A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change

R.J. Beamish [a,*], Conrad Mahnken [b]

[a] *Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC, V9R 5K6, Canada*
[b] *National Marine Fisheries Service, 7305 Beach Drive East, Port Orchard, WA 98366, USA*

Abstract

We hypothesise that salmon year class strength is determined in two stages during the first year in the ocean. There is an early natural mortality that is mostly related to predation, which is followed by a physiologically-based mortality. Juvenile salmon that fail to reach a critical size by the end of their first marine summer do not survive the following winter. In this study we describe our initial tests of this critical size and critical period hypothesis using data from ocean surveys of juvenile salmon and from experimental feeding studies on coho. Conservative swept volume abundance estimates for juvenile coho, and possibly chinook, indicate that there is high mortality in fall and winter during their first year in the sea. Studies of otolith weight show that the length and otolith-weight relationship for young coho changes in the early fall of their first ocean year. Studies of growth and associated hormone levels in feeding studies show that slow growing juvenile coho are stunted and deficient in an insulin-like growth factor-I (IGF-I). Juvenile coho sampled in September had low IGF-I values, indicative of poor growth. The results of these studies provide evidence for the general hypothesis that growth-related mortality occurs late in the first marine year and may be important in determining the strength of the year class (brood year). The link between total mortality and climate could be operating via the availability of nutrients regulating the food supply and hence competition for food (i.e. bottom–up regulation). © 2001 Elsevier Science Ltd. All rights reserved.

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* Corresponding author. Fax: +1-250-756-7141.
    E-mail address: beamishr@pac.dfo-mpo.gc.ca (R.J. Beamish).

1. Introduction

Climate and associated ocean ecosystem changes affect the abundance trends of Pacific salmon (Beamish et al., 1999; Mantua, Hare, Zhang, Wallace, & Francis, 1997). The failure of increased numbers of hatchery-reared smolts to boost the numbers of adults (Coronado & Hilborn, 1998; NRCC, 1996) demonstrates that it may not be the numbers of smolts entering the ocean that is limiting production. However, how climate and climate change cause these fluctuations in abundance is unknown. In this paper we are proposing a new hypothesis to explain these linkages. Our hypothesis is that numbers of returning Pacific salmon are linked to fluctuations in climate and ocean environment through growth. The regulation of the final abundance (total returns) occurs in two major stages. The first phase in marine mortality is mostly predation-based and occurs immediately after the smolts enter salt water. It is well known that rates of mortality are high at this stage (Parker, 1968) and partly related to size (Pearcy, 1992). We propose that there is a second subsequent period of major mortality in the fall and winter of the juvenile salmons' first year at sea, when those indiviuals that have not attained a critical size die, because they are unable to meet minimum metabolic requirements. We call our idea of a fall–winter growth-based mortality the 'critical size and critical period hypothesis'. According to our hypothesis, growth-based mortalities may occur throughout the summer, but mortalities predominantly occur after the summer of their first marine year (Fig. 1). A moribund animal may be more vulnerable to predators, or it may simply sink to the sea floor where it is consumed by scavengers. Here we describe the results of our initial tests of our hypothesis. We expect to continue with these studies and hope to encourage others to study the relationship between marine growth rates and marine survival because of the importance of understanding how climate and climate change will affect the productivity not only of salmon but also other commercial fishes.

