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**Natural regulation of the abundance of coho and
other species of Pacific salmon according to the
critical size and critical period hypothesis**

by

R.J. Beamish¹ and C. Mahnken²

¹Department of Fisheries and Oceans
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, British Columbia
Canada, V9R 5K6

²National Marine Fisheries Service
7305 Beach Drive East
Port Orchard, Washington
USA, 98366

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Abstract

We propose that the marine carrying capacity for coho and other Pacific salmon species is regulated naturally by the requirement to grow at a critical rate and thus achieve a critical size range by a critical period. Regulation occurs in two major stages. In the first stage, marine mortality is predation based and occurs immediately after entry into salt water. Mortality at this stage is partly related to the size as well as to the density of smolts and the density and type of predators. The second period of major mortality occurs in the fall and winter when juveniles that are not at a critical size, are unable to maintain minimum metabolic requirements and enter a growth trajectory that leads to death. Both density dependent and density independent factors interact through these mortality stages to establish the abundance after the first winter in the ocean. Shifts in the mean carrying capacity occur when there are regime shifts in the climate-ocean environment, despite the high levels of ocean mortality. Interannual variability in abundances at the stock level fluctuate around these trends in a mean carrying capacity.

According to this hypothesis, the freshwater stage of Pacific salmon is a period of relatively safe refuge for reproduction which results in the production of a large number of young with diverse genetic traits. The large number of young greatly exceed the available ocean habitat resulting in large marine mortalities. The diverse genetic traits and a two-stage process of marine mortality ensure that a few offspring always survive the variable ocean environment, despite the high levels of ocean mortality.

Introduction

How is the abundance of Pacific salmon regulated naturally? What is the natural mechanism that maintains relative abundance levels among Pacific salmon species despite 90% and greater marine mortalities. Why do some representatives of each of the thousands of stocks around the Pacific, always return to spawn despite the very high marine mortality? What is the relative importance of the fresh water and marine phases of their anadromous life history in the regulation of stock size? We suggest that not only are the answers of critical importance for management, they are also urgently required to ensure that threatened stocks do not become extinct (NRCC 1996).

Coho Salmon

In North America, coho salmon (*Oncorhynchus kisutch*) are perhaps the salmon species that has the broadest general recognition. They are both a sought after sport and commercial species and an indicator of the health of freshwater streams and rivers. They also are relatively easy to rear in hatcheries making the additions of hatchery-reared juveniles an attractive way of both addressing management problems and supplementing wild production. In the 1960s and early 1970s, off the west coast of North America, coho were readily available for fishing, but by the late 1970s there were signs that coho abundance was declining at the southern limits of their range. It is now roughly 20 years later and despite massive expenditures by governments as well as from the private sector, the decline has not been halted and some stocks are threatened (NRCC 1996). In the 1960s there was an increase in the production of hatchery-reared coho in British Columbia, Washington and Oregon that reached a

maximum 198,000,000 smolts in 1981 (Beamish et al. 1997). We estimated that hatchery production was about 1.5 times the wild coho production in these areas in the 1960s. By the late 1980s and early 1990s, the total number of coho smolts entering the ocean probably were double the wild production of the 1960s and 1970s. Despite this increase in total smolt releases, the total catch of coho has continued to decline, reaching astonishingly low levels in the mid-1990s (Fig. 1).

We propose that coho brood year strength currently is less a function of the number of smolts entering the ocean and more of a function of the ocean conditions at the time of ocean entry. We suggest that the final size of the population is determined in the fall and winter. We call our hypothesis, the critical size- critical period hypothesis and we propose that this hypothesis explains how carrying capacity for all Pacific salmon is affected by ecosystem changes. Carrying capacity can be defined in several ways, but we consider carrying capacity to be the mean biomass that can be supported in an ecosystem in a particular state or regime. We use the term regime as defined in Beamish et al. (1998a) to describe abrupt shifts in the mean of a biological or physical series. Within a regime, variation in abundance will occur; however, we consider carrying capacity to be the mean level. For example, the production of Pacific salmon stocks in Alaska has been shown to switch from one mean level to another (Hare and Francis 1995). We would consider that each mean level represents a distinct carrying capacity.

There is surprisingly little theory about the mechanisms that regulate the abundance of the various species of Pacific salmon naturally. There is, instead, a comprehensive

literature relating to fishery effects and to the management of fished salmon stocks. We use the word stocks to mean regional aggregations of salmon that are fished as a unit and population to represent distinct spawning groups, Ricker, (1975). Ricker (1954) addressed the impacts of fishing by showing that the relationship between the number of young salmon entering the ocean and subsequent returns followed a dome-shaped curve. If the ocean is as important as we propose, application of a Ricker type relationship to rebuild abundance (Perry 1995) would produce abundances appropriate for the current ocean conditions and not necessarily to levels observed in a previous regime.

