

ECOSYSTEM



ECOSYSTEM APPROACHES FOR FISHERIES MANAGEMENT

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Taking the Next Step in Fisheries Management

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Abstract

For several decades fisheries biologists focused their attention on the taxonomy, life history, and population dynamics of single species of fishes. Most attention went to the preferred commercial species, but less popular fishes were not totally ignored. There was always the intention to piece together the species relationships into some integrated big picture, but the incentive was never strong enough to bring enough people together for a long enough time to begin to understand how whole ecosystems could be understood and protected. Several recent events have now provided this incentive. The most serious is the recognition that climate impacts must be understood both for fisheries management and for the detection of global warming impacts. The lessons from recent fisheries management issues such as East Coast cod, Atlantic salmon management, and coho problems, clearly have shown that there are some problems with previous concepts and that it is cost effective to study marine ecosystems. It is also good politics. It is easier to make difficult decisions when people are well informed about what is known and what is not known.

It is time to manage and protect whole ecosystems. This will not be a linear extension of single-species thinking. A more abstract concept is needed in which the single species is seen in relation to the processes that affect ecosystems and less in terms of numbers of individuals. The timing of copepod production, the condition of juveniles at certain times of the year, and the abundance trends of associated species may all become ways of assessing fishing impacts. Ecosystem management requires an understanding of the influences that regulate species naturally. For salmon, we propose a new concept of natural regulation that we call the critical size-critical period hypothesis. According to this hypothesis, the abundance of

salmon is determined both in the early marine period and in the first fall and winter of ocean residence. The amount of mortality late in the first marine year is related to the rate of growth during the summer. Like all difficult but essential tasks, it is important to get started with ecosystem management. It is also important to recognize that the communication and coordination of relevant information for ecosystem management may be as challenging as acquiring the understanding of how to do it.

Introduction

In the 1960s and 1970s we first heard about ecology. I think most of us liked what we heard. If you remember, we considered ecology to be the interaction of living things and nonliving things. In fisheries, the interest in ecology always seemed to be curiosity-based. It was hard to see how the complexities of food chains and environmental factors would ever find their applications in fisheries management. It reminded us of this little poem called *The Purist*.

I give now Professor Twist
A conscientious scientist
Trustees exclaimed, "He never bungles"
And sent him off to distant jungles
Camped on a tropic riverside
One day he missed his loving bride
She had, the guide informed him later
Been eaten by an alligator
Professor Twist could not help but smile
You mean he said, "a crocodile."

The point, of course, is that we do not want to miss the message in the detail of the event.

Ecosystem interactions are complex, but we can no longer avoid dealing with the complexities. We do have to consider the impacts of associated species and we do have to consider the impacts of the environment. As fisheries science developed, we had to simplify the complexities of ecosystems, but it is time to understand how to incorporate ecosystem dynamics into management. This is an improved understanding, not a complication of the simplicities we had to use. We must always be careful not to elevate our intelligence above the species relationships we do not understand. We are, in reality, stewards, and not managers.

Two of the most frequent news topics in recent years have been fisheries and climate. They are newsworthy because the changes we observed were extreme or unexpected or both. Climate will continue to be an important item in the news as we begin to detect the impacts of global warming, but fisheries may become less newsworthy as we stabilize our expectations through an improved understanding of the interrelationships among species and their ecosystems.

For example, our forecasts on the west coast of Canada a decade ago bear little resemblance to the fisheries we have today, not because of poor management, but because of a poor understanding of how ecosystems function. Our rather embryonic understanding of processes that affect fish abundance is a product of single species thinking. Our well-intended emphasis on interpreting numbers without the associated emphasis on understanding how the system works was a response to a rapidly developing fishery and economy that needed quotas. The lesson from our experiences with Pacific sardines, northern cod, Atlantic salmon, Pacific coho salmon, and a number of other species is that there is a complexity that must be understood if we are to have fisheries and be good stewards of our resources. In the next decade we will recognize the need to separate natural abundance changes from fishing effects. The fluctuations in abundance will continue, but our response to these changes needs to be different. We need to be able to forecast the shifts in our marine ecosystems that will change the trends in abundance of salmon, herring, halibut, and other species. We need to assess the health of a stock in relation to its carrying capacity rather than its historic abundance or its demand by fishermen. I think that a decade from now all of us will be more comfortable with the state of our west coast fisheries, not because there will be more fish, but because we will better understand why changes occur. It requires a major change in the thinking of biologists, fishermen, managers, educators, and the public, but we have the resources, the people, and the policies to make it happen if we can just get started.

It may be fine to preach all this ecosystem stuff, but how do we use it in management? Does an Atlantic cod with a skinny body mean anything? Of course it does. Does a shift in the intensity of winter winds in the North Pacific mean anything? Of course it does. In this paper, we try to show why and how we think ecosystem management will make us better stewards.