2. Methods

We use results from research on coho, chum and chinook salmon from the Strait of Georgia, British Columbia, Canada (Fig. 2) to test our hypothesis. We compare the abundance of smolts in the late summer to the total returns, and the number of juveniles entering the ocean. Coho salmon return in their second year at sea, so they provide a rapid method of assessing the importance of fall and winter mortality relative to the early spring and summer mortality. If abundances in late fall are high relative to the total numbers of smolts entering the ocean, and also high relative to the total returns, then mortality in fall and winter is important relative to the
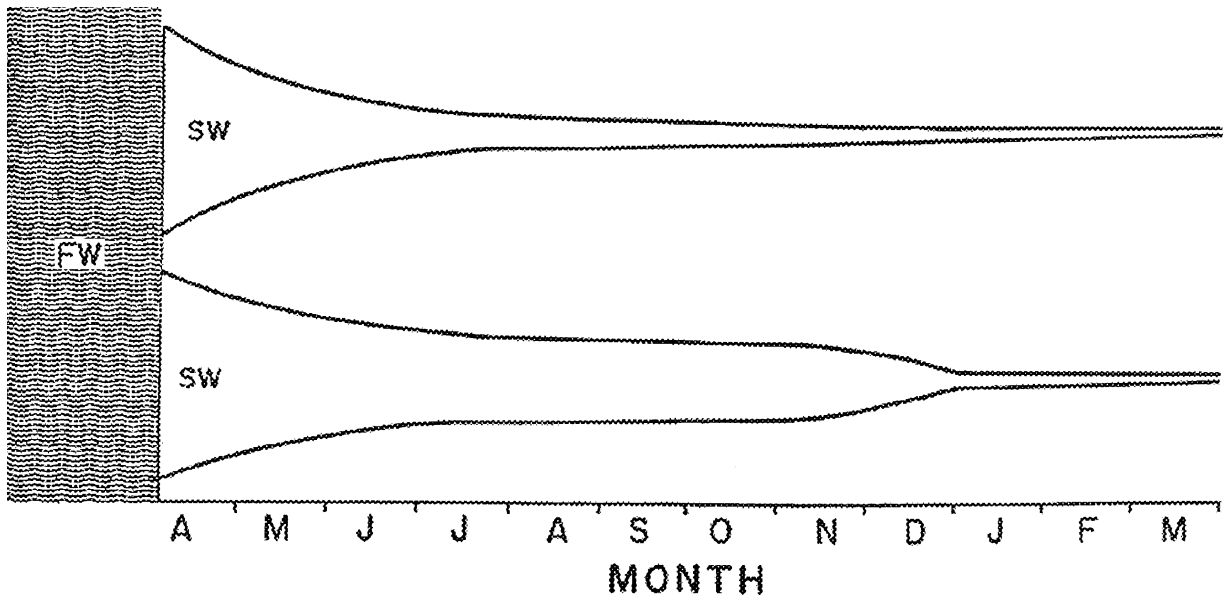
Fig. 1. A representation of the natural process that could determine the total number of salmon that survive in the ocean and return to spawn. In the upper panel the abundance of juveniles is greatly reduced immediately after juveniles leave fresh water (FW). By mid-July in salt water (SW) predation mortality after this period is relatively minor and there is little change in trend in the winter. In the lower panel, predation mortality accounts for about one half the loss in abundance by mid-July. There is minimal mortality until about mid-October when a second growth-based mortality occurs. The year-class size is virtually determined during the winter. Some mortality would occur after the first marine winter, but is small relative to the earlier mortalities. It is the second, growth-based mortality that links climate and salmon production, naturally.

earlier mortality. This means that the total marine mortality of juveniles has two important components, an early and a later phase of mortality, which we propose are driven by different mechanisms.

The survey design and the procedure for estimating abundances have been described in Beamish, McCaughran, King, Sweeting, and McFarlane (2000). The volume of water fished was calculated and the numbers of fish captured were standardised to a one hour tow. The survey design (Fig. 2) followed a pattern of fixed transects to facilitate comparisons between years. The daily tows were randomised among depth strata according to a stratified design that allocated the most tows to the upper 30 m of the water column. The total number of tows taken was a compromise between the amount of available ship time, and the need to keep the total catches of juveniles within reasonable limits. The rope trawl used in the surveys fished approximately 21 m deep and 64 m wide (Beamish & Folkes, 1998) and was smaller than standard rope trawls to ensure that individual catches were not too large. In general, the September surveys consisted of an average of 102 tows in which approximately 8000 individuals of all five species of ocean age-0 Pacific salmon were captured. The procedures for calculating abundance estimates are described in Beamish et al. (2000) and were based on the traditional swept volume procedures, similar to those used in Russian studies (Shuntov, Radchenko, Lapko, & Poltev, 1993). A major source of error is related to the efficiency or catchability of the net. We have assumed the catchability to be 1,
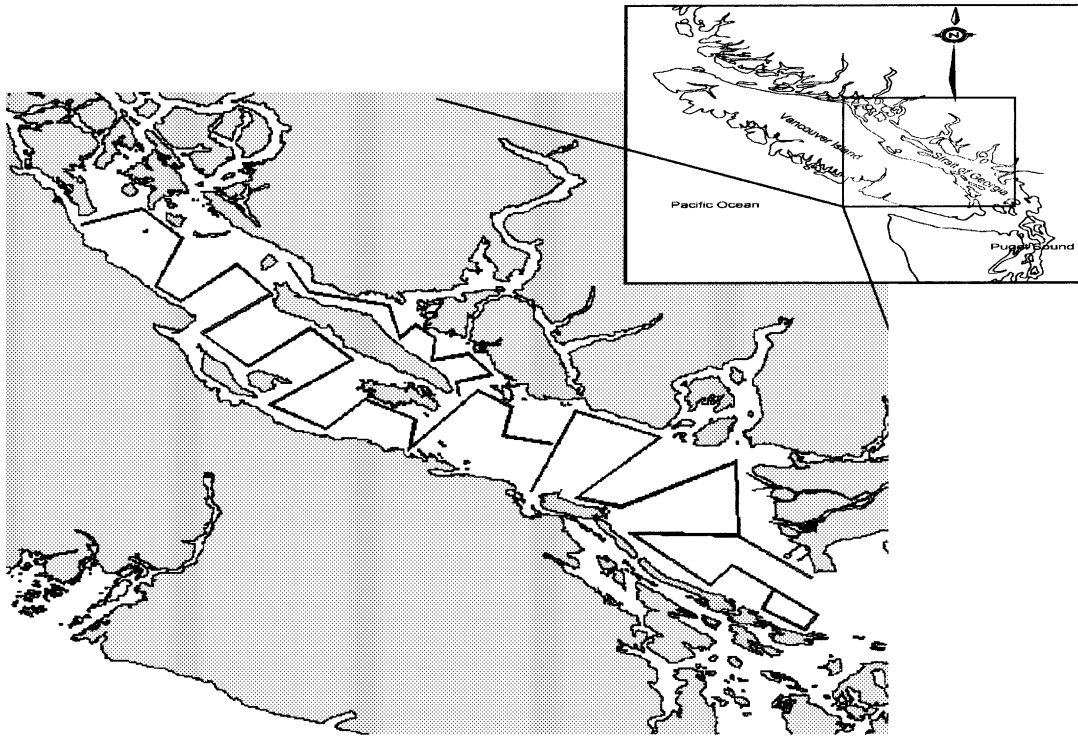
Fig. 2.   Location of the Strait of Georgia study area showing the track lines used in the surveys.

