al., 1994) was positively correlated with survival, indicating that high early marine growth lessens mortality due to predation. In our study, for three of the four years, growth rate was an excellent predictor of survival interannually, explaining 85% of the observed variability. The anomalous year was 1988 (1987 brood), which was also the year of highest overall growth rates. Fish from all release groups of the 1987 brood returned to the weir at consistently lower rates than fish from the other brood years. Fishery exploitation on returning adults may be a factor. We corrected the rate of survival each year for those fish taken in the commercial fishery with the correction factor used by the Alaska Department of Fish and Game; however, the correction factor was relatively crude with no measure of variance. It is conceivable that fishery exploitation could still have affected the growth and survival relationship. Changes in nearshore predation or conditions (both environmental and biological) after the fish had moved offshore could also have been the cause. Although we noted no unusually high concentrations of piscivorous sea birds or marine mammals in the Auke Bay area in the spring of 1987, that observation does not preclude the possibility that larger than normal populations of predators may have caused significant mortality on the juveniles beyond our study area of Auke Bay. Identification of the elements causing such anomalous years would provide insight into how these factors interact with growth conditions to drive interannual variation.

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