Regimes

A few years ago the word *regime* was not in the vocabulary of many fisheries biologists. It is today, even though we are not entirely sure how to define regimes. In general, regimes are large, linked climate-ocean ecosystems that shift in states over 10- to 30-year periods. In response to these changes, there may be changes in the dynamics of the resident fishes and other biota. A number of authors have written about regimes, but the best-known studies are studies by Hare and Francis (1995) and Mantua et al. (1997). Both these studies clearly demonstrated the persistence of trends and the abruptness of the periods of change. Most researchers studying trends in climate agree that there was a regime shift in 1977 and some feel that another change occurred in 1989 (Watanabe and Nitta 1998, Beamish et al. 1999). Beamish et al. (1998a) think that a recent change occurred in 1995. They use a number of indices to study regimes and regime shifts

(Beamish et al. 1999) and here we show how three indices changed about 1995.

The length of day (LOD) is the time it takes the solid earth to complete one rotation. The measure of LOD and the relevance of the measurement are discussed by Beamish et al. (1999). Changes in the annual trend of the LOD represent changes in the angular momentum of the solid earth and a redistribution of energy on the planet. The recent LOD time series shows changes in trends about 1973, 1987, and recently in 1994 (Fig. 1). The North Atlantic Oscillation Index (NAOI) is the normalized difference in the normalized winter sea level pressures between Lisbon, Portugal, and Iceland (van Loon and Rogers 1978). The NAOI clearly changed in 1989 and 1995. The changes in the 1970s were less clear (Fig. 2). The southern Oscillation Index (SOI) is commonly known on the “El Niño index.” It is analogous to the NAOI but in an east-west direction. It is the standardized series of the standardized Tahiti data minus the standardized Darwin data (Climate Prediction Center, National Center for Atmospheric Research, Boulder, Colorado). The trend in the pattern in the SOI changed in 1977 (Fig. 3) from an oscillation of positive (La Niña) and negative (El Niño) anomalies to persistent El Niño conditions up to 1989 and then to extreme, persistent El Niño conditions to 1995. Beginning in 1996, the oscillations were more like the pre-1977 state but more extreme.

Critical Size–Critical Period Hypothesis

It is now clear to salmon biologists that abundance changes in salmon can be related to natural changes in climate and in the ocean. We propose that the linkage of the climate/ocean environment to final abundance is through summer growth rates. We call our hypothesis the critical size–critical period hypothesis.

We propose that the marine carrying capacity for Pacific salmon species is regulated naturally by the requirement to grow at a critical rate and thus achieve a critical size by a critical period. Regulation occurs in two major stages (Fig. 4). 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 coho that are not at a critical size, are unable to maintain minimum metabolic requirements and enter a growth trajectory that leads to death. 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 coho salmon (*Oncorhynchus kisutch*) and possibly juveniles of other Pacific salmon species. The amount of fall and winter mortality is related to the condition of the fish at a

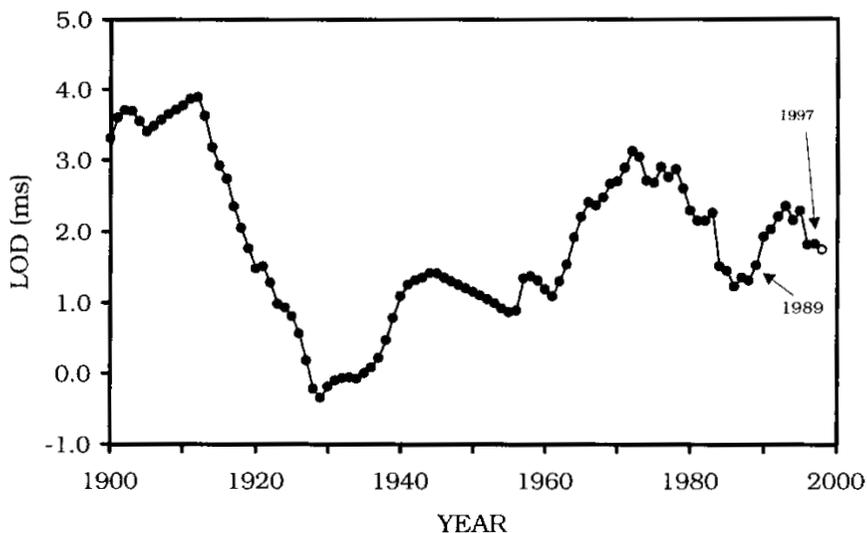


Figure 1. The length of day (LOD) time series from 1900 to 1997 in milliseconds (ms). Changes occur about 1974, 1989, and 1996.