because we wanted to ensure that major biases would be towards lower abundances. In Russian studies (Shuntov et al., 1993), which have used larger nets, catchability of 0.3 has been assumed. If a similar assumption were to be applied to our study, our estimates would be more than doubled. At least 90% of the catch for chum was taken in the top 30 m, for coho in the top 45 m, and for chinook in the top 60 m. We have used only these depths in our abundance estimates, which also produces conservative estimates.

   Previous studies had suggested that juvenile coho do not migrate out of the Strait of Georgia until the fall, but that some age-0 chum and chinook have migrated out of the sampling area by this time (Healey, 1980). Previously (Beamish et al., 2000) we showed that tagged coho released into the Strait of Georgia are rarely found outside the survey area until after September. Thus, our abundance estimates were probably representative of the entire population of coho, but of an unknown fraction of the population of chum and chinook. The upper and lower bounds of the abundance estimates are ± two standard deviations intervals. It is important to note that the pur-pose of our abundance estimates is to compare the size of the population in the fall of the first marine year with the numbers entering the ocean and with the final, total returns. Thus, either having estimated the catchability to be too high, or not having sampled part of the chum and chinook populations because some have migrated out of the survey area will reduce the estimate and bias any conclusion toward rejection of our hypothesis.

   It should be straightforward to test size-related mortality if the juvenile fish remain in the Strait of Georgia. If there are no sampling problems, the size of the salmon that survive the winter can

be back-calculated to the late fall period using their scales. The hypothesis would be supported, if the smaller fish in the observed length frequencies in the fall samples were shown to be missing from the back-calculated lengths of the samples collected after their first winter at sea. However, juvenile salmon including coho leave the rearing area of the Strait of Georgia in the late fall (Beamish, Mahnken, & Neville, 1997) and mix with other juveniles from other areas making it difficult to sample a single population. An additional difficulty is that the large rope trawl used to catch salmon (Beamish & Folkes, 1998) rubs off most of the scales. So in this paper we have used otolith weights of the salmon collected in the Strait of Georgia in September and in October/November to gauge if there was a change in the otolith weight and fish length relationship that coincided with the time we propose the smaller fish may suffer mortality.

One hundred pairs of undamaged otoliths were randomly selected from the late summer samples (September) and autumn samples (October/November) collected in each of the three years. Each pair of otoliths was cleaned in about 1 ml of 0.1 N NaOH for 6–8 h. They were then cleaned by hand in distilled water, washed in 95% ethanol and heated for 15 h at 55–60°C. Each otolith was examined using 10× magnification to ensure that it was undamaged. Each otolith was weighed separately and averaged. If one was crystalline, it was rejected if its weight differed by more than 10% from the non-crystalline otolith, but this was seldom necessary.

Seasonal variation in the growth rates appears to be universal in temperate water teleosts (Perez-Sanchez, Marti-Palanca, & Le Bail, 1994). Somatic growth is promoted through the action of pituitary growth hormone (GH) and is mediated through secretion of insulin-like growth factor-I (IGF-I). It has been shown that in juvenile salmon maintained in salt water, low hepatic IGF-I expression is associated with low growth rate (Duan, Plisetskaya, & Dickhoff, 1995). Thus, IGF-I is an important hormone in mediating somatic growth, osmoregulation and germ cell proliferation in salmonid fishes. We have used unpublished IGF-I data supplied by Brian Beckman, (National Marine Fisheries Service). Beckman used the methods described by Shimizu, Swanson, and Dickhoff (1999) to measure IGF-I in the blood of coho collected in the Strait of Georgia and Puget Sound in September, 1998. The values determined from these coho collected in the ocean were compared with samples obtained from fish used in seawater feeding studies in the laboratory. These seawater experiments attempted to induce stunting in coho salmon through the regulation of their growth. Growth was controlled by diet in two 'populations', one fast growing, and the other slow growing. An identical replicate set of fast and slow growing populations was reared for physiological assessments. All the fish in each of the four populations were individually PIT-tagged in order to determine their individual instantaneous growth. Individuals from the first set of populations were periodically measured for growth and returned to the rearing container. IGF-I samples were taken from sacrificed animals, representing the range of sizes, in the replicate set of populations.