Foerster (1968) proposed that under natural, unfished conditions, sockeye salmon abundance would be large and limited only by the rearing areas in fresh water. This reasoning appears to be associated with the estimated mortality of up to 99% of eggs and fry in fresh water. The high marine mortality was assumed to be constant over time, and apparently less important in the self-regulation of the population than the number of smolts produced in fresh water. The mortality that did occur in the ocean was believed to occur very early after ocean entry (Parker 1968, Percy and Fisher 1990, Furnell and Brett 1986).

Our hypothesis identifies fresh water as a safe refuge for reproduction. The young produced in fresh water greatly exceed the capacity of the marine environment to support them. However, the diverse, genetically based life history traits, help optimize survival in the ocean which is a more hostile environment than fresh water. Thus, even

though egg to smolt mortalities are extremely high, the marine environment regulates the final abundance in a manner analogous to the regulation of abundance of any plant or animal that produces very large numbers of young. It is a fundamental principle in ecology that in such cases the final abundance is a function of available habitat and not the large number of seeds or babies (Colinvaux 1978).

According to our hypothesis, regulation in the ocean occurs in two stages. The first mortality is predation based, and occurs soon after the juveniles enter the nearshore area. The second mortality occurs in the late fall and winter and is not predation based, rather it is a function of the condition of the juvenile. The "culling" impact of winter on land animals such as muskoxen (Ovibos moschatus) is a recognized mechanism of regulating abundance (Bartmann 1984, Gunn et al. 1989) and we suggest that an analogous mechanism occurs in the ocean for salmon. The amount of fall and winter mortality is related to the condition of the fish at a critical period in the late fall as well as to the stresses of winter. We use the term critical size, but we include growth rate as a measure of critical size. The combination of competition for food from other individuals in the cohort or from associated species, or physical changes to the ocean environment, all interact through the growth rate to initiate a growth trajectory that will sort out the fish that will survive the late fall and winter from those that will die. The actual cause of death is more a function of a physiological change, than a constant removal through predation. Smolts not able to achieve the critical size at the critical period quickly become programmed to a path resulting in death. The moribund animal

may end up in a predator's stomach or it may simply fall to the ocean bottom and be consumed by scavengers.

Ricker (1945) defined a critical size as the mean length or weight when the growth of a year class just balances mortality i.e., the average size of the year class when the total weight is neither increasing nor decreasing. For exploited populations, it is the mean size when the instantaneous rate of growth equals the instantaneous rate of natural mortality. The concept of a critical period is frequently associated with Hjort (1914) and has been interpreted to relate to larval survival in relation to predation and food. According to these earlier definitions, therefore, the critical period implies that a time in the larval stage is critical for stock size and the critical size identifies a stage in the growth and death of a year class. The critical size, according to our theory, is the minimum size (or growth rate) of the fish at the critical period, that will ensure it survives the first winter in the ocean.

Supporting evidence from rearing studies

Mahnken et al. (1982) studied coho from 12 hatcheries in Washington State to determine the size that would optimize their survival in net-pens in salt water. In the net-pens, coho were in a smolt, transitional, or parr-like stage (Fig. 2A,B). The parr-like stage resulted from some fish that did not develop into the other stages and coho that reverted to the parr stage. These changes occurred despite the addition of artificial food. The parr-like fish did not feed or grow normally and eventually died. The fish in

reversion fed and grew, but eventually became parr-like and died. It was possible for some of the fish in reversion to survive through the winter and resmolt the following spring (Folmar et al. 1982). The reversion process accelerated after the summer solstice and continued to the winter solstice. The association with photoperiod suggested that reversion was associated with genetically controlled osmoregulatory requirements that were linked to the time of year and a requirement to grow at a minimum rate to survive. The different growth rates resulted in reversion occurring throughout the year. In the net pens, the size of the largest parred coho (Fig. 2B) was a good indicator of the minimum size required for coho to continue in a growth trajectory leading to survival rather than reversion. Mahnken et al. (1982) called this size, the critical size (not our definition) which increased throughout the year. In fresh water during the smoltification of coho it was possible to predict the survival of coho after transfer to net-pens based on size and condition (Folmar and Dickhoff 1981). Mahnken et al. (1982) expanded this technique to salt water and used the percentage of the population in salt water smaller than the largest parred individual to predict saltwater mortality. The observations of Mahnken et al. (1982) identified a possible ecosystem and trophic relationship with growth that could result in death in the late fall and winter through osmoregulatory dysfunction. Although these studies were in net pens, we propose that a similar response could occur for hatchery and wild fish during their first marine year.