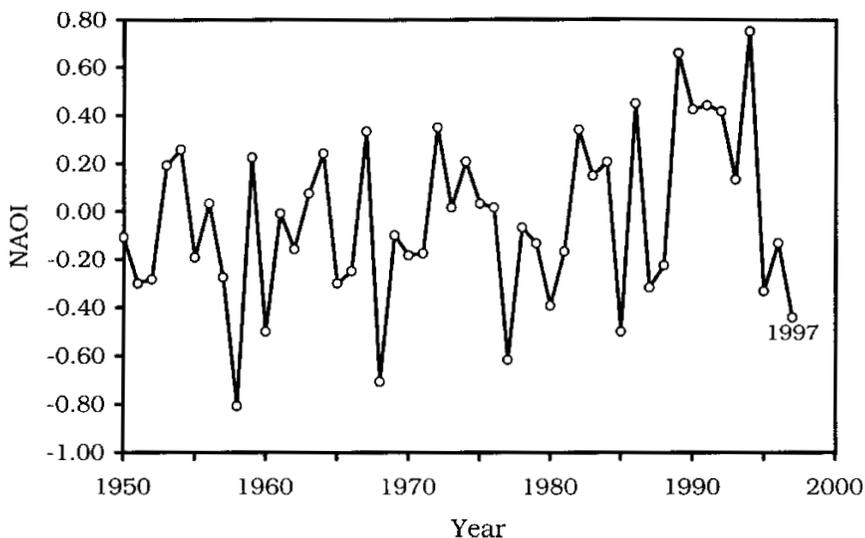


Figure 2. The North Atlantic Oscillation Index (NAOI) from 1950 to 1997 showing the change to positive anomalies in 1989 and a major change to negative anomalies in 1995.

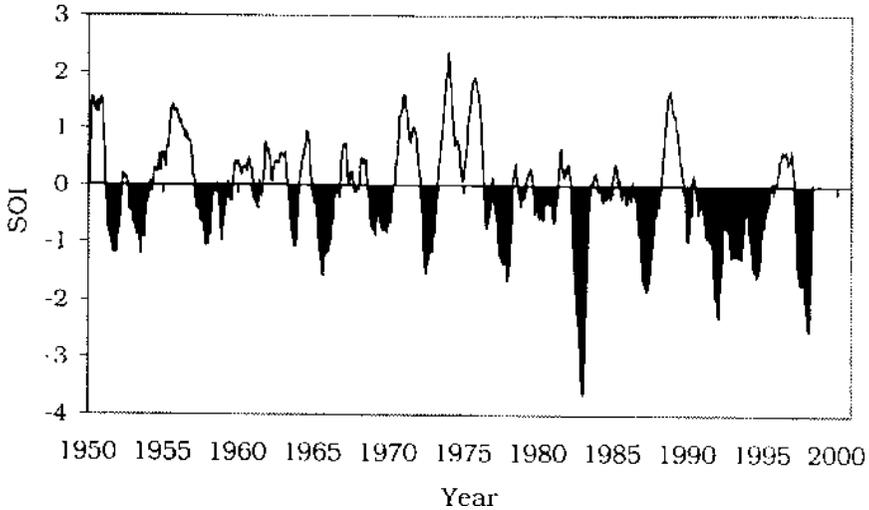


Figure 3. The southern oscillation Index (SOI) from 1951 to 1997, smoothed with a running average of 5s. The extreme negative anomalies are El Niño events and the extreme positive anomalies are La Niña events. Trends exist from 1951 to 1976 and from 1977 to 1989 and 1990 to 1995. The pattern may have changed again in 1996. The actual values are not shown.

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 timing of the fall transition from a stratified surface layer to a virtually unstratified ocean habitat, the fall solstice, and the “severity” of the winter may contribute to the timing of the critical period. The combination of competition for food, from other coho salmon and/or associated species such as juvenile chum salmon (*O. keta*), 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. Both density-dependent and density-independent factors interact through both these mortality stages to establish the brood-year strength after the first winter in the ocean. Interannual variability in abundances at the stock and regional levels will contribute to the variations about a mean carrying capacity that is characteristic of a regime. Shifts in the mean carrying capacity occur when there are shifts in a regime.

Critical Size - Critical Period

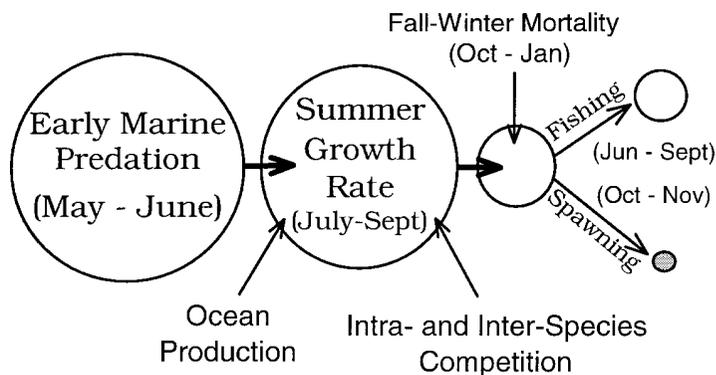


Figure 4. Diagram of the marine phase of critical size-critical period hypothesis. The areas of the circles are proportional to the speculated numbers of individuals in a stock. The early marine predation period reduces the number of juveniles to the abundance represented by the circle for the July to September growth period. It is during this time that the rate of growth in the summer determines the size of the stock after the first marine winter (October-January). The abundance after the marine winter will be the approximate brood-year size and during June to September fishing will remove a large percentage, leaving the spawning escapement in October and November.