3. Results

3.1. Abundance and survival of juveniles

In general, the abundance estimates were similar among the three years, ranging from 3 to about 6 million individuals for each of the three species (Table 1). Coho abundances were almost

Table 1
Minimal juvenile salmon abundance in the late summer in the Strait of Georgia and the comparable smolt production and total returns

Date		Mean length (mm)	SD	n	Abundance (lower interval–upper interval)	Smolt production	Total returns
1999							
Aug. 31–Sept. 19	Coho	230	22	1438	4,642,000 (2,293,000–6,991,000)	12,500,000[c]	328,000[b]
	Chum	189	27	515	6,147,000 (2,778,000–9,515,000)	–[e]	–
	Chinook	173	44	1035	3,382,000 (2,443,000–4,103,000)	–	300,000
1998							
Sept. 8–26	Coho	241	29	840	3,048,000 (1,566,000–4,103,000)	14,900,000[b]	315,000[b]
	Chum	187	13	647	5,584,000 (3,766,000–7,403,000)	–	–
	Chinook	172	40	692	4,102,000 (2,764,000–5,253,000)	–	300,000
1997							
Sept. 8–27	Coho	246	21	911	2,978,000 (1,693,000–4,261,000)	13,500,000[c]	–
	Chum	186	23	526	5,229,000 (1,772,000–8,686,000)	–	1,600,000[a,d]
	Chinook	157	55	919	6,015,000 (4,697,000–7,334,000)	–	300,000

[a] 1994 year class or brood year, 1995 year-to-sea.
[b] Holtby, Simpson, Tanasichuk, and Irvine (2000).
[c] Beamish et al. (2000) (updated).
[d] Ryall, Bailey, and Palevmo (1999).
[e] Dash indicates no data.

identical in 1997 and 1998 at 3 million, and larger in 1999 at 4.6 million (Table 1). The estimated number of coho smolts from Canadian hatchery and wild stocks entering the Strait ranged between 12.5 and 14.9 million (Table 1). Our abundance estimates indicated that between 22 and 37% of these juveniles survived through to the late summer. The adult returns in 1998 and 1999 were from the juveniles that went to sea in 1997 and 1998, respectively. The returns for 1997 are not listed since these fish entered the ocean as juveniles in 1996 before we made abundance estimates. The returns in 1998 and 1999 suggest that there was post-September mortality of 97.9 and 97.4% in the two years.

The chinook abundances were 6.0, 4.1, and 3.4 million in 1997, 1998 and 1999, respectively. The majority of juveniles that left the rivers in 1997, 1998, and 1999 are not expected to return until 2000 or later. We have used estimates of the total 1999 returns of approximately 300,000 adult chinook to the populations around the Strait of Georgia (unpublished estimates by B. Riddell, Pacific Biological Station, Nanaimo, BC, Canada) representing more than 90% of the production. These returns indicate that between 91 and 95% of the juveniles in the abundance estimates in Table 1 died after September if returns were about 300,000 adults.

Estimates of chum salmon abundances increased from 5.2 to 6.1 million from 1997 to 1999. The juvenile chum abundances estimated in this study cannot be compared to total returns, which occur about 3 years after they entered the ocean. We have again provided an approximate comparison using the returns from previous years as was done for chinook. The total adult returns from the range of 5.2–6.1 million juveniles estimated in our study would be approximately 26–30% of our population estimates of juveniles (Table 1).

3.2. Otolith weights

In September, the otolith weight and fish length relationship (Table 2) was weakly linear in all years r^2=0.21, 0.52, 0.37, for 1997, 1998, 1999, respectively with positive slopes of 0.1×10^{-4}, 0.2×10^{-4} and 0.2×10^{-4} for 1997, 1998 and 1999, respectively. Therefore, in September, larger fish had heavier otoliths [Fig. 3(A)]. However in October/November, this relationship changed [Fig. 3(B)] (r^2=0.01, 0.28, <0.00 for 1997, 1998, and 1999 respectively). In all samples, the average otolith weights in the fall were heavier than in September (Table 2) as were the fish lengths and weights. The skewness of the otolith weight frequencies changed between September and November for the 1998 and 1999 samples [Fig. 4(C–F)] but not for 1997 [Fig. 4(A,B)]. The lighter otoliths were less frequent in the November 1998 and 1999 sample.

