A Review of the Critical Size, Critical Period Hypothesis for Juvenile Pacific Salmon

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Abstract: In this review, we consider size of juvenile Pacific salmon (*Oncorhynchus* spp.) after the first summer at sea to be the trait on which size-selective mortality operates. The idea is based on the critical size, critical period hypothesis, where those individuals within a cohort that do not reach a critical size during their first summer at sea have higher rates of late fall and over-winter mortality. The results suggest that early marine growth of juvenile Bristol Bay sockeye (*O. nerka*), Prince William Sound hatchery pink (*O. gorbuscha*), and British Columbia coho (*O. kisutch*) salmon from geographically distinct regions (Bering Sea, northern Gulf of Alaska, coastal British Columbia, respectively) is important and that these salmon must attain sufficient growth during their first summer at sea to survive subsequent years at sea.

Keywords: critical size, juvenile Pacific salmon

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) experience relatively high mortality rates during the first few months at sea (Parker 1968; Hartt 1980), and it is believed that the high mortality rates may be partly related to size (Pearcy 1992). Size-dependent marine mortality of juvenile salmon may be concentrated during two specific early marine life-history stages. The first stage may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker 1968; Willette et al. 1999). The second stage is thought to occur following the first summer at sea, when smaller individuals may not have sufficient energy reserves to survive late fall and winter (Beamish and Mahnken 2001). Thus, larger individuals within a cohort likely have higher probability of survival, emphasizing the importance of size during the first summer at sea.

In this review, we consider size of juvenile Pacific salmon after the first summer at sea to be the trait on which selective mortality operates. The idea is based on the critical size, critical period hypothesis, where those individuals within a cohort that do not reach a critical size during their first summer at sea have higher rates of late fall and over-winter mortality (Beamish and Mahnken 2001). Here, we briefly discuss two different methods to examine critical size (longitudinal sampling and retrospective analyses) for Pa-

cific salmon and provide recent examples from the literature. In the next section, we examine the critical period concept by estimating marine stage mortality of juvenile Pacific salmon to determine the magnitude of over-winter mortality. Lastly, we provide examples of possible mechanisms affecting growth of juvenile salmon during their first year at sea.

RESULTS AND DISCUSSION

Evidence for Critical Size of Juvenile Salmon

Longitudinal Sampling

Ideally, comparisons of size distributions prior to and after the first winter at sea based on repeated measurements of size from the same population would best address size-selective mortality. This type of sampling, known as longitudinal sampling (Chambers and Miller 1995), provides a means to directly assess individual growth. Recent papers that employed longitudinal sampling utilized the fact that scale radius length is proportional to fish body length (Francis 1990; Ricker 1992) and compared average circuli spacing of first-year marine scale growth collected from juvenile and adult salmon within a cohort (Beamish et al. 2004; Moss et al. 2005). For example, mean intercirculi spacing for ocean-age-0 coho salmon (*O. kisutch*) was significantly smaller than the mean intercirculi spacing for ocean-age-1 fish from the same cohort (Beamish et al. 2004; Fig. 1) suggesting

that larger individuals within a cohort had higher marine survival. In another example, relative frequencies of scale radius length at various early marine circuli for Prince William Sound (PWS) hatchery pink salmon (*O. gorbuscha*) indicated that scale radii for surviving adult pink salmon were significantly larger than for juveniles from the same brood year and the same circulus (Moss et al. 2005; Fig. 2). Again, direct comparisons of size from a cohort of PWS hatchery juvenile pink salmon indicated that larger fish had higher marine survival. Because coho and pink salmon spend one year in the ocean, the mortality for the smaller fish within a cohort was believed to occur during late fall and winter.

