

Evidence That Reduced Early Marine Growth Is Associated with Lower Marine Survival of Coho Salmon

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Abstract.—Coho salmon *Oncorhynchus kisutch* from the Strait of Georgia were used to test the hypothesis that slower growing fish in their first ocean year had lower survival over the late fall and winter than faster growing fish. The Strait of Georgia provided a suitable area for this study because it is a semi-enclosed rearing area for juvenile Pacific salmon that is distinct from the open marine rearing areas off the west coast. Coho salmon that survived the winter had significantly larger spacing between circuli on scales, indicating that brood year strength is related to growth in the first marine year. Other studies have shown that smaller fish of a cohort are less able to survive periods of energy deficit than larger fish. Thus, size-related mortality in the first marine fall and winter may be an important determinant of brood year strength of some coho salmon stocks and stocks of other species of Pacific salmon.

In previous publications we proposed that most natural marine mortality of Pacific salmon *Oncorhynchus* spp. in general and coho salmon *O. kisutch* in particular occurred in two major episodes (Beamish and Mahnken 1999, 2001). The first episode, predation in the early marine period, is commonly believed to be the major determinant of brood year size (Parker 1968; Pearcy 1992). We hypothesized that a second major episode of mortality occurred later in the year and was related to growth. According to our hypothesis, Pacific salmon had to achieve a sufficient size by the end of the first marine summer to be able to survive the metabolic demands during a period of energy deficit in the late fall and winter. This critical-size and critical-period hypothesis linked natural mortality directly to the productivity of the ocean ecosystem and indirectly to climate and climate change.

We examined scales of coho salmon to assess size-dependant mortality. The spacing between circuli is an index of relative growth among individuals within a cohort because scale growth and circuli formation are a permanent record of growth

(Fisher and Pearcy 1990; Friedland and Haas 1996; Friedland and Reddin 2000). We selected coho salmon because of their short life span in the ocean and because we were able to sample a population in their first and second years in the ocean. In 2000 and 2001 we were able to study a relatively large and discrete brood year of coho salmon throughout their marine phase in the Strait of Georgia, which is located on the west coast of Canada between Vancouver Island and the British Columbia mainland.

Coho Salmon Biology

Coho salmon spawn in freshwater in the late fall, and eggs hatch in the following spring (Sandercock 1991). Most coho salmon spend the next year in freshwater and enter the ocean late in the following spring. Some coho salmon may spend 2 years in freshwater, but these fish are relatively rare in the Strait of Georgia; for example, about 70% of the juvenile coho salmon in this area are from hatcheries that release their fish after 1 year (Sweeting et al. 2003). Coho salmon spend about 16–18 months in the ocean before they return to spawn in freshwater in their natal rearing areas. The recent behavior of coho salmon in the Strait of Georgia differs from the behavior reported in Healey (1980). Coded wire tag data indicated that

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most juvenile coho salmon remained in the Strait of Georgia until about September (Beamish and Sweeting 1999). From 1995 to 2000 virtually all ocean-age-0 coho salmon left the Strait of Georgia in the late summer and fall. Maturing, ocean-age-1 coho salmon did not return to the Strait of Georgia until the late summer of the following year (Beamish et al. 1999). It was not until 2001 that maturing coho salmon returned to the Strait of Georgia in the spring, providing us with the opportunity to test our hypothesis. Another change from the observations of Healey (1980) was an increase in the percentage of hatchery-reared coho salmon from less than 20% during Healey's study to about 70% (Sweeting et al. 2003). Coded wire tag studies indicated that these coho salmon are from hatcheries around the Strait of Georgia or around Puget Sound (Sweeting et al. 2003). Virtually no hatchery-reared coho salmon in the Strait of Georgia are from any other hatcheries.