3.3. IGF-I as an indicator of instantaneous growth rate in coho salmon

A positive relationship (r^2=0.5) was found in the laboratory feeding experiment between fish size and IGF-I in both the fast and the slow growing populations sampled in September (Fig. 5), indicating that smaller animals in the population were exhibiting signs of stunted growth. In the laboratory study an even stronger relationship (r^2=0.7) was found between instantaneous growth (early August to mid-September) and IGF-I. A similar significant and positive relationship between IGF-I and fish size (Fig. 5) was found for two populations collected in September, 1999 in the Strait of Georgia (r^2=0.2) and in Puget Sound (r^2=0.1). Thus, the same positive IGF-I/fish size relationship observed in the feeding studies holds for natural populations sampled at sea. It

Table 2
Weights (g) of samples of otoliths in relation to mean weight (g), and length (mm) of coho collected in September and October–November 1997, 1998 and 1999

		September			October–November		
		Fish weight	Fish length	Otolith weight	Fish weight	Fish length	Otolith weight
1997	Mean	184	248	0.00474	200[a]	260[a]	0.00523[a]
	SD	63	233	0.000653	45	17	0.00058
	n	95	100	100	99	99	99
1998	Mean	173	239	0.00448	322[a]	297[a]	0.00593[a]
	SD	72	30	0.000679	84	24	0.000735
	n	100	100	100	100	100	100
1999	Mean	141	229	0.00436	203[a]	259[a]	0.000523[a]
	SD	38	21	0.00057	49	20	0.000625
	n	100	100	100	125	125	125

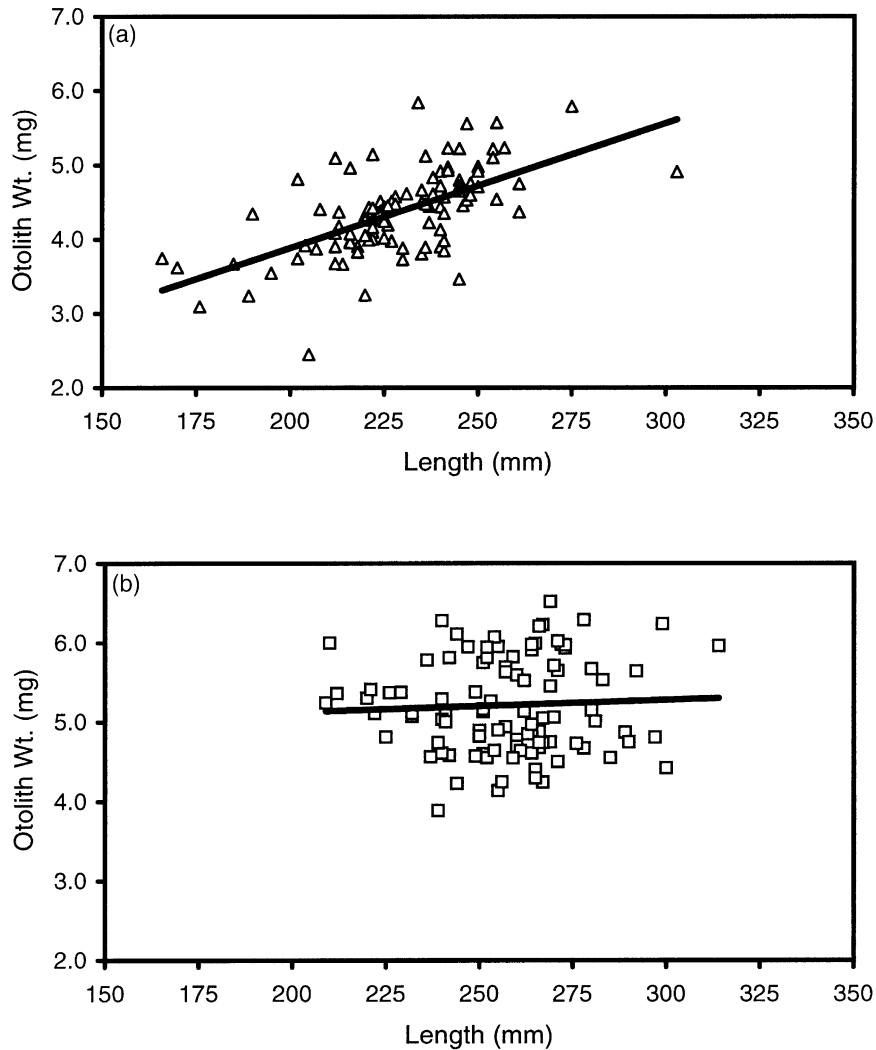[a] Significant difference compared with September of the same year, ns (not significant).

Fig. 3. Examples of the otolith weight, fish length relationship in 1999 between (a) September and (b) November. The solid line is the calculated regression. The change shown in this relationship was typical for all three years.

is noteworthy that the fish sampled in Puget Sound and the Strait of Georgia all had low IGF-I concentrations relative to the range observed in the feeding studies.