Retrospective Analyses

According to the critical size, critical period hypothesis, the number of juvenile salmon reaching the critical size after the first summer at sea will vary, but the critical size should be more stable because it is likely a function of the intrinsic physiology of juvenile salmon (Beamish and Mahnken 1999). One way to test the critical size element of this hy-
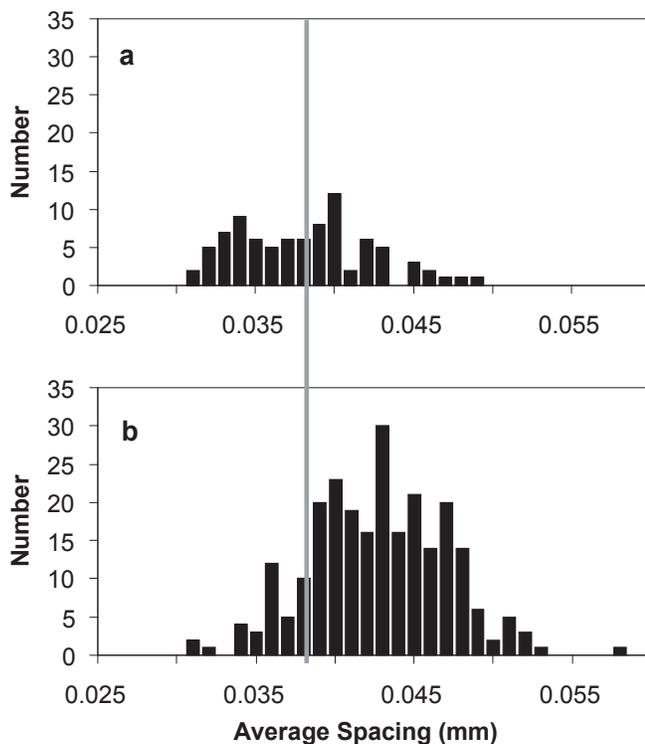
pothesis is to examine inter-annual variability in a time series of fish size from a sample of ocean-age-1 salmon during spring or early summer, as these fish comprise the surviving population after the first winter at sea. An example of a time series (1972 – 2000) of fork lengths (mm) for ocean-age-1 chum (*O. keta*) and sockeye salmon (*O. nerka*) captured in the central Bering Sea during July aboard Japanese research cruises (Ishida et al. 2002) is shown in Fig. 3. There was no significant trend in size for either ocean-age-1 sockeye or chum salmon (Ishida et al. 2002). These data provide strong evidence of size-selective mortality during the first year at sea, especially given that these fish likely represent mixed stocks from western Alaska, Russia and Japan (chum salmon) and experienced vastly different ocean conditions during their first year at sea.

Another way to get size after the first year at sea for salmon is to examine scale radius length from the focus to the first marine annulus for scales taken from adult salmon. As mentioned above, scale radius length is proportional to fish body length for Pacific salmon, thus, measuring the distance (mm) from scale focus to the first marine annulus provides an index of size of the salmon after their first winter at sea. If salmon reach a critical size to survive their first winter at sea, then we would expect to see little variation in their size index, as the adult scale samples available for analysis only reflect those juvenile salmon that had attained sufficient size in order to survive to adulthood, and not those that died at sea (Crozier and Kennedy 1999). For example, analyses of time series of size after the first year at sea measured from adult Bristol Bay sockeye salmon scale samples indicated a constant mean and variance for time series of freshwater age-1.0 and -2.0 sockeye salmon with coefficients of variation for size of less than 4% (Farley et al. 2007). The authors speculated that the low variability in size after the first year at sea and the fact that the size of these fish after their first year at sea was not significantly related to survival was due to size-selective mortality during the first year at sea.

As an additional test of the critical size, critical period hypothesis, we used the time series of Bristol Bay sockeye salmon scale and smolt size data to test for differences in the size of smolts and juveniles after their first year at sea between freshwater age groups within a river system or among freshwater age groups between river systems. If size at the first ocean winter is related to survival, then we should see a decrease in the differences between smolt size at age and size after the first year at sea among and between river systems. To examine this concept, we first compared the mean fork length for Egegik River and Kvichak River age-1.0 and -2.0 smolts (Egegik – 28 years of data from brood years 1953–1998 with some missing years; Kvichak – 46 years of data from brood years 1953–1998; data provided by the Alaska Department of Fish and Game) between freshwater age groups (1.0 and 2.0) and river systems. Next, we compared differences in average size measured from adult scales between age-1.0 and -2.0 sockeye salmon after their