Importance of Size during First Marine Winter

In general, weight-specific rates of energy use decline with increasing size for a wide range of animals (Calder 1984; Schmidt-Nielsen 1984; Shuter and Post 1990). Thus, larger individuals are better able to survive periods of starvation or energy deficits than smaller individuals because larger fish deplete their energy reserves less rapidly than smaller fish. This emphasizes the importance of growth during the first summer because Pacific salmon are at their smallest size entering the first ocean winter compared with sizes at subsequent winters. Thus, factors that reduce growth during the spring and summer and factors that increase the period of energy deficit in the late fall and winter would contribute to size-related mortality. There is evidence from controlled feeding experiments that mortality occurs directly from physiological changes (Oliver et al. 1979; Mahnken et al. 1982). Therefore, it would not be necessary to be killed by a predator, although the moribund fish may become easy prey for another species.

Methods

Ocean-age-0 coho salmon (1998 brood year) were collected from the Strait of Georgia using a large pelagic trawl net that was fished from a high-powered research vessel (Beamish et al. 2000a). Males maturing in their first marine year (jacks) were excluded from the analysis because they would return to freshwater before the first marine

winter. Scales were selected from the preferred area below the dorsal fin and above the lateral line. Scales were taken from the same preferred area from ocean-age-1 coho salmon (1998 brood year collected in the Strait of Georgia from March to September 2001) via commercial troll gear, except for the March sample that was from a trawl. Scales from ocean-age-1 coho salmon of the same brood year were also collected from adult coho salmon returning to the two hatcheries that release the largest numbers of coho salmon smolts into the Strait of Georgia. Big Qualicum Hatchery is located on Vancouver Island on the west side of the Strait of Georgia. Chilliwack Hatchery releases coho salmon into the Fraser River, which enters the Strait of Georgia on the east side.

The scale samples were stored in scale books, which were later used to make acetate impressions. Only scale impressions with a well-defined focus were used. Acetate impressions were viewed and digitized using a Bioscan Optimas image processing system. A line was drawn from the focus to the edge of the scale, such that the line was approximately perpendicular to the circuli. This position was similar to the 360° axis reported by Friedland and Haas (1996). Individual circuli were marked, and the distances between circuli were measured electronically. The freshwater annulus was identified, and any closely spaced circuli that formed in freshwater after this annulus were noted. The first widely spaced circuli pair after the narrowly spaced circuli was considered to be the first ocean intercirculi space. The first ocean circulus appeared wider and more robust than the last freshwater circulus.

Results

We analyzed 47 scales from 1,497 ocean-age-0 coho salmon (1998 brood year) captured in the Strait of Georgia in September and 40 scales from a catch of 138 in November 2000 (Table 1). After the winter of 2000–2001, 184 scales were analyzed from ocean-age-1 coho salmon (1998 brood year) from the Strait of Georgia and 102 scales from fish collected at the hatcheries (Table 1). In our sample of 87 ocean-age-0 and 184 ocean-age-1 coho salmon captured in the ocean, 43% and 47%, respectively, were missing adipose fins. The length frequency of the 40 coho salmon used in the ocean-age-0 November 2000 sample for scale analysis was not significantly different from the length frequency in the total catch of 138 coho salmon (*t*-test, $P > 0.05$). However, the mean length of the 47 fish used for scale analyses in the September

TABLE 1.—Sample size, average coho salmon fork length, and average intercirculi space of two ocean-age-0 samples collected in 2000 and six ocean-age-1 samples collected in 2001.

Date or hatchery	Ocean age	Number collected	Number sampled	Average \pm SD fork length (mm)	Average \pm SD intercirculi space (mm)
Sep 2000	0	1,497	47	254.4 \pm 17.22	0.037 \pm 0.004
Nov 2000	0	138	40	271.4 \pm 21.99	0.039 \pm 0.005
Mar 2001	1	32	32	327.6 \pm 18.76	0.040 \pm 0.004
Jul 2001	1	320	50	497.6 \pm 23.46	0.042 \pm 0.004
Aug 2001	1	231	50	532.9 \pm 28.96	0.041 \pm 0.004
Sep 2001	1	201	50	541.4 \pm 32.19	0.040 \pm 0.003
Chilliwack Hatchery	1	79	52	629.6 \pm 64.4	0.043 \pm 0.005
Big Qualicum Hatchery	1	50	50	609.5 \pm 62.01	0.044 \pm 0.003

2000 sample (254 mm) was significantly larger than the mean length (247 mm) of the total catch of 1,497 coho salmon (t -test, $P < 0.01$).