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 exceeds the available ocean habitat, thus high marine mortalities will occur. 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).

In North America, coho salmon 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 addressing management problems or supplementing wild production with the expectation of producing more. In the 1960s and early 1970s coho salmon were readily available for fishing but by the late 1970s there were signs that 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 considered threatened (National Research Council 1996). In the 1960s there was an increase in the production of hatchery-reared coho salmon in British Columbia, Washington, and Oregon that reached a maximum of 198 million smolts in 1981 (Beamish et al. 1997). We estimated that this hatchery production was about 1.5 times the wild production in these areas in the 1960s. By the late 1980s and early 1990s, the total numbers of coho salmon smolts entering the ocean probably were double the wild production of the 1960s and 1970s. Despite this increase in hatchery-reared smolt releases, the total catch of coho salmon continued to decline, reaching astonishingly low levels in the mid-1990s (Fig. 5). In the states of Washington and Oregon, and the Province of British Columbia, total government expenditures over the past 20 years have probably exceeded 1 billion U.S. dollars. The exact amount is less important than the inability to manipulate the population dynamics of coho salmon despite the good intentions of a large number of very concerned individuals. We propose that the explanation is that except for very low abundances, coho salmon abundance is less a function of the number of smolts entering the ocean and more of a function of the ocean conditions. We suggest that the final size of the population or brood-year strength is determined in the fall and winter. This hypothesis explains how carrying capacity 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. 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.

Ricker (1945) defined critical size as the mean length or weight at which 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 at which 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.

Evidence to Support Hypothesis

In this report we describe results from three studies that support the hypothesis that growth during the first marine summer is an important factor in the determination of brood-year strength. Additional studies are currently in progress.

Swept Volume Abundance Estimates

The results of abundance estimates of coho salmon in the Strait of Georgia (between Vancouver Island and mainland 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 1998). The net was fished at a speed of approximately 5 knots, with an average mouth opening of 18 m × 15 m, and was effective at catching all species and sizes of Pacific salmon in most weather conditions. In the Strait of Georgia in September 1997, over 75% standardized catch of coho salmon occurred in the top 15 m and virtually all coho were in the top 45 m.

Swept volume estimates were made according to the procedures described in Beamish et al. (1998a). The estimates were for the top 45 m only and the net was assumed to have a catchability of 1. This means that all juvenile coho salmon 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 2,280 ocean-age-0 coho salmon were captured, with an average, standardized catch of 44.0 coho salmon per hour in the top 45 m. The abundance estimate was 2,840,000 with 95% error limits of 1,583,000-4,097,000. This is a minimal abundance and if the catchability is smaller (as it probably is), the estimates would be larger. In Russia, studies of the catchability of larger rope trawls (mouth opening 45 m × 45 m) 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 salmon smolts into the Strait of Georgia. Our studies in September 1997 showed that approximately 77% of the ocean-age-0 coho salmon were from hatcheries (Beamish et al. 1998c). Therefore, the remaining 23% were either wild fish from Canada or hatchery and wild fish from the United States. We estimated the hatchery and wild percentage from the United States to be 7.3% based on the marked and unmarked coho salmon released into Puget Sound and samples we collected in our surveys in Puget Sound in 1997 (Beamish et al. 1998b). Assuming that there was no selective

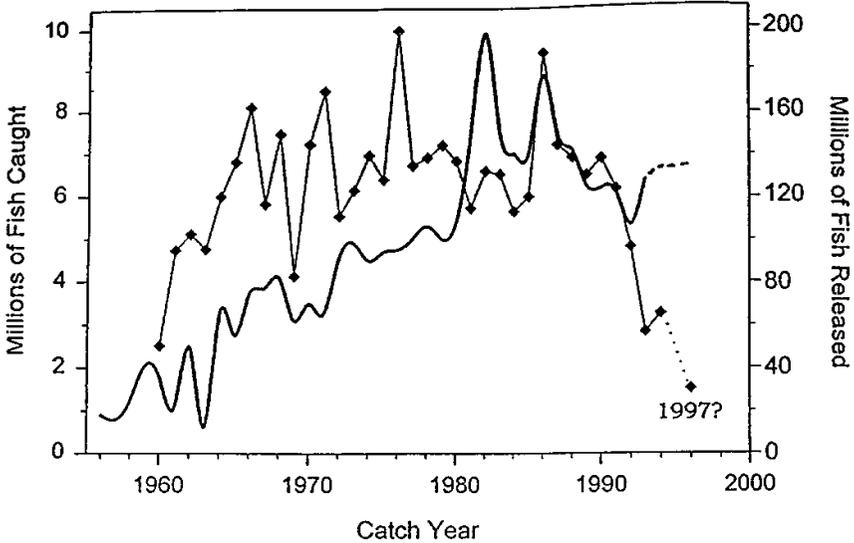


Figure 5. The estimated catch of coho salmon (line with diamonds) from British Columbia, Washington and Oregon (International North Pacific Fish Commission, statistical year books). Data from 1974 to the present include sports catch. The total hatchery production from British Columbia, Washington, and 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 million with a harvest rate of 50%. Assuming an equal sex ratio, 3,000 eggs per female, and a 2% survival from egg to smolt, there would be about 180 million smolts produced annually. Hatchery production averaged about 60 million (Beamish et al. 1997), leaving about 120 million wild smolts. Hatchery release year is lagged +1 year to match catch year.