Fig. 1. The distribution of the average circuli spacing of the first 10 saltwater circuli from (a) ocean-age-0 coho salmon collected in the Strait of Georgia in September and November, 2000 (mean 0.038, SD 0.004; brood year 1998) and (b) ocean-age-1 coho salmon collected in March, July, August, and September in the Strait of Georgia and from Chilliwack and Big Qualicum hatcheries (mean 0.042; SD 0.004; brood year 1998). The vertical line through the histograms shows the mean intercirculi spacing for the ocean-age-0 sample in relation to the distribution of mean intercirculi spacing for ocean-age-1 fish, of which 82% are larger than the ocean-age-0 mean. (Figure from Beamish et al. 2004).
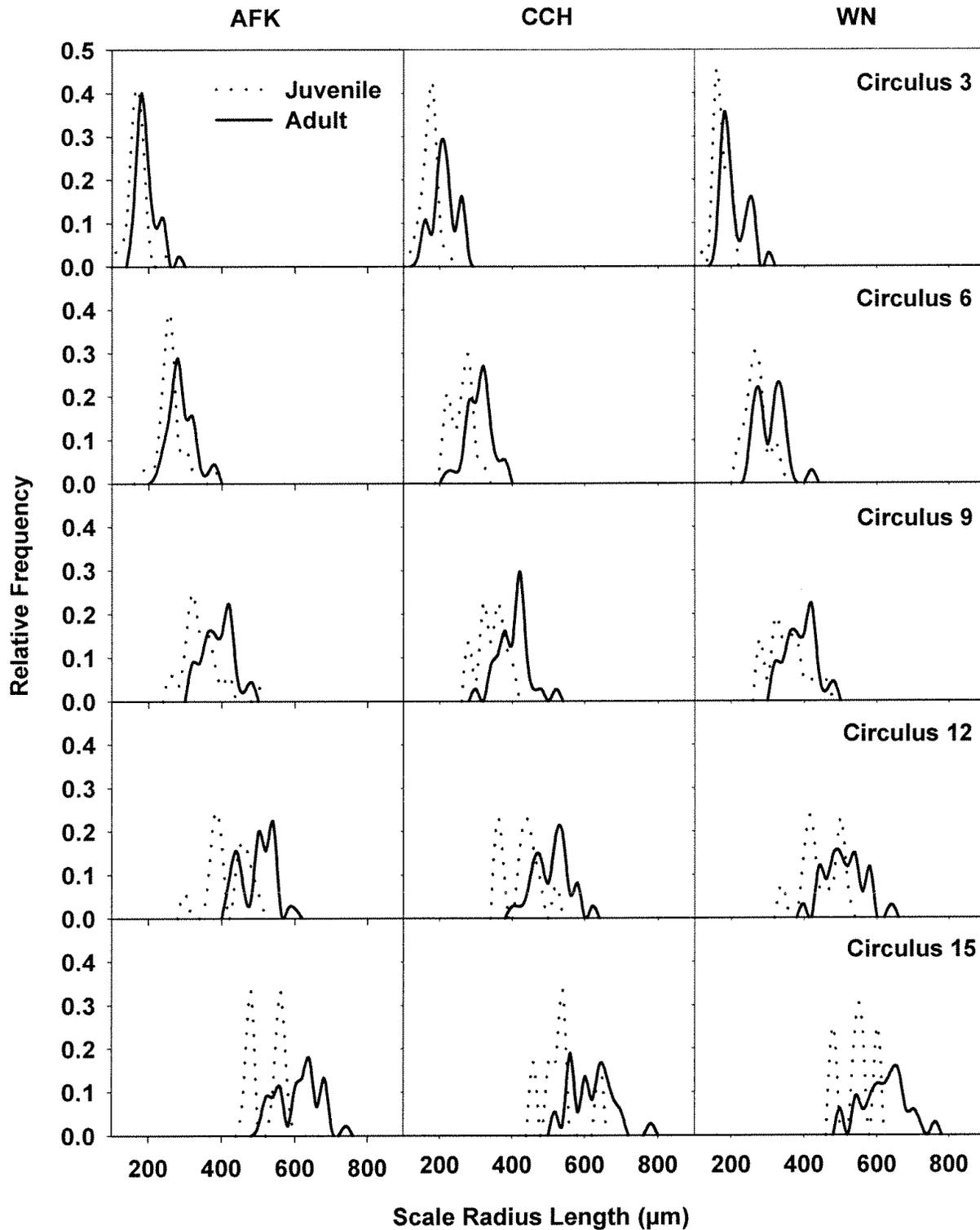
Fig. 2. Relative frequencies of scale radius length to circuli 3, 6, 9, 12, and 15 for hatchery pink salmon (dotted lines) and individuals of that cohort returning the following year as mature adults (solid lines) released by Armin F. Koernig (AFK), Cannery Creek (CCH), and Wally Noerenberg (WN) hatcheries in 2001 (brood year 2000). (Figure from Moss et al. 2005).
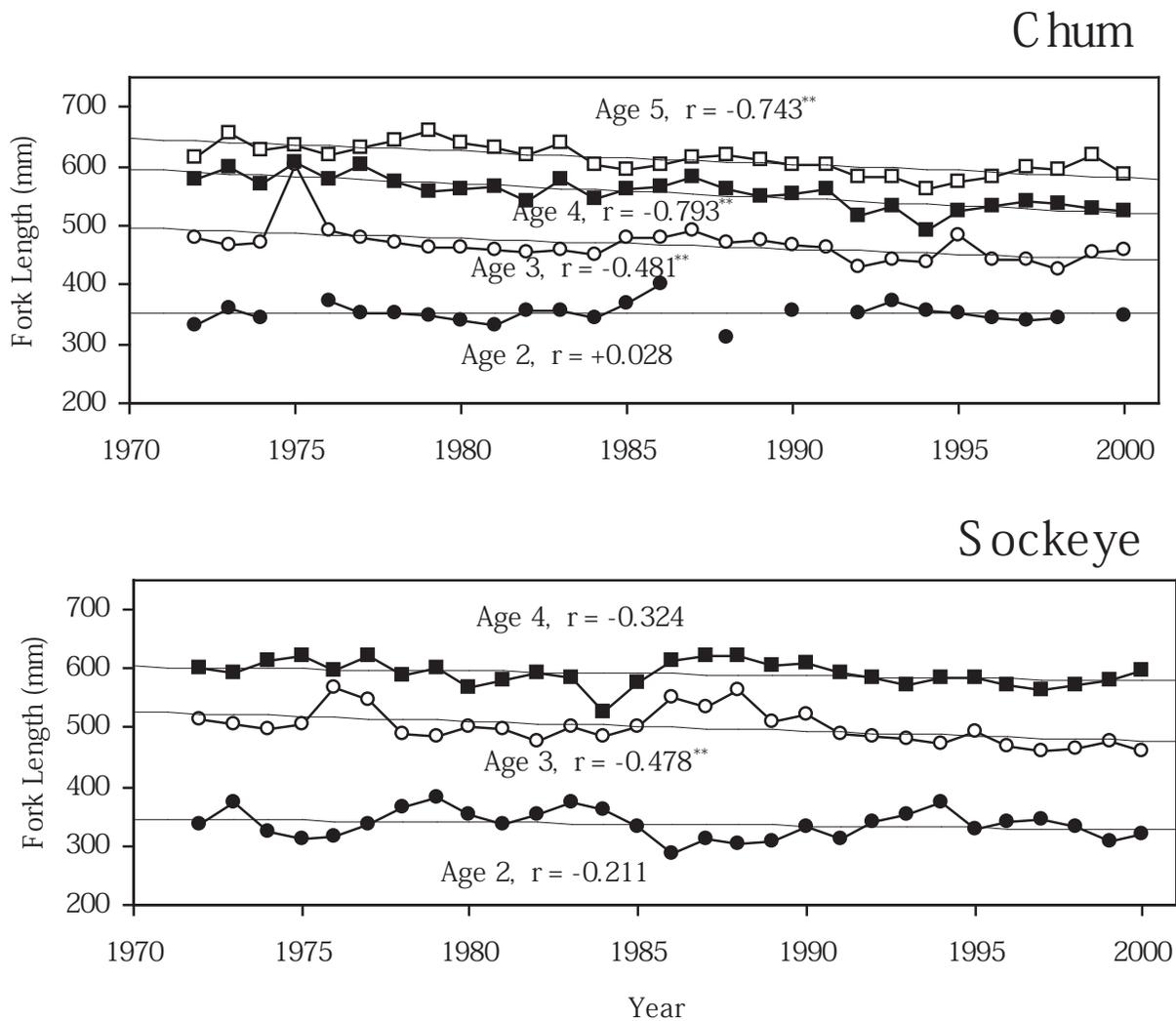
Chum