We re-analyzed the data of Mahnken et al. (1982) to compare ration size with cumulative mortality (Fig.3A,B). In all experiments there was an abrupt increase in the trend between mid-September and early October in the low ration experiments ranging from

13 to 17%. The ration size was also related to the cumulative number of fish in poor condition or stunts (Fig. 3A,B), although there was not an abrupt change in the trend in late September.

It is apparent from the feeding experiments that ration size is related to marine survival in controlled environments. The mechanism causing death is associated with physiological changes that are detectable, both as reversions to parr-like stages and stunting. As predation is not a factor in net pens, it is clear that coho require specific growth conditions in order to survive the changes that occur in their environment beginning in the fall of their first marine year.

Supporting evidence from juvenile abundance surveys

It was the results of abundance estimates of coho in the Strait of Georgia (between Vancouver Island and British Columbia) provided the initial evidence that relatively large numbers of juveniles were still alive by the fall of their first marine year. A number of surveys have been completed, but here we report the results from the September 1997 cruise, as an example of the methods used to estimate abundance.

Surveys were conducted in the Strait of Georgia using a large rope trawl (Beamish and Folkes 1997). The net was fished at a speed of approximately 5 knots, with an average mouth opening of 18m x 15m and was effective at catching all species and sizes of Pacific salmon in most weather conditions. In the Strait of Georgia in September 1997, 53% of coho were caught in the top 15 m and 90% all coho were in the top 45m.

Swept volume estimates were made according to the procedures described in Beamish et al. (1998b). The estimates were for the top 45m only and the net was assumed to have a catchability of one. This means that all juvenile coho in front of the net opening would be captured. We doubt that this is correct, which means that the abundance estimates are minimal estimates. In September 1997, 96 sets were completed throughout the Strait of Georgia. A total of 2280 ocean age 0 coho were captured, with an average, standardized catch of 44 coho/hr in the top 45m. The abundance estimate was 2,840,000 with 95% error limits of 1,583,000 to 4,097,000. This is a minimal abundance and if the catchability is smaller (as it probably is), the estimates could be considerably larger. In Russian studies the catchability of larger rope trawls fishing at the surface has been estimated to be 0.3 (Shuntov et al. 1988, 1993).

In 1997, Canadian hatcheries released approximately 10 million coho smolts into the Strait of Georgia. Our studies in September 1997 showed that approximately 77% of the ocean age 0 coho were from hatcheries, (Beamish et al.1998d.). Therefore, the remaining 23 % were either wild coho from Canada or hatchery and wild coho from the United States. We estimated the hatchery and wild percentage from the United States to be 7.3% based on marked and unmarked coho released into Puget Sound, and samples we collected in our surveys in Puget Sound (Beamish et al. 1998c). Assuming that there was no selective movement of rearing types, Beamish et al. (1998d), the number of wild Canadian coho entering the Strait could be determined using the known number of hatchery releases and was approximately 3 million. Therefore, the total

hatchery and wild smolt production would be approximately 13 million fish. The minimal abundance estimate of 2.8 million represents 22% of its total smolt production or 19% if only smolts of Canadian origin are counted. If the actual catchability is about 0.5, the abundance is approximately double the percentage of coho remaining in the Strait of Georgia in September, using a catchability of 0.5 could produce an abundance that would approach about 40% of the number that entered salt water in the spring. In 1997, the total returns of coho that entered the Strait in 1966 (catch and spawning abundance) was less than 500,000 fish. The abundance estimate in September 1996 using a catchability of one was 3.6 million (with 95% error limits of 5.1 to 2.1 million). Again, the actual number could be higher if the true catchability were known. Even at 3.6 million, the total return of less than 500,000 in 1997 indicates that the mortality in the fall and winter is substantial. It is too early to estimate the total returns in 1998 to compare with the 1997 abundance estimate, but if marine survivals are similar to 1996 and 1997, the 10,000,000 hatchery coho and 3,000,000 wild coho amount to about 300,000 (1.8% for hatchery and 4.2% for wild, DFO 1998). This indicates that the marine mortality that occurs after September of the first year in the ocean is of major importance in the determination of the final brood year strength

