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.
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.
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.

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.
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 $18 \times 15$ 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 $45 \times 45$ 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-
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 6. Fork length frequency distribution of coho salmon maintained in netpens 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 parred 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).
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
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

Figure 8. Index of growth of Chilko 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.
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.

References


Climate Variation, Ecosystem Dynamics, and Fisheries Management in the Northwestern Hawaiian Islands

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Abstract
A dramatic ecosystem shift from high to low carrying capacity occurred in the late 1980s in the northern portion of the Hawaiian Archipelago. This shift was observed for a range of trophic levels and species including seabirds, monk seals, spiny lobsters, and reef fishes. Concurrent with the ecosystem shift were physical changes associated with weakening of the Aleutian Low Pressure System and the Subtropical Counter Current. A trap fishery operating at Maro Reef rapidly depleted the spiny lobster population after the ecosystem shift. At an adjacent bank, Laysan Island, closed to commercial lobster fishing, the spiny lobster population declined much more gradually but ultimately was depleted as well. Harvest from the lobster fishery during much of the 1990s averaged about 25% of the harvest in the 1980s. Fishermen adjusted to the reduced harvest by moving into the pelagic longline fishery which was apparently not impacted by the ecosystem shift.

Introduction
The Northwestern Hawaiian Islands (NWHI) comprise a 1,500 km chain of islands, atolls, coral reefs, and banks in the northern portion of the Hawaiian Archipelago (Fig. 1). The region has no permanent human population but supports a rich marine ecosystem. In the mid-1970s a comprehensive research effort began to study various components of this ecosystem which
led, in subsequent years, to standardized time series of indices of ecosystem productivity and population abundance for some components of this ecosystem. These indices and other survey data will be used to describe the sudden ecosystem shift which occurred concurrently with a climate shift in the late 1980s. One of the resources we will examine is the spiny lobster which is targeted by a commercial trap fishery and hence provides an example of interactions between both fishery and climate impacts.

The Climate Shift

A North Pacific climate event characterized by an intensification and southward shift in the Aleutian Low Pressure System occurred during 1977-1988 (Trenberth and Hurrell 1994). This climate shift impacted the northern portion of the Hawaiian Archipelago, probably through a southward shift of winter storm tracks and increased wind speed and stress, resulting in a deepening of the mixed layer depths by 30-80% during the winter (Polovina et al. 1994, 1995). An ecosystem model of nitrate, phytoplankton, and zooplankton driven by mixed layer depth was used to evaluate the impacts to the plankton ecosystem from the lower light but greater nutrient levels caused by the deeper mixed layer depth during the 1977-1988 period. The model suggested that due to nutrient limitation in the NWHI, the deeper vertical mixing observed during this climate shift could increase both phytoplankton and zooplankton production by 50% (Polovina et al. 1995).
Changes in vertical mixing are only one physical response; another is a change in horizontal transport. Data from tide gauges along the archipelago suggest that the Subtropical Counter Current (SCC), which crosses the northern portion of the Hawaiian Archipelago, was stronger during 1977-1985 and weaker subsequently (Polovina and Mitchum 1992). A positive correlation between an index of the strength of the SCC and recruitment to the fishery 4 years later at Maro Reef has been documented (Polovina and Mitchum 1992). It is not known whether the stronger SCC was the result of the more intense Aleutian Low or just coincidental, but both features were strong from 1977 until the mid-1980s and then shifted to weaker states which have persisted at least through the mid-1990s. Concurrent with this shift in physical features, a drop in ecosystem carrying capacity in the NWHI was observed, which we believe resulted from this climate shift.