The scale length–fish length relationship for all ocean-age-0 and ocean-age-1 coho salmon used in the analysis was strongly linear (F -test, $P < 0.05$; $r^2 = 0.94$). The number of circuli that formed in

the ocean for the September 2000 sample of ocean-age-0 fish ranged from 15 to 30 (mean 22, SD = ± 3.6). The mean width of the first 10 intercirculi spaces was not significantly different from the first 15 intercirculi spaces or the first 20 circuli (analysis of variance [ANOVA], $P > 0.05$). Therefore, we used the circuli spacing for the first 10 spaces as a measure of scale growth.

The average intercirculi spacing of the first 10 circuli in the September and November samples was not significantly different (t -test, $P > 0.05$), so we combined the two samples. The ocean-age-0 fish in 2000 (1998 brood year) showed a significant correlation between capture length and average circuli spacing of the first 10 intercirculi spaces, although the relationship was weak ($r^2 = 0.26$, $P < 0.01$). The frequency distribution of average circuli spacing of the first 10 intercirculi spaces for ocean-age-0 fish from the September and November 2000 samples (Figure 1) was normal (mean = 0.038 ± 0.004 mm; Kolmogorov–Smirnov test, $P > 0.05$). The frequency distribution of the mean width of the first 10 ocean intercirculi spaces for the ocean age-1 fish was also normal for each sample and for the aggregate (mean 0.042 ± 0.004 ; Kolmogorov–Smirnov test, $P > 0.05$; Figure 2). There was a significant difference in the mean intercirculi widths of the first 10 intercirculi widths for the six ocean-age-1 samples (ANOVA, $P = 0.022$). However, the mean intercirculi space of each of these six samples was significantly larger than the average intercirculi space of the ocean-age-0 sample (t -test, $P < 0.05$).

The intercirculi spacing of the July sample and the two hatchery samples were similar and larger than the other samples. Therefore, we made three comparisons with the ocean-age-0 fish, using (1) all ocean-age-1 samples, (2) the July plus the hatchery samples, and (3) the remaining sample of ocean-age-1 fish (total sample minus July plus

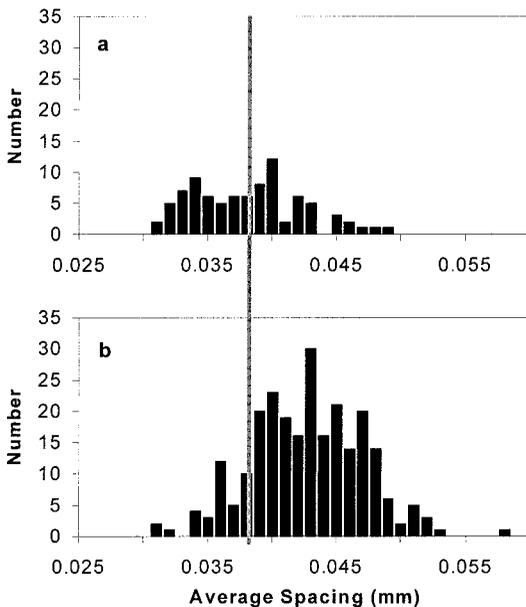


FIGURE 1.—The distribution of the average circuli spacing of the first 10 saltwater circuli from (a) ocean-age-0 coho salmon collected in the Strait of Georgia in September and November, 2000 (mean 0.038, SD 0.004; brood year 1998) and (b) ocean-age-1 coho salmon collected in March, July, August, and 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.