movement of rearing types (Beamish et al. 1998c), the number of wild Canadian coho salmon entering the Strait of Georgia could be determined using the known number of hatchery releases and would be approximately 2.2 million. The total hatchery and wild smolt production, therefore, would be approximately 13 million fish. The minimal abundance estimate of 2.8 million represents 22% of this total smolt production or 19% if only smolts of Canadian origin are counted. If the actual abundance approximately is double because of a catchability of 0.5 rather than 1.0, the percentage of coho salmon remaining in the Strait of Georgia could approach about 40% of the number that entered salt water in the spring. In 1997, the total returns of coho salmon that entered the Strait of Georgia in 1996 (catch and spawning abundance) was less than 500,000 fish. The abundance es-

timate in September 1996 was 3.6 million (with 95% error limits of 5.1 million-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 preliminary estimates are that the total returns will be less than in 1997. 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.

Marine Pen Rearing Studies

Mahnken et al. (1982) studied coho salmon 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 salmon were in a smolt, transitional, or parr-like stage (Fig. 6). The parr-like stage resulted from some fish that did not develop into the other stages and fish 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 (Fig. 6B). In the net-pens, the size of the largest parred coho salmon (Fig. 6B) was a good indicator of the minimum size required for the fish 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 salmon it was possible to predict survival 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 reanalyzed the data of Mahnken et al. (1982) to compare ration size with cumulate mortality (Fig.7). In all experiments there was an abrupt increase in the trend between mid-September and early October in the low-ration experiments, with abrupt increases in mortalities ranging from 13 to 17%. The ration size was also related to the cumulative number of

stunted fish (Fig. 7), although there was not an abrupt change in the trend in late September. The rate of stunting (Fig. 7A) was greatest immediately following summer solstice. By winter solstice the commutative percentage of stunted fish was 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 (Fig. 7B) between September and November, with highest mortality in populations containing large numbers of stunted fish. Stunting continued to produce significant mortality at low-ration levels from November through termination of the experiment in March/April.

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 salmon require specific growth conditions in order to survive the changes that occur in their environment beginning in the fall of their first marine year.

Growth and Survival of Sockeye Salmon in the First Marine Year

One of the most extensive studies of marine growth and survival of Pacific salmon has been for Fraser River sockeye salmon (*O. nerka*). A number of investigators have produced some excellent data and analyses (Foerster 1954; Ricker 1962, 1982, 1995; Henderson and Cass 1991; Cox 1997). However, the relationship between size of smolts and total return remains unclear. Henderson and Cass (1991) showed that the larger smolts entering the ocean had higher marine survival. However, the years in which the average size of the smolts entering the ocean was larger did not produce higher average marine survivals; i.e., producing more larger smolts at the time of ocean entry would not necessarily produce a larger return. Henderson provided us with an extensive set of scale measurements of distance to the first ocean annulus (Fig. 8) for the 1949-1985 brood years, (1951-1987 years-to-sea). The scale measurements showed that the distance to the first marine annulus remained relatively constant, indicating that there could be a critical size of Chilko Lake sockeye salmon at the time of the first annulus formation in the ocean. Only the 1975 brood year, or the smolts that went to sea in 1977, were significantly different in size (much smaller). Despite this absence of a trend in sizes at the time of first annulus formation, others had observed a trend in adult sizes Ricker (1995) that changed with the regime change in 1976-1977 (Cox 1997).

According to our hypothesis, the explanation would be related to the two types of mortality in the first 12 months of ocean residence. The early marine mortality is size-related and predation-based, but the final regulation is size- or growth-related, which is a function of the carrying capacity. The numbers of juveniles reaching the critical size will vary, but the critical size would be more stable as it is a function of the intrinsic physiology of the sockeye salmon juvenile. The trend in adult size, however, is re-