The Ecosystem Shift
Time series of indices of productivity for spiny lobster (*Panulirus marginatus*), the Hawaiian monk seal (*Monachus schauinslandi*), and two species of seabirds, the red-footed booby (*Sula sula*) and the red-tailed tropicbird (*Phaethon ruricauda*), all show declines between the 1980s and 1990s (Fig. 2). In the case of spiny lobsters, indices of recruitment of 3-year-olds at two banks, Necker Island and Maro Reef, are measured as the catch rates from an annual standardized research survey. At Maro Reef 3-year-old recruitment completely collapsed in the late 1980s and has not shown any recovery since, while at Necker Island, 750 km southeast of Maro, recruitment dropped about 50% in the late 1980s but has shown some subsequent recovery (Fig. 2). In the case of monk seals, pup survival, measured as the fraction of pups born which survive to age 2, sharply declined at French Frigate Shoals in the late 1980s with no subsequent recovery, while at Laysan Island, north of French Frigate Shoals, the decline was more gradual (Fig. 2). For both species of seabirds at French Frigate Shoals reproductive success, measured as the fraction of eggs laid which result in fledgling chicks, shows a sharp drop of about 50% between the early 1980s and the period since the mid-1980s (Fig. 2). When lobster and monk seal time series are shifted backwards 2 or 3 years to account for the appropriate time lags (lobster data are for 3-year-olds, monk seal data are based on 2-year-olds), temporal coherence between the time series is seen. While the causes of these declines have not been completely determined, in the case of monk seals and seabirds field observations suggest reduced food availability during their winter fledgling season is a likely factor. A reduction in food availability has been cited as the reason for declines in reproductive success in other seabird populations (Baird 1992). In the NWHI in the 1990s, the higher egg mortality appears to be the result of longer exposure to the sun and higher chick mortality to be the result of starvation, all of which are consistent with lower food availability for adults.
resulting in more time spent away from the nest foraging and less food for the chicks. These seabirds forage primarily on flying fishes and squids which are linked to oceanic rather than reef productivity.

The decline in monk seal pup survival has also been inferred to be the result of a decline in prey, based on widespread observations of emaciated pups and the lack of other identifiable causes including direct human impacts and disease (Gilmartin and Ragen 1992). The diet of monk seal pups is not known but generally the areas and depths where they are seen foraging suggest they forage on prey in the benthic coral reef and shelf ecosystem. Like the seabirds, winter appears most critical to monk seal pup survival since the pups first forage then.

The reef fishes are a major component of the NWHI ecosystem, and given the remote location of the region, are not impacted by human exploitation. While a continuous time series of reef fish densities is not available, comparisons between densities at the same reefs at French Frigate Shoals and Midway Atoll between the early 1980s and early 1990s show that densities in the early 1990s are about one-third lower than in the early 1980s, providing still another indication of the drop in carrying capacity seen in other elements of the ecosystem (DeMartini et al. 1996).
Climate and Fishery Interactions

The catch rate of 3-year-old spiny lobsters at Maro Reef, obtained from standardized research cruises and used as an index of recruitment to the fishery, showed a dramatic collapse in 1990 (Fig. 2). Age composition of the trap catches from these research cruises shows an abundance of 3-year-olds along with some older and younger lobsters in 1987 and 1988, but since 1990 and persisting through the present, the spiny lobster population at Maro Reef appears to be severely depleted (Fig. 3). Unfortunately, 1989 age-frequency data which might show a transition between 1988 and 1990 levels are not available due to the lack of a research cruise in 1989.

Maro Reef and Necker Island were the two primary fishing grounds for the lobster trap fishery during the 1980s, and annual harvest at Maro Reef during that period ranged from about 200,000 to 450,000 lobsters (Fig. 4). The picture from Figs. 2-4 suggests a collapse in recruitment of 3-year-old spiny lobsters to the fishery in 1989, as a result of a sudden weakening of the SCC during the mid-1980s (Polovina and Mitchum 1992). The fishery was largely harvesting a single age group, 3-year-olds, and with the collapse in recruitment to the fishery in 1989, the remaining population of older lobsters was quickly depleted by the fishery.