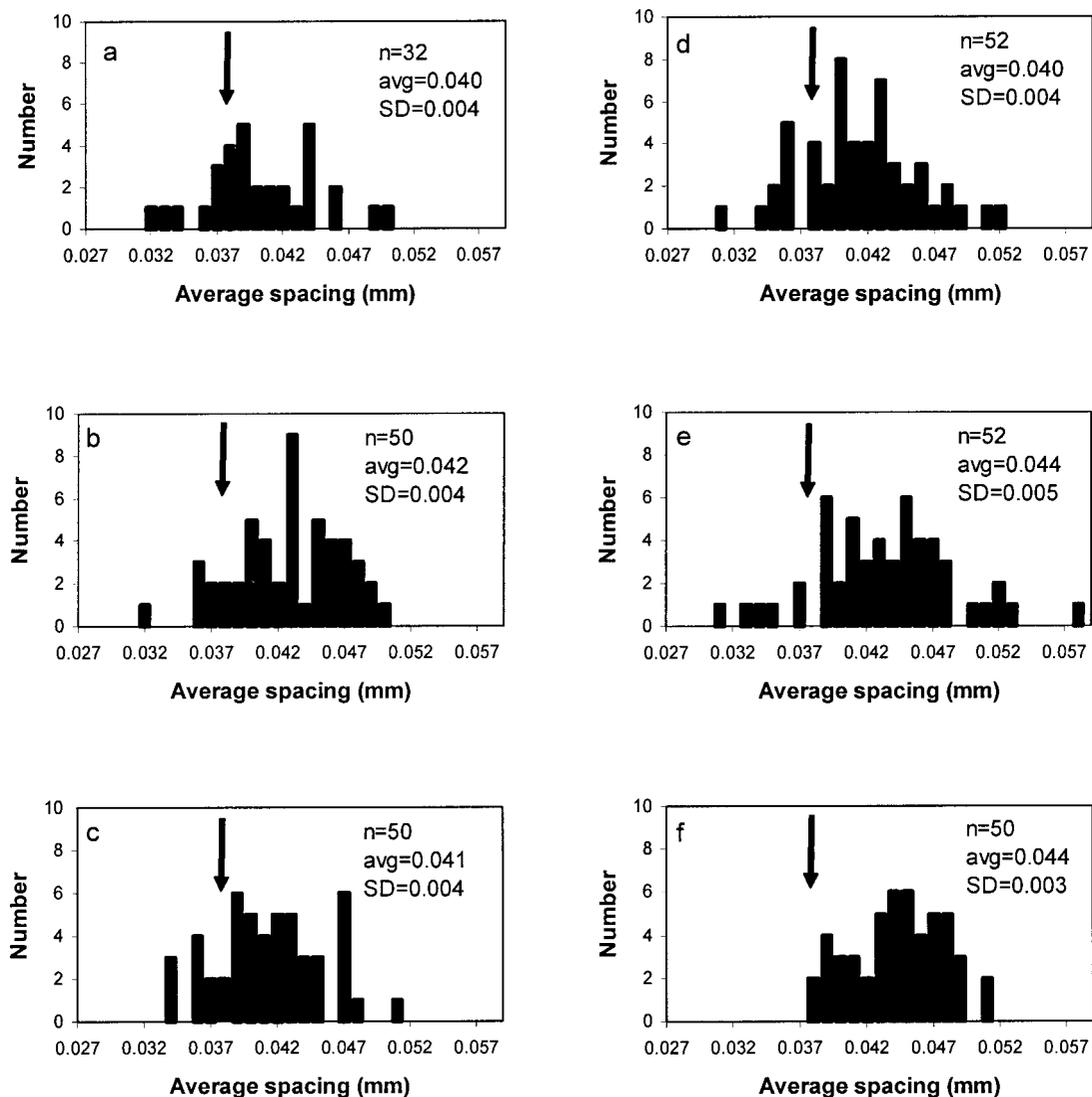


FIGURE 2.—The distribution of the average circuli spacing for the first 10 saltwater circuli from ocean-age-1 coho salmon (brood year 1998) collected from the Strait of Georgia in (a) March 2001, (b) July 2001, (c) August 2001, and (d) September 2001 and from the (e) Chilliwack Hatchery and (f) Big Qualicum Hatchery. The arrow identifies the mean intercirculi space from the ocean-age-0 sample.