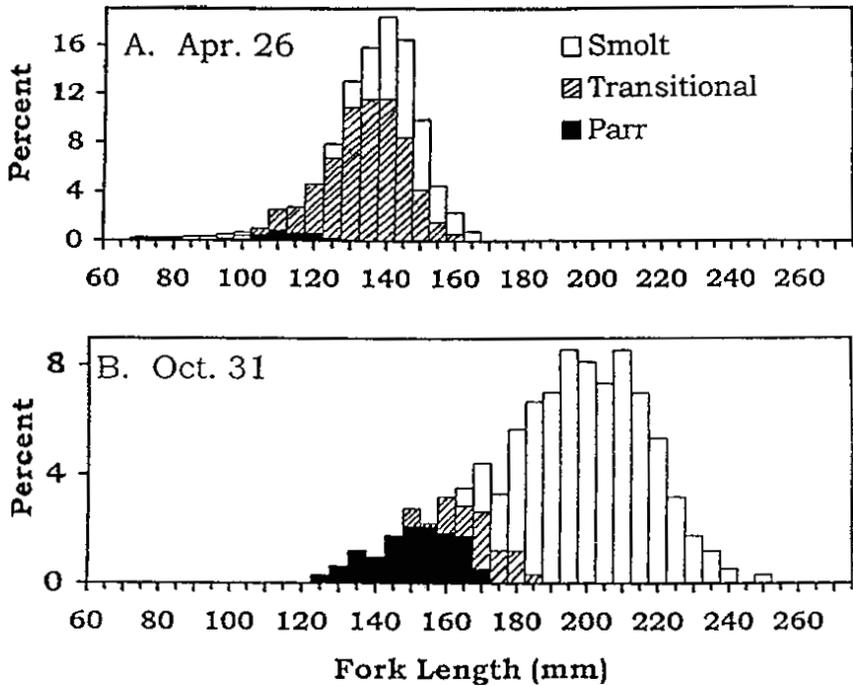


Figure 6. Fork length frequency distribution of coho salmon maintained in net-pens in salt water. (A) Early in the year (April 26) when coho salmon from 12 hatchery stocks were added, most fish were in a transitional state between parrs and smolts. (B) By October 31 few transitional fish were present. These fish would not survive winter conditions. The largest parrred fish (i.e., 170 mm on October 31) was considered to be the size below which coho salmon would not survive after the critical period. From Mahnken et al. (1982).

lated to the available food after the carrying capacity was established. We emphasize that at this stage in the development of this hypothesis, critical size may also be a critical growth rate which would allow for more variation in the size at the time of the formation of the first marine annulus. Our hypothesis, therefore, appears to explain the observations on marine growth and survival of Chilko Lake sockeye salmon. One problem is the anomalous 1975 brood year. Why would the critical size be different only for 1 year out of 27 years? These juveniles entered the ocean in 1977 and exceptional survival was recorded for many species in this year (Beamish 1993). It is possible that the winter conditions were exceptionally favorable and smaller juveniles were able to survive the winter according to the mechanisms reported previously by Folmar et al. (1982).