4. Discussion

One test of our hypothesis was that there should be much higher abundances of juveniles late in the first marine summer relative to total returns in order to show that mortality in the first marine fall and winter is important. This we observed for coho and possibly also for chinook. The catching efficiency of the net we used is probably smaller than we have assumed, and is
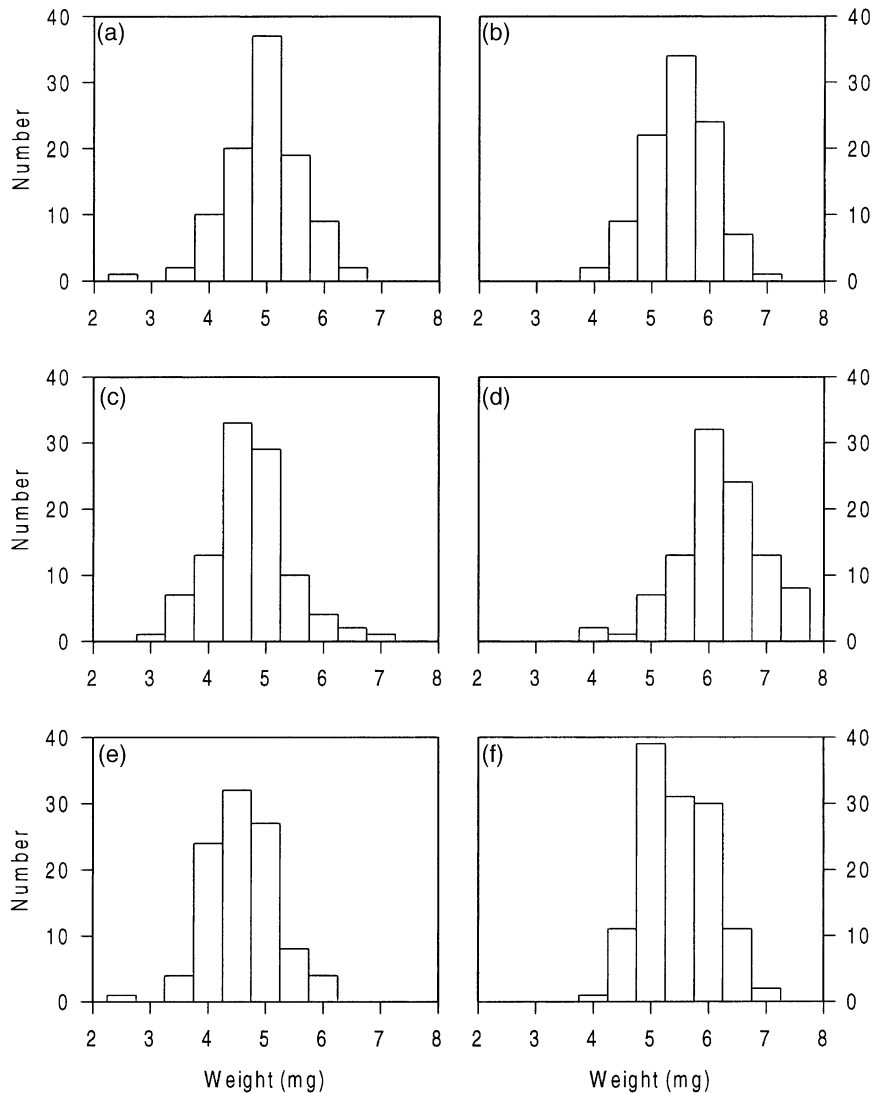
Fig. 4. The otolith weight frequencies in (a) September 1997, (b) November 1997, (c) September 1998, (d) November 1998 and (e) September 1999.

likely to be more inline with the Russian estimates; hence our abundance estimates in the fall should be much larger. The total return estimates remain unchanged, so estimates of fall and winter mortality are in all probability even higher than we have reported. The substantially larger abundance of young coho in the Strait of Georgia in September relative to the numbers entering the Strait and eventually returning is evidence that the mortality they suffer in the fall and winter during the first marine year is an important component of the total marine mortality.