Sockeye

Fig. 3. Fork lengths (mm) of pink, chum, and sockeye salmon in the central Bering Sea in July from 1972 to 2000.   * significant at the 5% level; ** significant at the 1% level. Figure from Ishida et al. (2002). Note: age is designated as total age of the fish (i.e., Age 2 = "X.1 or 0.1", indicating size of the fish during July after their first year at sea (pers. comm., Y. Ishida, Ishiday@fra.affrc.qo.jp).

first year at sea. The results indicated that the average fork length of age-2.0 sockeye salmon smolts was 18.5% larger than age-1.0 smolts in the Kvichak River and 12.5% larger than age- 1.0 smolts in the Egegik River. The difference in mean size of juvenile sockeye salmon after the first year at sea between age groups and among river systems fell to 5.3% for the Kvichak River and 7.9% for the Egegik River. Comparisons in size among ages and between river systems indicated that age-1.0 and age-2.0 smolts were 19.6% and 11.9% larger in the Egegik River than in the Kvichak River. However after the first winter at sea, the differences between average size of Egegik River and Kvichak River smolts were reduced to less than 1% for age-1.0 fish and 2.8% for age-2.0 fish. These results suggest smaller age-1.0 sockeye salmon within and between river systems are either growing faster than larger age-2.0 sockeye salmon or that their mortality is much greater during their first year at sea. Evidence for

higher rates of mortality includes low survival of Kvichak River sockeye salmon with respect to other major sockeye salmon-producing river systems in Bristol Bay (Fair 2003).

Ricker (1962) proposed that marine survival of sockeye salmon increased with increasing smolt size. Henderson and Cass (1991) tested this idea for sockeye salmon from Chilko Lake located in the Fraser River, BC watershed.   There was no significant relationship between the mean length of smolts leaving the lake and the marine survival for brood years 1949 to 1985. However, adults returning to spawn had significantly larger scale-based indices of growth in fresh water than the corresponding smolts of the same brood year. This indicated that there was higher mortality for smolts that were smaller as indexed by their scale growth. Beamish and Mahnken (1999) published new data from the Henderson and Cass (1991) study that was an index of scale growth up to the first marine annulus (Fig. 4). The data in Fig. 4 repre-
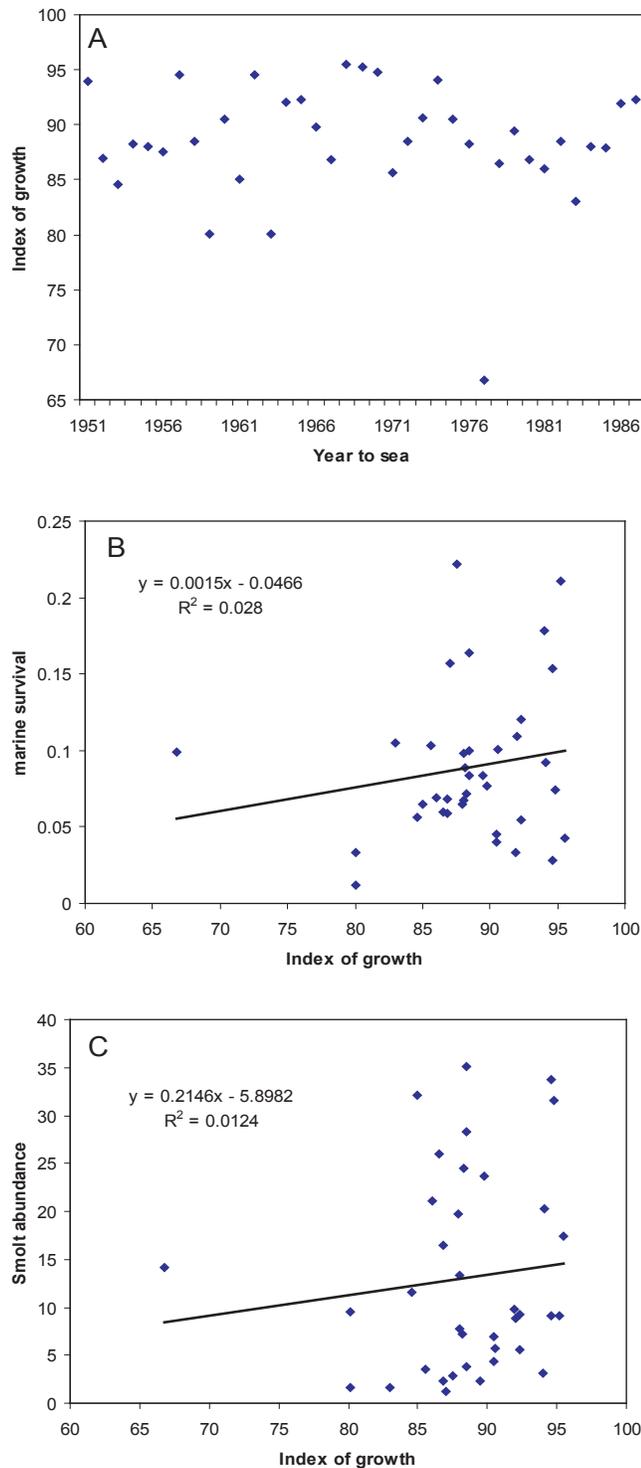
Fig. 4. Index of fish growth using scale measurements according to the methods of Henderson and Cass (1991) for sockeye salmon from Chilko Lake, British Columbia Canada. A: Index of the scale growth to the first circuli of the first marine annulus from scales removed from adult fish in fresh water. Brood year is two years earlier than the year to sea. B: The index of growth in (A) compared to the marine survival for the same brood year. C: The estimated abundance of smolts leaving Chilko Lake and the index of scale growth used in (A). Marine survival and smolt abundance data available from A. Cass (CassA@pac.dfo-mpo.gc.ca).