Supporting evidence from other studies

A linkage between summer growth in the first marine year and total survival has also been proposed for Atlantic salmon (Salmo salar) by Friedland et al. (1996). Recognizing that they were studying the surviving fish and not knowing the sizes or growth of the ones that died, they concluded that a hatchery stock that grew slower in

the first summer in the ocean had higher marine mortalities even though they were from the same gene pool as stocks in another hatchery that grew faster in another rearing area. The cause of the mortality was believed to be predation that occurred throughout the summer period. In another study (Friedland et al. 1993), they found that the overall survival of North Atlantic salmon was related to ocean conditions in the winter, indicating that the carrying capacity for Atlantic salmon is linked to natural mortality during the first marine winter. Survival appeared to be more a function of growth rate than actual size as surviving fish from different stocks had different spacing between circuli during the period of summer growth. Friedland et al. (1996), Friedland and Haas (1996) and others have also shown that the timing of maturation of Atlantic salmon was related to growth in the first summer in the ocean. Slower growth resulted in fish remaining in the ocean for 2 winters before returning to spawn.

Shuter et al. (1980) examined the relevance of growth, size, and winter mortality for freshwater fishes. They point out the importance of the first growing season in the life of a temperate zone fish. Such fish are most susceptible to winter starvation in their first year because they must endure winter at their smallest size. After extensive laboratory and field experiments, they succeeded in quantifying young-of-the-year growth and starvation rates under summer and winter conditions for both yellow perch and small mouth bass. In laboratory experiments conducted at typical winter temperatures and photoperiods, unfed yellow perch (Perca flavescens) and small mouth bass (Micropterus dolomieu) lost conditioning and died in a size-dependent manner. When food was supplied ad libitum to young-of-the-year perch held under

typical winter conditions, mortality was low but the fish lost condition in a size-dependent manner. At natural winter densities in enclosure studies, young-of-the-year yellow perch exhibited size-dependent levels of total mortality that were similar to the levels exhibited in laboratory experiments with starved fish (Post and Evans 1989). Shuter et al. (1980, 1989) and Cunningham and Shuter (1986) showed that wild young-of-the-year small mouth bass exhibited large declines in body condition and appeared to suffer size-dependent variations in winter mortality that were consistent with the variation observed in laboratory starvation experiments. They concluded that size-dependent, winter mortality could explain the overwinter changes in the young-of-the-year size distributions observed in wild populations of both yellow perch and small mouth bass (Thoneys and Coble 1979, Shuter et al. 1980, Post and Evans 1989). Shuter extended this concept to explain limits in the distributions and impacts of climate change. For any species there is a point where viable populations can no longer be maintained in the face of a short growing season and a long period of resource scarcity (Schmidt-Neilsen 1984). Through this general mechanism, climate may determine the northern limit of a species range. Climate through its influence on the length and warmth of the growing season affects the autumn size of young-of-the-year fish. This autumn size and winter duration produced a synchronized relationship between climate and mean year-class strength. It is clear from the work of Shuter and others that the amount of summer growth is related to the ability of young-of-the-year yellow perch to survive their first winter.

One of the classic studies of coho survival in relation to size was carried out by Bilton and reported in several publications i.e. Bilton (1978), Bilton et al. (1982). This was a study of the optimal time and size to release coho from hatcheries. Amazingly they concluded that a better understanding of the ecological dynamics of time of entry into salt water and the feeding and growth of juveniles in the coastal marine waters could achieve a marine survival approaching 50%. Despite their recognition that factors other than time and size at release were important in determining the success of the total return, little emphasis was placed on identifying the mechanisms that regulated marine carrying capacity. Why were these projections so far from the present reality of 2% survival or 25 times less than they calculated to be possible? We propose that the answer is that the marine carrying capacity is not determined in the “several months following migration to salt water”, but in the late fall and winter. Optimizing release size and timing may minimize the size related, predation based early marine mortality, but it is the rate of growth during the summer that we propose minimizes late fall and marine survival. Releasing large coho at or after June 29 in the Bilton study resulted in very poor survival. We suggest that this mortality could be more a function of poor growth rates than predation as the period to adapt to saltwater feeding conditions would be shorter than for coho introduced earlier in the year. Bilton’s size and time-release studies, according to our hypothesis experimented with the first phase of the regulation of marine carrying capacity but not the second.

A study of coho growth and survival off Oregon and Washington (Fisher and Pearcy, 1988) concluded that years of low marine survival were not a result of reduced food

supply resulting in reduced growth and poor condition. As, growth rates in June were not related to marine survival, the authors proposed that there was not a strong relationship between growth rate and mortality. Variations in mortality were proposed to result from the switching of predation to and away from coho as alternative prey became more or less abundant. Year class strength (or carrying capacity), therefore would be determined early in the summer (before the end of June) and would be predation based. Although the authors did not observe a relationship between growth rates in June and survival they did observe that the growth rate of coho caught in the late summer was related to survival. Year classes in which the fish caught in the late summer had higher average growth rates also had higher survival. Thus there was a relationship between growth rate observed in the fall and survival but this relationship was not evident in low survival years during the early summer.