Our conservative estimates of mortality between the fall of the first ocean year and the total returns of adults one year later exceeded 90% for chinook salmon. The evidence we found of substantial mortality after the first marine summer for chinook supports our hypothesis, even
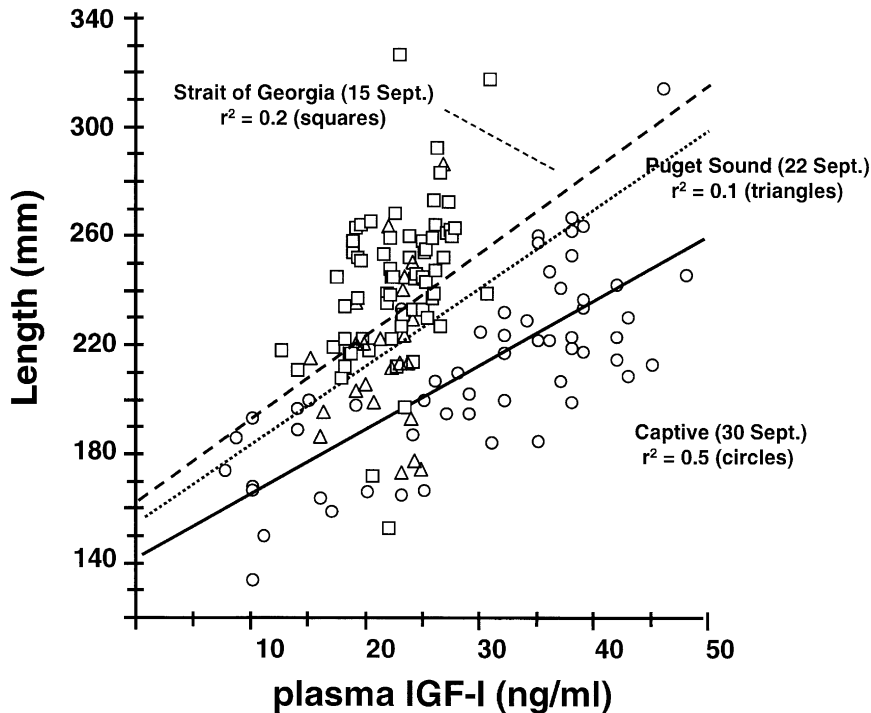
Fig. 5. The relationship between plasma IGF-I and length for ocean age 0 coho sampled in the feeding studies in seawater net-pens September 30, 1999 (○) and from samples collected in September 1999 in the Strait of Georgia (□) and in Puget Sound (△).

though the juvenile abundance estimates probably do not account for the entire population. One difficulty with estimating the abundance of juvenile chum and chinook is that we do not know what proportion of the population migrates out of the sampling area before September of their first marine year. Another difficulty with chinook is that they remain in the ocean for an average of 3–4 yr. So their mortality may be far more spread throughout their time at sea and, unlike coho, it cannot be expected to occur only during their winter in the ocean. The estimates of mortalities for chum salmon after the first marine winter were lower than for coho or chinook. The numbers of juvenile chinook and chum in our September estimates are probably not large relative to the numbers entering the Strait; we believe that we sampled only a part of the juvenile population of smolts that entered the ocean. Our hypothesis, in relation to abundance-measures, therefore, applies best to coho in our study.

Russian scientists pioneered the ocean survey methodologies used to establish juvenile Pacific salmon abundance. In one study, large numbers of pink salmon were commonly found late in their first ocean year in the southern Okhotsk Sea, north of the Kuril Islands (Shuntov et al., 1993). These juveniles were migrating out to the central North Pacific where they spend less than a year before they return to spawn in the rivers flowing into the Okhotsk Sea. In late October 1998, 46 1-h tows caught 9501 pink salmon with a mean length of 26.4 cm. The net was towed at speeds similar to ours, but their net had a vertical opening of 38–42 m and so its mouth area was about four times larger than the net we used. Melnikov, Radchenko, and Staovoitov (1999)

used a cachability (i.e. a net retention efficiency) of 0.3 (compared to our 1.0) to derive an estimate of the abundance of juvenile pink salmon of 1,070,000,000 fish or 209,600 t. The origin of these salmon was determined using scale patterns and the resulting abundances were compared to the catch and escapements in the summer and fall of 1999. By comparing the total returns of 94,500,000 pink salmon to the Sakhalin Islands area with stock they estimated to be 700 to 800 million juveniles in late October of the previous year, they estimated mortality between the October 1998 survey and the total adult returns in 1999 to be 88%. However, note that the abundance estimates of juveniles in this Russian study were based on the assumption that most of the population had been in the sampling area. If the entire population had not been sampled, the abundance would have been underestimated and mortality would have been even higher. Melnikov et al. (1999) also estimated that there were 517,600,000 chum and 11,210,000 coho in their survey area, confirming that juveniles of a variety of species tend to remain in the nearshore feeding areas late into the first marine year.

A second test of our hypothesis is that the fish that did survive and return were all derived from the larger fish in the juvenile population in the fall and winter of the first marine year. We have not tested this assumption directly in this paper, but we have shown that there was a change in the otolith size/fish size relationship in the fall of the first marine year. The changes in skewness in relationship we observed in November 1998 and November 1999 resulted from a decrease in the proportion of lighter otoliths in the samples, which indicates there had been a disproportionate reduction in the numbers of smaller fish in our samples. In November in all three years, the slope of the otolith weight and fish weight relationship declined, but the change in skewness was detected only in 1998 and 1999. There are other possible explanations for this change between September and October/November, such as the smaller fish may have migrated out of the sampling area. However, we consider that the change in the relationship we observed was not the result of a sampling artifact but at that stage of their life cycle growth related mortalities are important; this we interpret as support for our hypothesis.