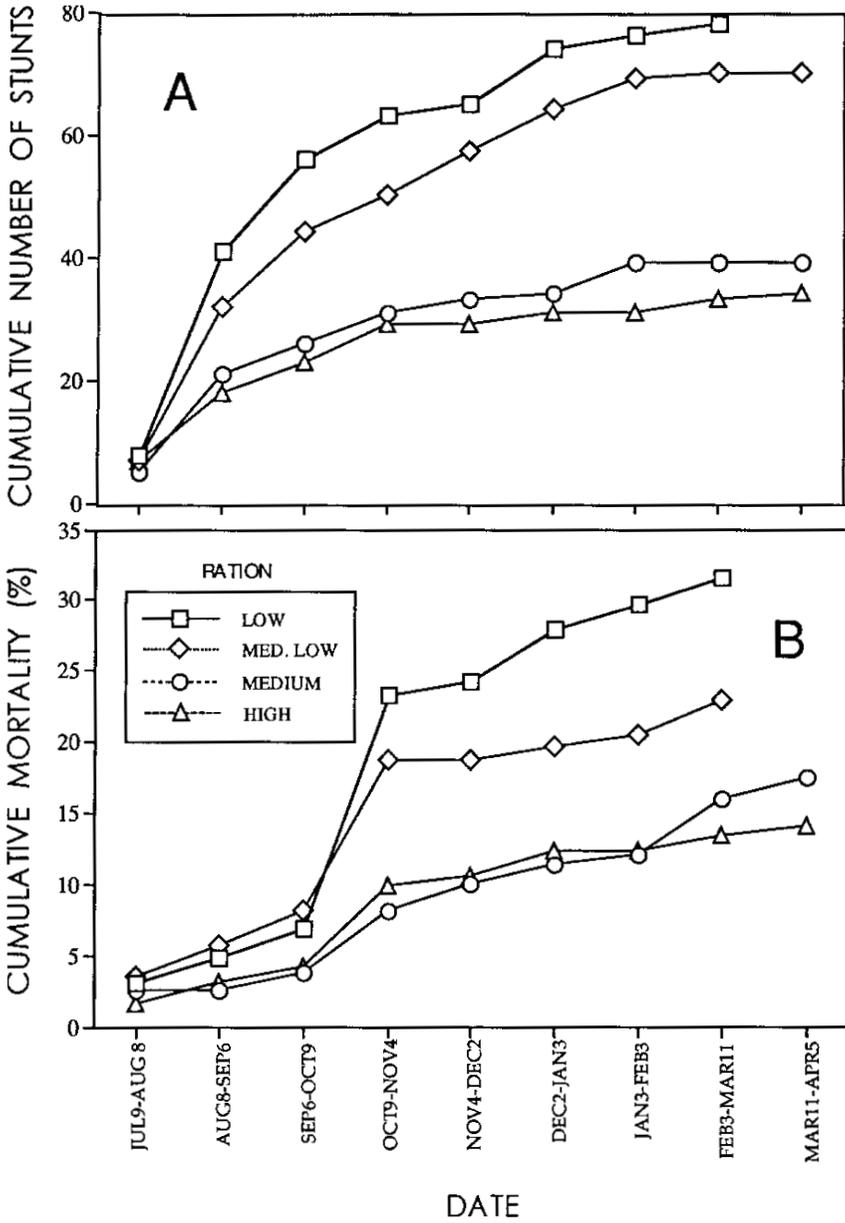


Figure 7. The data used in Fig. 5. (A) There was a larger number of stunted fish in the two experiments with the lowest rations that continued to increase in numbers throughout the study. (B) If aggregated by ration size there was a large increase in mortality between October 19 and November 4 for the two experiments with the lowest ration.

Climate Change and the Critical Period–Critical Size Hypothesis

There is an increasing amount of evidence indicating that Pacific salmon abundance is closely linked to long-term trends in climate (Beamish and Bouillon 1993, Hare and Francis 1995, Mantua et al. 1997). The linkage between the ocean environment and salmon abundance may be thought of in terms of carrying capacity. According to our hypothesis, changes in climate that affect ocean productivity and temperatures change carrying capacity by affecting the ability of juveniles to achieve a critical size in their first ocean year. According to this view, carrying capacity would be affected by the amount of food available in the summer months, competition for this food by other species, density-dependent competition from other juveniles of the same species, and physical conditions that affect the amount of energy required to find and metabolize food. It is apparent that a number of situations could interact to affect carrying capacity. For example, very high early marine predation-based mortality could reduce competition for food and improve summer growth and survival over the winter even if total food production was low. Warmer sea surface temperature can have the confounding effect of being associated with lower ocean productivity and higher metabolic rates, resulting in fewer juveniles surviving the winter. Adding more smolts to the ocean in a less favorable regime would probably reduce returns as competition for food and intrinsic population dynamics of a species may reduce the numbers of fish that achieve a critical size. Climate changes that alter the timing of food production could favor the survival of competing species. Again, the addition of more smolts should not be expected to improve returns, as it is the amount of food available to each fish in the summer that regulates returns and not the number of fish feeding. In periods of exceptional ocean productivity, as apparently occurred after the 1976-1977 regime shift (Beamish 1993), survivals tend to be better because competition for food is reduced. Perhaps the most dramatic impacts of climate impacts on carrying capacity are the changes in survival that occurred for coho salmon off Oregon and chinook salmon (*O. tshawytscha*) in the Strait of Georgia after the 1976-1977 climate change. Pearcy (1992) and Beamish et al. (1995a) both showed that abrupt declines in abundance and survival occurred even though more smolts were added into the ocean from hatcheries. In both cases, there was no evidence of large increases in predators and no explanation for the reduced returns. Clearly something changed, and we suggest that the change was increased winter mortalities resulting from reduced summer growth.

Density-Dependent and Density-Independent Effects

Traditional interpretations of the mechanisms regulating population size incorporate natural mortality that is density-dependent and density-independent. In simple language, density-dependent mortality is death from

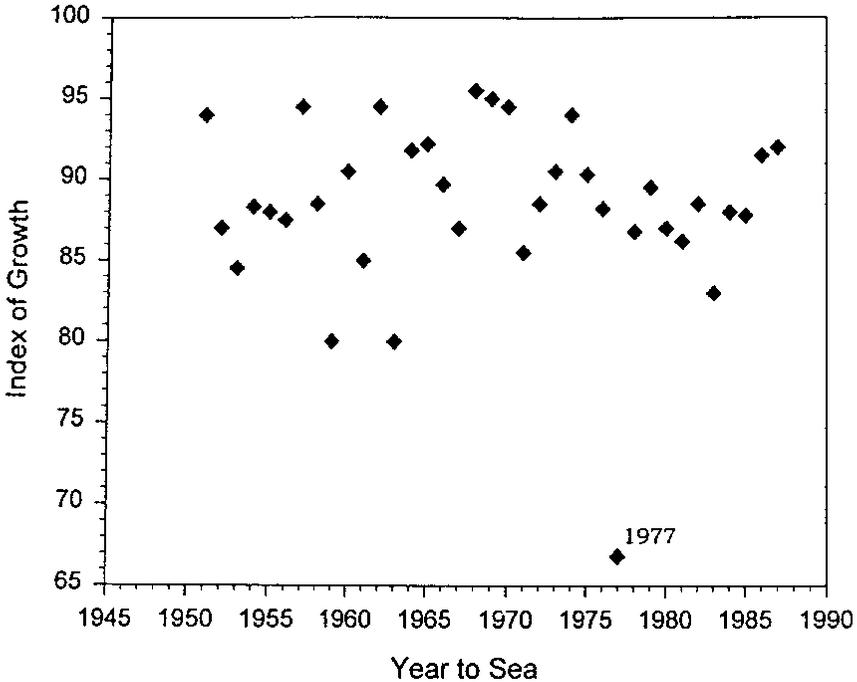


Figure 8. Index of growth of Chilkol Lake sockeye salmon during the first year of marine growth. Index is the scale distance between the last freshwater circulus and first marine annulus, magnified 87 times, using 100 scales each year collected from the spawning ground.