hatchery samples). The mean intercirculi space for the first 10 ocean intercirculi widths of the aggregate of all ocean-age-1 fish was significantly larger than the mean intercirculi space for ocean-age-0 coho salmon sampled from the same population in the previous year (t -test, $P < 0.01$; Figure 2). The intercirculi spacing of the first 10 ocean circuli for the July plus hatchery sample and remaining sample of ocean-age-1 fish were also significantly larger than the corresponding spacings for the ocean-age-0 sample (t -test, $P < 0.05$). For the total sam-

ple, 65% of the ocean-age-1 fish had intercirculi spacings observed in only the largest 25% of the ocean-age-0 fish (Figure 1).

A small number of the hatchery-reared coho salmon were tagged with a coded wire tag. In September and November 2000, 78 of the ocean-age-0 fish captured had coded wire tags, of which 81% were from Canadian hatcheries around the Strait of Georgia and 19% were from U.S. hatcheries around Puget Sound. In July 2001, 12 of the 320 ocean-age-1 fish (Table 1) had a coded wire tag,

of which 83% were from some of the same Canadian hatcheries around the Strait of Georgia as observed in 2000. The remaining 17% were from hatcheries in Puget Sound. In 2001, 7 coho salmon with coded wire tags were detected in the August and September samples, but these tags were not recovered. In 2000 and 2001, no coded-wire-tagged fish were observed from any location outside of either Puget Sound or the Strait of Georgia.

Discussion

The comparison of circuli spacing between coho salmon from the Strait of Georgia population in their first and second marine years showed that a significantly larger number of fish with the widest circuli spacing survived over the late fall and winter. Approximately 65% of the ocean-age-1 coho salmon in the Strait of Georgia in 2001 had mean circuli spacing that was observed in the 25% of the fish with the widest spacing in the previous year, indicating that more of the larger fish survived the first marine winter. We propose that the ocean-age-1 coho salmon sampled in 2001 are from the same population sampled in 2000.

Because about 70% of the coho salmon in the Strait of Georgia are from hatcheries (Sweeting et al. 2003), we included samples of ocean-age-1 fish from the two largest hatcheries that combine to produce 39% of all hatchery-reared coho salmon. The mean intercirculi spacing in these two samples was 0.043 mm and 0.044 mm (Figure 2e, f), which was larger than the aggregate of all six samples (0.042 mm; Figure 1b) and significantly larger than the spacing observed in the previous year. Clearly, the coho salmon that returned to these two hatcheries were larger than the average size of the juveniles sampled in the previous year, as indicated by their intercirculi spacing.

The other four samples of ocean-age-1 coho salmon had a percentage of missing adipose fins of 57, 47, 44, and 40% or a combined percentage of 45%, that was similar to the percentage of 43% observed in the ocean-age-0 catch of juveniles in the previous year. This is an indication that the population sampled in the Strait of Georgia in 2001 had a percentage of hatchery fish very similar to the percentage in 2000. The similarity in the percentages also indicates that the mortality over the late fall and winter was not selective for rearing type. The average intercirculi spacing in these four samples varied, but all average spacings were significantly larger than observed in the juveniles in the previous year. In 2001 the 12 coded-wire-tagged coho salmon recaptured in the July sample

were from hatcheries around the Strait of Georgia or Puget Sound, and the percentage from Canadian hatcheries was similar to the percentage observed the previous year. Although this was a small sample of tags, it provided additional evidence that the coho salmon sampled in 2001 were from the same population as those sampled in 2000.