Laysan Island, about 110 km north of Maro Reef, has been closed to commercial lobster trapping since the beginning of the fishery to protect the large population of monk seals on Laysan from becoming entangled in lobster traps and line. Limited research trapping at Laysan shows an absence of 2- and 3-year-olds in 1991 compared to 1977 and 1986, suggesting that the recruitment collapse which impacted Maro Reef also impacted Laysan by 1991 (Fig. 5). However, apparently due to the absence of a fishery at Laysan, unlike at Maro Reef, there was still a significant population of older animals at Laysan. Unfortunately, by 1996, even in the absence of a fishery, the lobster population at Laysan was severely depleted, apparently the result of the collapse of recruitment in the mid-1980s and the subsequent impact of natural mortality (Fig. 5).

Response of Fisheries Management

Since 1983, the fishery has been regulated under a fishery management plan by the Western Pacific Regional Fishery Management Council, primarily with a minimum size set slightly above the size at onset of maturity, escape vents in traps to allow escapement of sublegal lobsters, and some areas closed to fishing. These closed areas, although not specifically designed to protect lobsters but rather to reduce fishery interactions with protected species, did close perhaps as much as 10% of the lobster habitat to trapping, including all of Laysan Island and all portions of banks shallower than about 20 m.

The sudden collapse of the spiny lobster population in 1990 caught fisheries managers by surprise. In 1989 a dynamic production model was
Figure 3. Age-frequency of spiny lobsters from Maro Reef research cruises.

Figure 4. Commercial landings of spiny lobsters from Maro Reef.
used with historical commercial fishery data to estimate a maximum sustainable yield (MSY) for the NWHI fishery (slipper and spiny lobsters combined) of 1 million lobsters, with an effort of 1 million trap-hauls (Polovina 1990). The 1989 fishery catch and effort of about 1.2 million lobsters and 1.1 million trap-hauls suggested the fishery was at about MSY levels. However, by 1990 it was obvious that the population of spiny lobsters at Maro Reef and other northern banks had collapsed. The report on status of the stocks in 1990 (Polovina 1991) noted that the spiny lobster spawning biomass was estimated at 22% of the pre-fishery level and recommended both a seasonal closure from January through August to protect spawning biomass, and a reduction of annual effort to 200,000 trap-hauls.

Catch and effort were not restricted during 1990, and about 775,000 lobsters were caught with 1.2 million trap-hauls. The collapse of a portion of the spiny lobster population in 1990 without any reduction in effort, meant that the performance of the fishery measured as the catch rate (the ratio of total catch divided by total effort) dropped 40% between 1989 and 1990. Prior to 1990, industry was not generally supportive of restrictions
on catch or effort. Their argument was that it was unnecessary since the fishing grounds are remote and effort would cease once catch rates fell below an economically viable level which was sufficiently high to protect against recruitment overfishing. However, the 1990 season showed that there was excessive fishing capacity in the industry given the reduced population size and raised concern that an economic threshold might not prevent overfishing. Responding to this concern, the Western Pacific Regional Fishery Management Council closed the fishery under an emergency closure from May 8 to November 11, 1991, and implemented new management regulations in 1992. These new measures added regulations to the existing management measures, including a closure during the first half of the year to protect spawning biomass and a harvest quota to control harvest during the second half of the year. Initially the new harvest quota approach resulted in high interannual variation: a combined slipper and spiny lobster NWHI harvest of about 850,000 for 1992 followed by a closure of the fishery in 1993. However, from 1994 to 1997 quotas were in the range 101,000-310,000, well below the long-term MSY of 1 million lobsters estimated prior to the collapse at Maro Reef. Under this lower harvest, catch rates for spiny lobsters at Necker Island recovered about 50%, from 0.5 to 0.75 lobsters per trap-haul, but spiny lobsters at Maro Reef have not recovered since the 1990 collapse, although there has been a substantial increase in slipper lobsters at Maro Reef.