Nickelson (1986) concluded that the conditions in the ocean were responsible for the determination of the size of the total returns. Optimal conditions for survival of coho appeared to occur when upwelling was strong and ocean temperatures were cool. Although growth rates were not determined, we suggest that such conditions are optimal for growth during the summer. Optimal growth at this time according to our hypothesis improves the condition of fish and the survival in the late fall and winter, rather than allowing individuals to grow out of a predation window.

An extended study of the factors affecting the variability in marine survival of coho from a small stream concluded that growth rates in the ocean were related to marine survival (Holtby et al. 1990). It was proposed that the mechanism related to size selective

predation. However, the authors did not find a relationship between the size of marine entry and survival, particularly for the larger smolts that spent two years in fresh water. It is their observation that growth in the ocean was related to mortality that may support our hypothesis.

Anderson (1988) argued that maximizing surplus energy by the end of the first season of growth would improve winter survival of temperate water fishes. It is not a new idea to link growth and mortality (Gulland 1965) as many investigators have related survival to growth (Ware 1975) with mortality occurring through predation. However, the concept of a two stage mortality process with the mortality in the second stage resulting from physiological changes caused by low energy reserves is not the usual explanation for the determination of final carrying capacity. Surplus energy levels at the end of the growing season, therefore, are a function of both food availability and temperature. Temperatures above optimal will require an increase in feeding to maintain growth rates as the standard metabolic rate increases nonlinearly (Brett 1979). Thus, the gradually increasing surface temperatures in the Strait of Georgia in the 1980s and 1990s could reduce the number of coho that reach a critical size, if food availability did not increase.

Discussion

It is important to understand how Pacific salmon abundance is regulated naturally as this information provides the basis to understand how ecosystem changes will affect the abundance trends. Once it is known that changes in ecosystems may be shifts among

mean productivity levels, it is no longer acceptable to consider the impact of the environment, associated species, or associated individuals of the same species to be random over a decadal time scales. If we accept that there are limits to the abundance of all Pacific salmon and that these limits vary for different species, we can ask what the natural limits are and how are they regulated. If the regulation is in fresh water, then escapement, spawning area, and rearing conditions would regulate smolt output. Marine mortality rates in the ocean would have an impact, but if they fluctuated randomly, the ocean impact would tend to be constant. While this theory of abundance regulation does not appear to be stated explicitly in the literature, it often appears to be the underlying concept for the management of Pacific salmon. Our hypothesis is consistent with observations in other studies that marine size and growth rates are related to survival. The concept of size related, predation based mortality is easily accepted as there is sufficient scientific literature to support the concept. Less familiar and rarer is the literature relating to mortalities resulting from poor condition resulting from reduced food intake. Slow growth in virtually all the studies reviewed does not result in good returns. The reduced growth was usually considered to result from low food abundance, or reduced availability because of competition. We suggest that slow growth may also occur from reduced appetite which may be a function of smolt density.

. Fast growth in the ocean can be related to higher percentages of coho returning to spawn in their first ocean year (Pearcy 1992). Furthermore, he proposes that adult coho production is regulated in the ocean because both upwelling and jack returns are related to adult returns. He believes, that predation ultimately regulates abundance and that the intensity of predation is affected by ocean conditions that alter the densities

and abundances of prey. He reports observations of difficulties finding predators as we did in our studies, but proposes that most of the mortality occurs within several months of saltwater entry. Pearcy (1992) argues that high condition factors in the early summer in years of poor survival is evidence that marine survival is not regulated by food limitation. We propose that his observations were based on fish sampled in the early summer and that the observations made later in the summer more accurately measured the growth and survival relationship. We stress that our critical size and critical period hypothesis is testable and we present it here so that other investigators may study its applicability.

Our hypothesis identifies food limitation as the reason for the mortality that occurs after the critical period. Food limitation or availability may appear to be an unlikely factor controlling mortality because it can be shown that there is a large amount of food in the ocean relative to the amount eaten by some salmon (Walters et al. 1978). However, we propose that availability of food is not measured by total abundance. Laevastu and Favorite (1977) consider that partial starvation is an important component of marine mortality and this is consistent with our hypothesis of programmed death, if the critical size is not achieved by the critical period. This concept of minimal growth rates required to maintain a genetically determined rate of growth or perish is a familiar concept for larval fish survival (Iles 1980).