sented the mean scale length from the focus to the first circulus of the first marine annulus for 100 adults sampled for 37 years. The mean size of each sample was not related to the marine survival of that brood year ($R^2 = 0.028$, Fig. 4b) or to the mean size of smolts leaving the lake ($R^2 = 0.012$, Fig. 4c). The study showed that larger smolts leaving fresh water had higher survival than smaller smolts of that brood year. However, the size of adult fish at their first marine annulus was poorly related to survival. We suggest that the reason is that most of the size-related mortality had occurred prior to the first ocean annulus. The sizes in Fig. 4, as indexed by the scale measurements, are the critical sizes for this population of sockeye salmon. Large size when leaving fresh water improves survival, but it is the individuals that achieve the critical size in the ocean that make it through the first ocean winter.

These analyses provide growth after the first year at sea. If the species of salmon under investigation does not spend time growing in fresh water (i.e., pink and chum salmon), then the measurement of growth during the first year at sea provides the total size of the fish. However, examination of growth during the first summer growing season for species that spend one or more years rearing in fresh water does not provide the total size of the fish after the first summer at sea. As shown above for sockeye salmon from the Egegik and Kvichak rivers, size of juvenile sockeye salmon differs between river systems and freshwater age groups. Further, it is likely that the larger size of freshwater sockeye salmon from the Egegik River correlates to higher survival for these fish (i.e., Henderson and Cass 1991). Thus, freshwater growth may be an important component of size after the first year at sea and not including it may confound the importance of a critical size after the first summer at sea.

Evidence for Critical Period

One other test of the critical size, critical period hypothesis is that mortality after this period should be large relative to other sources of early marine mortality (Beamish et al. 2004). Estimates from the literature of marine mortality of coho, pink, and sockeye salmon at different early marine life-history stages are shown in Table 1. Estimates of early marine mortality of PWS pink salmon were not provided by Moss et al. (2005), thus, to estimate marine mortality, we used data on hatchery pink salmon releases and returns provided by the PWS Aquaculture Corporation, Cordova, AK. Our summer abundance indices of hatchery PWS pink salmon come from surveys conducted during August 2001 by the Ocean Carrying Capacity Program (Farley et al. 2001). Otoliths of pink salmon were examined to determine hatchery origin. Abundance indices for each hatchery followed the methods described in Farley et al. (2007) where the estimated survey area was 56,384 km². Information on distribution of juvenile PWS hatchery pink salmon indicated that 71% of these fish were still within PWS (Armstrong et al. 2005).