Recent research suggests that the source of spiny lobster larvae at Maro Reef is the spawning population at Maro Reef and hence the recovery of the spiny lobster population at Maro Reef may be a long, slow process based on rebuilding the resident spawning biomass (Polovina et al. 1999). The industry has been generally supportive of the management action reducing harvest levels. One important reason for this support was that all 15 permit holders were also able to obtain permits for the pelagic longline or bottomfish fishery, so their economic condition was not tied solely to the lobster fishery.

In the absence of the evidence of a climate and ecosystem shift, management might have a goal of rebuilding the fishery to achieve an MSY of 1 million lobsters. This would require closing the fishery for an extended period, but it is unlikely this recovery is achievable under the current less productive regime. Current management action recognizes there is a much lower MSY under the new physical and ecosystem regime.

**Summary**

A shift in climate occurred in about 1989 in the central North Pacific characterized by a weakening of the SCC and Aleutian Low Pressure System. The NWHI ecosystem shifted, apparently triggered by the climate shift, from a high carrying capacity to a low one. The shift occurred rapidly and nearly simultaneously over a range of trophic levels. There are significant spatial patterns; for example, the drop in spiny lobster recruitment was
greatest in the northern portion of its range while the drop in pup survival for monk seals was greatest at the southern end of its range. It is likely that there is not one physical cause for this ecosystem shift. In the case of lobster, evidence suggests that a reduction in lobster larval retention at Maro Reef occurred with the weakening of the SCC. In the case of seabird reproductive success and monk seal pup survival, evidence suggests a decline in prey arising from lower primary productivity attributed to weaker vertical mixing.

At Maro Reef, fishing prior to the drop in productivity reduced that population age structure, making it less resilient to interannual recruitment variation. After the recruitment collapse, a few years of unrestricted fishing at Maro Reef quickly eliminated most of the remaining spawning biomass. These results illustrate interactions between fishing and climate shifts: fishing alters the age-structure and can rapidly deplete a stock when the ecosystem shifts to a regime of lower carrying capacity. At Laysan, protection from fishing preserved more of the age structure but after a decade of poor recruitment, the spawning biomass was apparently depleted from natural mortality. Thus marine reserves may not always provide the protection many proponents assume.

One consequence of the collapse in the spiny lobster fishery at Maro Reef is that it raised concern about the ability of open access management to protect the spiny lobster population and provided the impetus to managers and industry to move to a limited access fishery with harvest controls. The ability of management to reduce catch and effort to about one-fourth the level prior to the stock collapse at Maro Reef was greatly facilitated by the permit holders who all had permits for the pelagic longline fishery and were able to move into another fishery not impacted by the ecosystem shift. Therefore, one step fisheries management can take to prepare for the impacts of climate variation is to encourage fishermen to diversify between fisheries that are not likely to fluctuate together. Unfortunately, the current trend toward limited access fisheries may restrict the ability of fishermen to diversify.

It has been a decade since the last climate and ecosystem shift. An issue of great interest to all those involved with the NWHI ecosystem is whether these states alternate on a decadal cycle so we can look forward to a return to a more productive period in the near future or whether these shifts are rare and irregular events.

References


Spatial and Temporal Patterns of Covariation in Components of Recruitment of British Columbia and Alaska Sockeye Salmon

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Extended Abstract

Sockeye salmon (Oncorhynchus nerka) populations typically show large year-to-year variation in survival rates, body size at maturity, and age at maturity. To better manage these stocks, it is important to understand the spatial and temporal scales over which environmental processes drive this variation in each component of recruitment. We used a multi-stock comparison to identify these spatial and temporal characteristics of variability using data from the late 1940s through brood year 1992 returns for 29 sockeye stocks from a wide geographical area across British Columbia and Alaska: 16 Fraser River stocks (southern British Columbia), the Skeena and Nass River stocks (central British Columbia), the Copper River and Upper Cook Inlet stocks (central Alaska), and 9 Bristol Bay stocks (western Alaska). These stocks overlap to varying degrees during their marine life stage.