In general, the inclusion of two hatchery samples in the aggregate of ocean-age-1 coho salmon in 2001, the similarity in the percentage of adipose clipped-fish in the samples in 2000 and 2001, and the coded wire tag observations are evidence that the same population was sampled in 2000 and 2001. In the September sample used for scale analysis of ocean-age-0 fish, the mean size of the fish was larger than the total sample from the trawl catches. Because larger fish had better survival over the winter, larger fish in the scale sample would tend to reduce the difference in mean circuli spacing between ocean ages 0 and 1. Thus, the larger fish in the September ocean-age-0 sample would not affect the observation of a significant difference in circuli spacing between ocean-age-0 and ocean-age-1 fish.

Scale Growth versus Fish Length

There was a strong relationship between scale length and fish length. This was expected because scales function to protect the fish; however, confirmation of this relationship is also verification of the reliability of the measurements. Bilton and Jenkinson (1977) compared the average spacing between the circuli in the first and second ocean years for 155 coho salmon grouped into 6 lots according to different release strategies into the Strait or Georgia. In all but one case, the final length of adults was significantly correlated with circuli spacing, indicating that wider intercirculi spacing was associated with a larger size of adults at capture. We also observed that ocean circuli spacing was related to fish length. Other studies have confirmed that the spacing between circuli is an index of growth for coho salmon (Fisher and Percy 1990), sockeye salmon *O. nerka* (Bugaev 1984; Barber and Walker 1988), pink salmon *O. gorbuscha* (Bilton 1966), and other fish species (Doyle et al. 1987). In some studies this relationship is simply assumed (Friedland et al. 1993) because it appears self-evident that the faster-growing fish will have wider spacing. Thus, there is an established literature that relates increased circuli spacing to increased size. The observation that the spacing of the first 10 circuli was not only an index of the growth rate through mid-September but also

of survival over the winter was surprising because it indicated that growth-based marine survival could be determined as early as July of the first marine year for some individuals.

Changes in Abundances Overwinter

The critical-size and critical-period hypothesis posits that brood year survival is determined by the number of fish in the population of ocean-age-0 coho salmon that have grown to critical size by the late fall and stored enough energy to survive periods of energy deficit over the late fall and winter. However, for this mortality to be important, it is necessary to show that the mortality that occurs is large relative to other sources of early marine mortality. We showed in Beamish et al. (2000a) and Beamish and Mahnken (2001) that abundances of juvenile coho salmon in the Strait of Georgia in September were large relative to the abundances of fish that returned as adults. Estimates of abundances in September were considered to be minimal estimates (Beamish et al. 2000a) and varied from 2,978,000 ($\pm 1,283,000$) in 1997, 3,037,000 ($\pm 1,370,000$) in 1998, and 4,642,000 ($\pm 1,370,000$) in 1999. If the catchability of the net was not 1, as assumed, but less, as is probable, the abundance estimates would be larger, perhaps double. The total returns in 1997, 1998, and 1999 can be approximated by using estimates of marine survival from Simpson et al. (2002) and the total Canadian smolt production from the Strait of Georgia (Sweeting et al. 2003). Conservative estimates of marine survival would be approximately 2% (Beamish et al. 2000b) and total releases would be approximately 15 million smolts (Sweeting et al. 2003). Therefore, adult returns would be about 300,000. If the abundance estimates that are considered to be minimal are compared with these total estimated returns, then the fall and winter mortality approximates 90%. If the true abundance estimates are double our estimate (Beamish et al. 2000a), then the fall and winter mortality exceeds 90%. Thus, it is clear that the mortality that occurs over the fall and winter is a major factor in determining final brood year abundance.