We have also shown that the smaller coho have lower levels of IGF-I which are associated with their stunting. We also show that low levels are typical of most of the coho we sampled in the Strait of Georgia and Puget Sound in September 1999. We should also note that there was very little fishing for coho during our study period. Our conclusion, therefore, is that the evidence so far does not allow us to reject the critical size and critical period hypothesis. There also was much less variation in the ocean-caught fish. We also showed that between 97 and 98% of the population of the coho we sampled in September failed to survive to return and spawn the following year, so we conclude that there is a growth related, physiologically based process that is associated with these high fall and winter mortalities. We have observed a relationship between size and IGF-I concentration in controlled feeding studies. The presence of small fish with low levels of plasma IGF-I in September is the first evidence that stunting is occurring in natural populations. These data indicate that while size may be a good proxy for coho growth, plasma IGF-I levels are even better related to the instantaneous growth rates, which reflect actual differences in the physiological mechanisms controlling fish growth.

In another experiment, coho yearlings were transferred to marine net-pens shortly after summer solstice, and the growth of four experimental groups was controlled by ration size (Beamish & Mahnken, 1999). After eight months of seawater culture, the populations receiving the high to medium rations contained 33 and 39% stunted fish, and had sustained mortalities of 13 and 16%,

respectively. The populations receiving medium-low and low rations contained 70 and 78% stunted fish and sustained mortalities of 23 and 32%, respectively. Thus stunting and mortality in these experimental populations were be controlled by energy intake. Coho data indicate that increasing food availability resulted in an increase in survival (Beamish & Mahnken, 1999). These results together with those presented here suggest that coho with the low IGF-I values in the fall suffer higher mortality. This could also indicate that the majority of ocean-caught coho with the low IGF-I values fail to survive the fall and winter and this could explain the large mortality that occurs in the juveniles between late September and their return as adults the following year.

An understanding of the physiological process involved in stunting is central to the critical size, critical period hypothesis. Duan et al. (1995) studied temporal changes in levels of IGF-I in tissues of normal and stunted juvenile coho salmon in seawater. Hepatic expression of IGF-I in juvenile coho salmon increased in springtime, following an increase in plasma growth hormone. Stunts were deficient in the production of IGF-I. As in normal seawater smolts, growth hormone remained high in stunted animals, but IGF-I levels were depressed. By contrast, stunted fish had significantly lower IGF-I levels in the liver from May to September compared to the normally growing fish. Growth hormone is the primary positive regulator of IGF-I synthesis, and a decrease in hepatic IGF-I synthesis in salmon can be associated with prolonged starvation (Storebakken, Hung, Calvert, & Plisetskaya, 1991; Sumpter, Le Bail, Pickering, Pottinger, & Carragher, 1991; Duan & Plisetskaya, 1993). However, stunted fish do eat, and aggressively so, even when kept together with their normally growing counterparts, but intestinal nutrient uptake is significantly reduced in stunted salmon (Collie, 1985) and protein synthesis rates in the body are reduced. Therefore, stunted fish may suffer from protein and/or energy deficiency, even though they feed aggressively. If individual fish do not receive sufficient food and fail to achieve a critical threshold size by late spring, they stunt, grow poorly and fail to survive winter (Mahnken et al., 1982). Thus the entire segment of small fish in the populations could be removed.

The critical size and critical period model proposes to explain Pacific salmon year class strength in general and coho year-class strength in particular on the basis of the need to maintain a weight-specific maintenance metabolism in the face of changing environmental conditions. A complex metabolic relationship exists whereby a juvenile must attain a critical size dictated by a certain weight-specific maintenance metabolism that is governed by growth trajectory and changing environmental variables like water temperature and photoperiod. Failure to attain the critical size required to maintain this state will result in endocrine dysfunction, stunted growth, and eventually death. Mortality will occur either through predation (compromised swimming ability), or through physiological death. Laevastu and Favorite (1977) considered that partial starvation is an important component of marine mortality, and this is consistent with our hypothesis. This concept that survival is determined by the need to achieve a genetically determined minimum growth rate, is a familiar concept for larval fish survival (Iles, 1980). Our hypothesis that Pacific salmon in general, and coho salmon in particular, experience a growth-based mortality late in their first marine year is consistent with the ideas of Houde (1997) and Cowan, Rose, and DeVries (2000). Houde (1997) expressed the view that body size and life stage-specific productivity contribute to the processes that regulate recruitment in teleosts. Cowan et al. (2000) after reviewing the extensive literature on the factors affecting the early marine survival of freshwater and marine fishes, concluded that density-dependent growth most likely occurs late in larval or juvenile stages at a critical weight. It is the ability of individuals to achieve a critical size, late in their first year of life that determines the variability in recruitment.

Although the results of our study and evidence from other research have not provided the final confirmation of our hypothesis of a fall and winter growth based mortality, they do provide supporting evidence. Understanding the sources and time sequence of marine mortality is an important part of the management of many marine fisheries (Bailey, Brodeur, & Hollowed, 1996; Bailey, 2000). We propose that understanding mortality at this critical stage in the life cycle of the various species of Pacific salmon will improve the efficiency and effectiveness of salmon management. It will result in more realistic expectations in the general public, and provide some of the knowledge required if we are to be successful in adapting our management practices to changes in their productivities expected to result from climate change.

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