overcrowding. The causes are seldom known. Density-independent mortality is mortality associated with physical changes in the environment and is independent of the number of animals in a population. In a classical Ricker type of population response, these two factors affect the shape of the stock and recruitment curve (Ricker 1975).

Our critical size-critical period hypothesis identifies the ocean environment as having a powerful impact on the final stock size. In the Strait of Georgia, the conditions were clearly unfavorable for chinook salmon immediately and for coho salmon later (Beamish et al. 1995a, 1995b). At issue is the relationship to density. Because mortality is measured as a percentage, some biologists feel that if mortality is independent of density, the reduced percentage of survival caused by a change in the environment can be mitigated by producing more juveniles. Our hypothesis considers that the environmental effect is most important in the conditioning of juveniles for late fall and overwinter survival and is related to

the density of competitors for the common food resource, including other fish in the population.

At some theoretical level of smolt abundance, the population must stop increasing and the mechanisms must involve density-dependent interactions within the population, otherwise the populations would not be limited in abundance. Our hypothesis accounts for this theoretical control by proposing that competition for food in the summer is both external and internal to a population. As density increases, the internal processes become increasingly active.

Discussion

Ecosystem management of our fisheries is a logical progression from single-species management. There is growing concern about overfishing, a developing appreciation of biodiversity, and an understanding that we must protect our marine plants and animals. This interest has fostered a desire to broaden our protection of aquatic resources and the concept of stewardship of whole ecosystems has become a priority of many management agencies. Ecosystem management is not a new concept but it has not advanced very far because the urgency of single-species management overwhelmed the work required to understand associations with other species and with the environment. It is now time to establish a practical set of guidelines and begin to manage on a more holistic basis. There is a wealth of literature on the concept so it remains to find ways to apply the theories. Most importantly it is *time to begin the process*, which will be experimental in the beginning.

We recognize that it has been difficult to model marine ecosystems. We also recognize that it will not be possible to maintain annual sampling programs for all the appropriate parameters for all of the key species in the various ecosystems. However, we believe it is important to maintain a process that looks at general or larger-scale relationships. It is easy to be pessimistic about the possibility of managing ecosystems. It is equally easy to be optimistic about the information that can be obtained by participating in processes that practice this approach. Several authors have suggested that ecosystem management depends upon the good effort, good judgment and good faith of those involved.

Ecosystem management is a philosophical change in our management approach. Ecosystem management is an exercise in developing realistic expectations for our fisheries. Realistic expectations are a function of improved understanding of how the system works and ensuring that the public are informed about what we know and what we do not know. Ecosystem management is an exercise in long-term, precautionary thinking. It is acceptable not to know things. It is not acceptable to place self-interest ahead of a resource. In some respects we may have to start over again. Native species and natural ecosystems need to be recognized and protected.

We do not have to defend our inability to understand the impacts of everything humans want to do to ecosystems. We do need to ensure that we are not preventing species from replenishing themselves. Be careful about promising stability. We need to recognize that extreme events may be rare but they are a normal factor in the natural selection process. One of the most difficult aspects of ecosystem management is communication among scientists. Experts in the private or public sectors are going to have to find ways to communicate their knowledge so that a collective wisdom is provided to managers. You have to be able to talk to your colleagues. You do not have to like them: just be able to work together.

We suggest that our hypothesis of the natural regulation of salmon abundance can be used as a simple example of ecosystem management. Abundance of salmon is more than a function of the abundance of spawning females. Climate is important. 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).

Some biologists believe that studies of the mechanisms that regulate salmon abundance in the ocean are not useful in management because we cannot control the ocean. First, it certainly is debatable if our perceived "control" is real. Second, 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 dismal understanding of how they work. We may expect that a better understanding of the mechanisms regulating carrying capacity will provide a better understanding of both how many fish should spawn and the importance of maintaining diversity within the life history types. We would no longer equate the straightforward production of smolts with the expectation of ever-increasing returns until some desirable historic catch is achieved. We also would understand why it is so difficult to identify stock and recruitment relationships using recruitment estimates determined before smolts enter the ocean. With such a complex set of factors in the ocean that regulate the final returns, the process of estimating the returns before any marine mortality has occurred is particularly difficult. Improving our understand-

ing of the mechanisms that regulate abundance of salmon in fresh water and in salt water improves the credibility of management for those that either harvest salmon or value knowing that stocks are healthy. Improving our understanding of ecosystems improves everyone's appreciation of the impact of our own intervention into our ecosystems.

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