Table 1. Estimates of marine mortality during the first 40 days at sea, prior to mid-August, and after the first winter at sea for juvenile coho, pink, and sockeye salmon from various regions in the North Pacific Ocean. Catchability of 1.0 assumes every fish in front of the trawl net was caught. Catchability estimate of 0.3 for juvenile salmon is from Shuntov et al. (1993).

			Marine mortality		
Catchability	Species	Region	1st 40 days	Mid-August	Over-winter
1.0	Coho	Strait of Georgia, BC[1]			> 90%
1.0	Sockeye	Bristol Bay, Alaska[2]			66–84%
1.0	Pink	Prince William Sound Hatcheries, Alaska		> 93%	26–34%
Unknown	Pink	NE Kamchatka[3]	55–94%		55%–95%
Unknown	Pink	Bella Coola, BC[4]	55–77%		
0.3	Pink	Prince William Sound Hatcheries, Alaska		80–97%	67–78%
0.3	Sockeye	Bristol Bay, Alaska			20–30%
0.3	Coho	Strait of Georgia, BC			> 90%

[1]Beamish et al. 2004; [2]Farley et al. 2007; [3]Karpenko 1998; [4]Parker 1968.

Therefore, we appropriately expanded our estimates on the shelf to reflect those fish still in PWS.

Conservative estimates, assuming the catchability of our net is 1, for over-winter mortality of PWS hatchery pink salmon ranged from 26% to 34% (Table 1). These estimates are lower than the conservative estimates of the post-summer mortality for juvenile Bristol Bay sockeye salmon which ranged from 66% to 88% (Farley et al. 2007). Conservative estimates of over-winter mortality for PWS pink salmon were also lower than those estimated for Strait of Georgia coho salmon (> 90%) and northeast Kamchatka pink salmon (from 55% to 95%). However, if catchability were lower, (i.e. 0.3 as suggested by Shuntov et al. (1993), then estimates of mortality for PWS pink salmon increase to > 70% and are more in line with estimates for Strait of Georgia coho salmon and northeast Kamchatka pink salmon (Table 1). In either case, it is apparent that the over-winter mortality estimates for juvenile Pacific salmon from various locations in the North Pacific are substantial and indicate a need for greater understanding mechanisms that may impact growth of juvenile salmon during their first year at sea.

There is evidence that juvenile Pacific salmon in their first ocean year will use lipids for growth early in the marine period (MacFarlane and Norton 2001), but have their highest energy content later in the summer (Yerokhin and Shershneva 2000), an indication that fish store energy prior to winter. The mechanism that alters the use of lipids is not known, but it may be related to day length or it may be related to size. A critical period would be the date that would ensure that sufficient lipids were accumulated to provide energy needed during the winter. If the mechanism that changes the utilization of lipids is only partly related to size, smaller fish would not be able to compensate for their small size after the end of the critical period. Presumably, there may be a relationship with winter ocean conditions. However, in general, it may

be possible to identify a time in the summer when fish of a certain minimal size have a defined probability of surviving average winter conditions.

A critical size, critical period relationship to marine survival is a reflection of the carrying capacity of an ecosystem. A recognition that insufficient growth in the first marine spring and summer probably will result in death during the winter is also recognition that there is a matching of numbers of juveniles entering the ocean with the prey that is immediately available to juvenile salmon. Natural regulation in the absence of fishing or hatcheries would result in reduced adult returns in periods of reduced prey production and large returns in periods of favourable ocean environmental conditions. In managed populations, it should be possible to use early marine growth to optimize the production of smolts entering the ocean and to forecast marine survival. Producing too many smolts during years with low ocean productivity simply results in salmon dying in the first marine winter either directly from starvation or indirectly by being easy prey.

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