A mechanism that is a two step process, one by predation early after ocean entry, and a second that is a function of the physiological condition during the winter period would

explain why some fish always return to each stock under natural conditions. If abundance was regulated entirely by predation, it would seem possible that in some years all juveniles would be consumed and stocks would disappear. If our hypothesis is correct, the value of understanding the mechanisms that produce final stock sizes is the wise use of funds and in the careful identification of expectations of yield. If our hypothesis is correct, it is clear that we can neither expect to change the carrying capacity of the ocean, nor should we want to attempt such an intervention into the marine ecosystem with our rather basic understanding of how they work.

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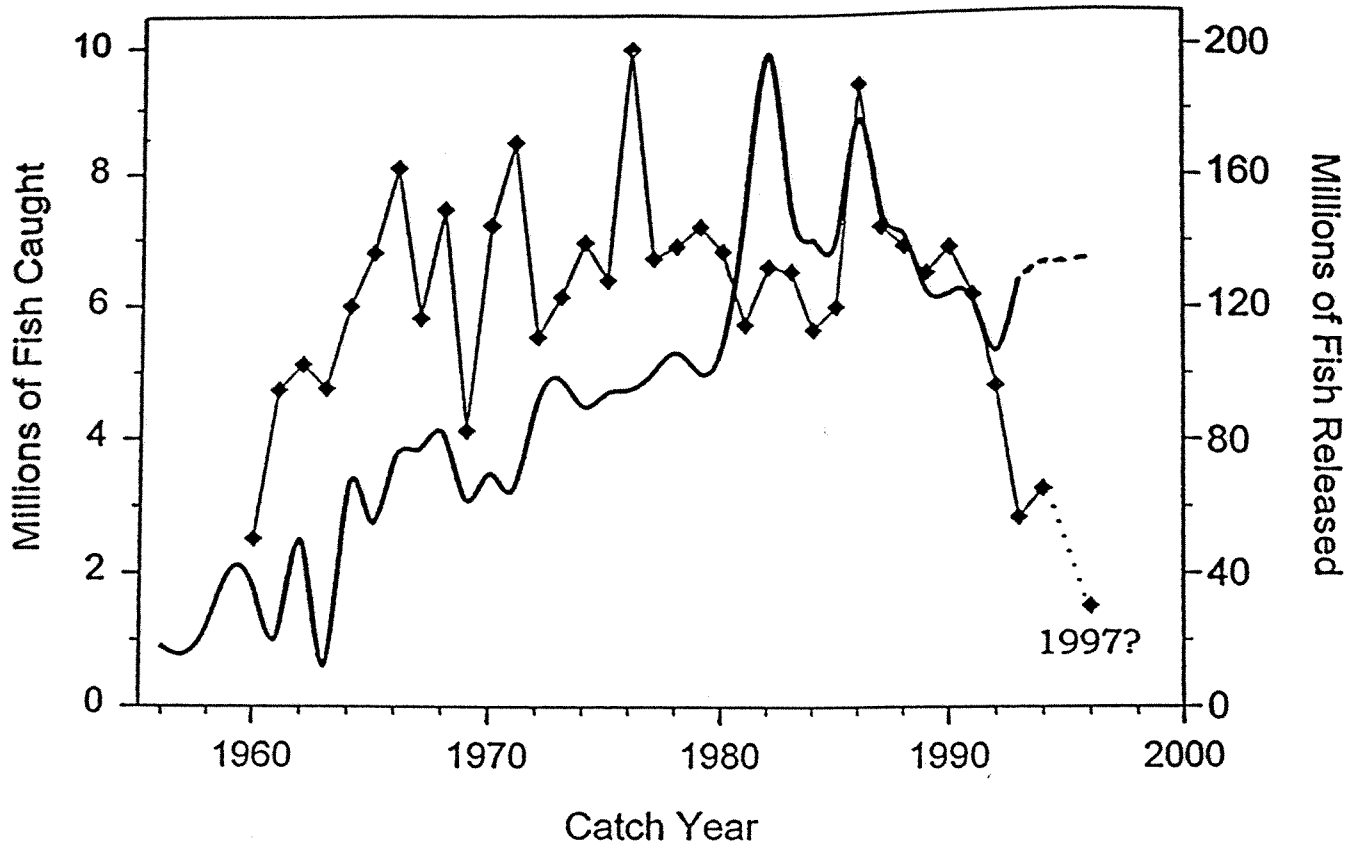
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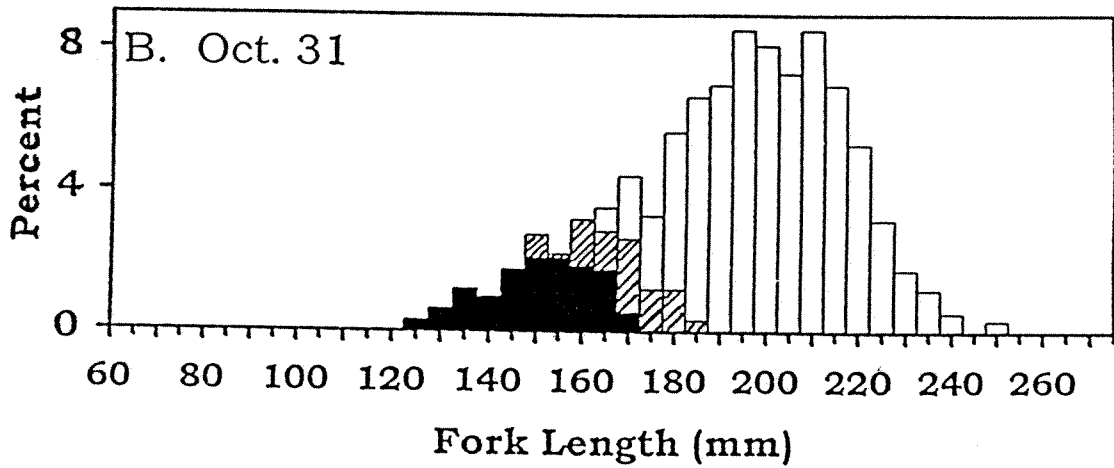
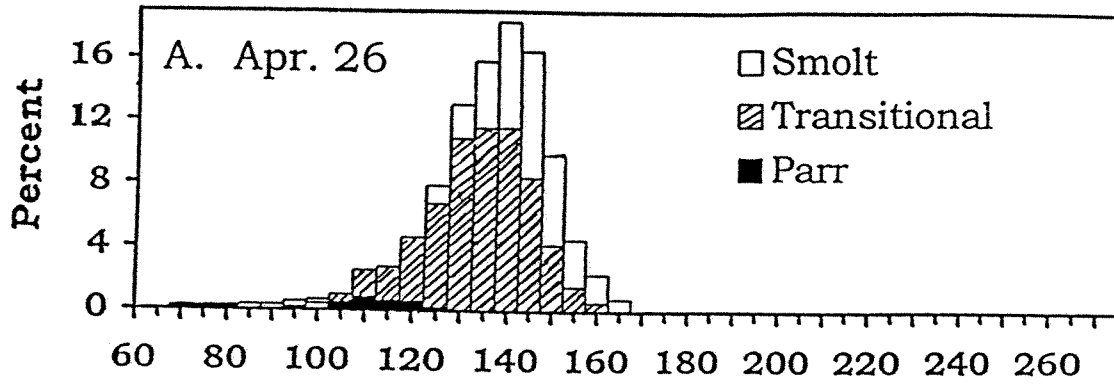
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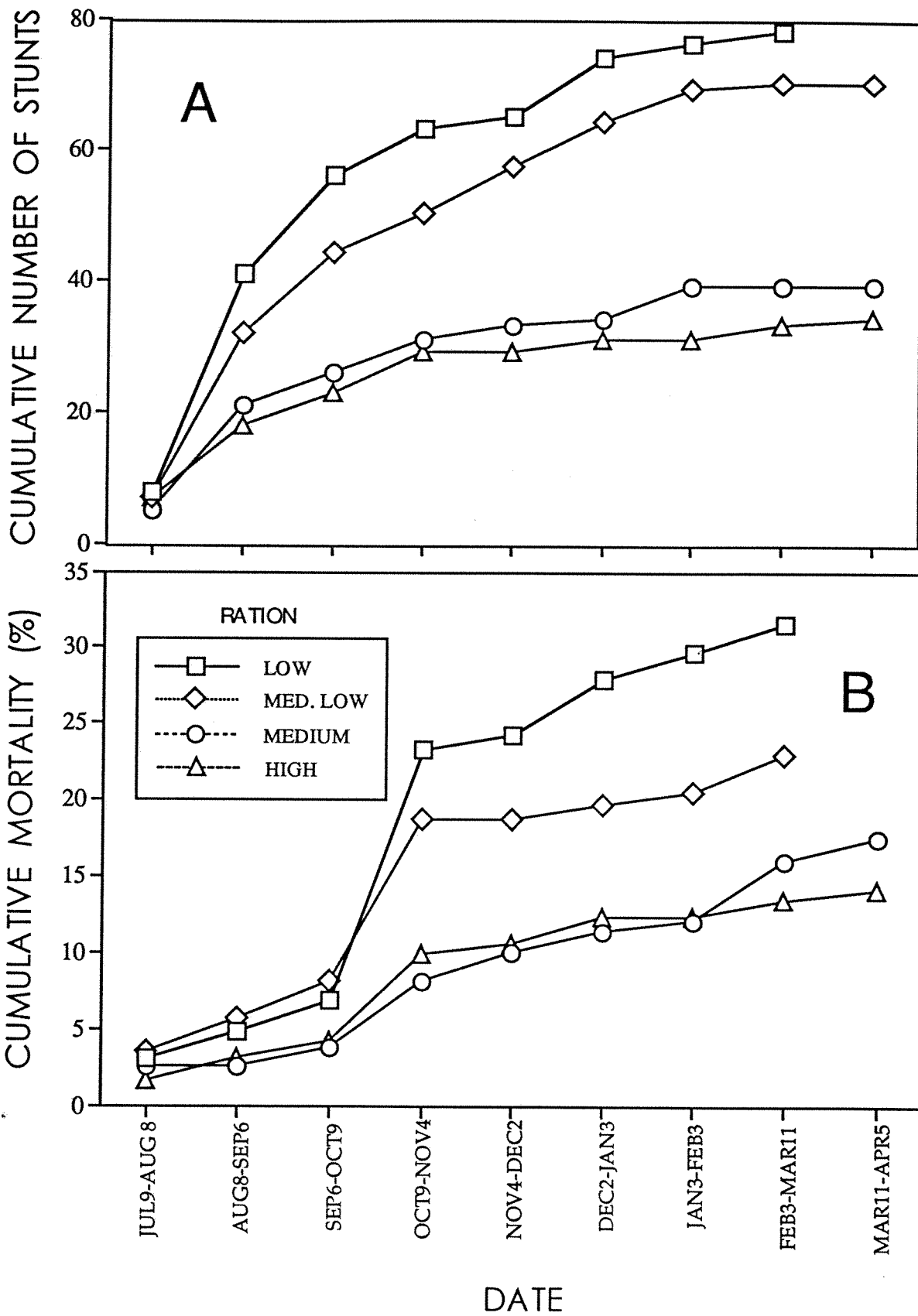
Figure Captions:

- Fig. 1 The estimated catch of coho salmon (thin line, diamonds) from British Columbia, Washington and Oregon (From, International North Pacific Fish Commission, INPFC, statistical yearbooks. Data from 1974 to the present include sports catch. The total hatchery production from British Columbia, Washington, and Oregon is shown as a solid line to 1992 and an estimate (dashed line) to 1996. We estimated smolt production in the 1960s by assuming that the combined harvest of sport and commercial catches would be approximately 6,000,000 with a harvest rate of about 50%. Assuming an equal sex ratio, 3000 eggs per female and a 2% survival from egg to smolt, there would be about 180,000,000 smolts produced annually. Hatchery predation averaged about 60,000,000 (Beamish et al. 1997) leaving about 120,000,000 wild smolts. Hatchery release year is lagged + 1 year to match catch year.
- Fig. 2 Fork length frequency distributions of coho salmon maintained in net-pens in salt water. Early in the year when coho from 12 hatchery stocks were added most fish were in a transitional state between parrs and smolts (Fig. 2A). By October (Fig. 2B) few transitional fish were present, but a relatively large number of parr-like fish or stunts were present. These fish would not survive winter conditions. The largest parred fish (i.e. 170 mm in October 31) was considered to be the size, below which, coho would not survive. (From Mahnken et al. 1982).
- Fig. 3 The data used in Fig.2. (A)There is a larger number of stunts that continue to increase in numbers throughout the study in the two experiments with the lowest rations. The rate of stunting (3A) was greatest immediately following summer solstice. (B) If aggregated by ration size, there is a large increase in mortality between October 19 and November 4 for the two experiments with the lowest rations. By winter solstice the commutative percent of stunted fish is large (60-75%) in the populations fed the two lower rations, and low in fish fed the two high rations. There was a large, but delayed increase in mortality (3B) between September and November, with the highest mortality in populations containing large numbers of stunts. Stunting continued to produce significant mortality at low rations levels from November though termination of the experiment in March/April.



Beamish and Mahnken Fig. 1





Beamish and Mahnen Fig. 3