Other Studies of Size-Related Mortality in the First Winter

The observation that small fish have higher mortalities than larger fish in their first winter appears to be well-known (Lindroth 1965; Hunt 1969). Cowan et al. (2000) reviewed studies of density-dependent growth in young-of-the-year fishes and proposed that density-dependent regulation is

more likely to occur in the late larval or juvenile stage for both marine and freshwater fishes. Their critical-weight hypothesis proposes that density-related food limitation is more likely to occur after a "critical weight" is achieved. This concept is similar to our hypothesis that mortality late in the first marine year is an important component of the total natural mortality. Their critical weight concept differs from our hypothesis because we propose that there is a critical period around the time of the fall equinox during which growth-based mortality begins to be expressed. If it is confirmed that circuli spacing before the end of July is an index of marine survival over the winter, then the critical period could be as early as the summer solstice, when day length begins to shorten. Friedland and Haas (1996) showed that wider circuli spacing in the first ocean year of Atlantic salmon *Salmo salar* was related to earlier maturity. In laboratory studies, Sogard and Olla (2000) showed that age-0 walleye pollock *Theragra chalcogramma* could survive extreme winter conditions as long as sufficient body size was obtained during the summer. Early juvenile growth of walleye pollock was an important determinant of survival during periods of low food availability, such as during the first winter. Energy reserve depletion generally varied inversely with size for the Atlantic silverside *Menidia menidia* under winter conditions (Schultz and Conover 1999). Small and large age-0 largemouth bass *Micropterus salmoides* had similar percentages of lipids in the late fall, but over the winter, the smaller fish used the lipid reserves at a faster rate (Miranda and Hubbard 1994). Mortality of these smaller fish was accelerated in the late fall and winter, resulting in a decrease in abundance that was seven times greater than for the larger fish. Winter mortality of age-0 white perch *Morone americana* was strongly influenced by body size, winter duration, temperature, and food availability (Johnson and Evans 1990). Oliver et al. (1979) carried out laboratory studies to determine if there was a critical weight or energy level that would define the level at which smallmouth bass *Micropterus dolomieu* would not survive the first winter. Although these critical levels were not identified, the investigators did confirm that the longer fish survived the winter better than shorter fish. Mortality was physiological because no predators were used in the experiment. The northern limits of distribution for Eurasian perch *Perca fluviatilis* and smallmouth bass were shown to be related to an inability to store sufficient energy to survive the period of energy deficit during the win-

ter (Shuter and Post 1990). The beginning of a period of energy deficit was proposed to be cued by a factor such as temperature or day length, or perhaps the loss of stratification in the water column.

Our hypothesis of a critical size and critical period for growth in the first ocean year is consistent with the results of Foy and Paul (1999) for age-0 Pacific herring *Clupea pallasii* in Prince William Sound. They observed a decline in the nutritional status of recruiting Pacific herring over the winter. The decrease in total zooplankton biomass contributed to a net energy loss (energy gained from feeding minus energy lost to metabolism). Juvenile Pacific herring depended on their stored energy to survive the winter, smaller fish being more affected by starvation than larger fish. Foy and Paul's study identified a process for overwinter survival that is virtually identical to the process we propose for growth-based overwinter mortalities for Pacific salmon, in general, and coho salmon in particular. Interestingly, Foy and Paul (1999) also proposed that the duration of the winter starvation period may be more related to the length of day than to temperature.

Management Implications

Our study identified a disproportionate loss of smaller coho salmon over the late fall and winter, indicating that a critical-size and critical-period hypothesis is valid, at least for coho salmon in this one brood year. Other studies also showed that smaller fish of a cohort are less able than larger fish to survive periods of energy deficits or starvation during the late fall and winter. Thus, density-related processes that reduce growth through competition or density-independent processes that reduce growth through reduced prey production may contribute to increased total marine mortality and, thus, decrease the abundance of adults. We recognize that our study is of one brood year of coho salmon from one ecosystem. However, there are a number of other studies, as previously indicated, that have identified a relationship between reduced growth and decreased survival during periods of energy deficit, such as during the winter. Thus, there is evidence from other studies that changes that reduce the productivity of an ecosystem and reduce growth of juvenile Pacific salmon could also decrease their marine survival. This is important because climate can affect the productivity of Pacific salmon (Beamish and Bouillon 1993) and this means that the sur-

vival of Pacific salmon can be affected by alterations to the atmosphere, as well as to water.

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