Specifically, we examined patterns of covariation among these stocks using time-series indices of (1) survival rate (residuals from the best-fit
stock-recruitment curve); (2) length at a given adult age; and (3) mean age at maturity. For each component of recruitment, we computed pairwise correlation coefficients among the various stocks. In addition, we used (step) intervention analysis to quantify changes in survival-rate indices coinciding with the regime shift in climatic and oceanographic conditions that occurred in the North Pacific in the mid-1970s (Graham 1994). For indices of body size and mean age, we used principal components analysis (PCA) to further identify the temporal patterns of variability shared among stocks.

For indices of survival rate, we found strong positive covariation among the nine Bristol Bay stocks (all 36 correlations were positive; average $r = 0.44$), and weaker but predominantly positive covariation among the 16 Fraser River sockeye stocks (102 of the 120 correlations were positive; average $r = 0.16$). However, there was no evidence of positive covariation between Bristol Bay and Fraser River stocks (average $r = -0.05$) or with stocks of other regions in British Columbia and Alaska. These results suggest that regional-scale environmental processes influence survival rates of sockeye stocks within each region (i.e., Bristol Bay or Fraser River), and that these processes are distinct for each of these two regions. Furthermore, intervention analysis showed that there were large and persistent increases in the mean productivity of all nine Bristol Bay stocks coinciding with the mid-1970s climate shift. In contrast, survival rates of the 16 Fraser River stocks did not show a consistent response to the climate shift: some increased, some decreased, and many remained largely unchanged. Thus, these results and others presented in Peterman et al. (1998) and Adkison et al. (1996) suggest that environmental processes driving variability among survival rates of Fraser River sockeye stocks differ from those processes affecting Bristol Bay sockeye, and that only the latter were strongly influenced by the mid-1970s climate shift.

For body size at maturity, we found widespread positive covariation across all ages and stocks from British Columbia and Alaska (2,335 of the 2,556 correlations were positive; average $r = 0.37$). There was evidence of both distinct, within-region patterns of covariation, as well as positive covariation between regions. For example, for lengths of age 1.2 fish, there was a strong tendency toward positive covariation among Bristol Bay stocks (all 28 correlations were positive; average $r = 0.50$) and among Fraser River stocks (all 190 correlations were positive; average $r = 0.60$), with weaker but predominantly positive covariation between these two regions (136 of 160 correlations were positive; average $r = 0.23$). The stronger covariation within regions indicates that regional-scale processes are important determinants of final body size of sockeye salmon. In addition, the positive covariation between regions suggests that, to some extent, either fish of different regions share similar distributions during periods critical to growth, or that these fish have different distributions at such times but are influenced similarly by large-scale environmental processes. In addition, we found that much of the covariation in body size across ages and
stocks was due to shared declining trends over time. The dominant principal component for body size, which accounted for 58% of the total variation, had a significant decreasing time trend \( (P < 0.001) \) over the period 1971-1997. These declining trends in body size of British Columbia and Alaska sockeye salmon may be related to physical oceanographic variables and ocean abundance of salmon (Cox and Hinch 1997).

Indices of age at maturity also showed positive covariation within and between regions, although the covariation was weaker (394 of the 496 correlations were positive; average \( r = 0.17 \)). The dominant principal component (accounting for 33% of the total variation) for mean age had a significant increasing time trend \( (P < 0.001) \) from 1971 to 1994. These patterns of covariation and time trends in mean age suggest similar hypotheses about important environmental processes as discussed above for body size. Pyper et al. (1999) provides more detailed results on these analyses of body size and age at maturity.

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Predictability of Returns of Sockeye Salmon (*Oncorhynchus nerka*) to Bristol Bay, Alaska, 1-4 Years in the Future

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**Extended Abstract**

A variety of forecasting methods has been used to forecast Bristol Bay sockeye salmon (*Oncorhynchus nerka*) returns 1 year into the future (Fried and Yuen 1987, Rogers 1997, Cross 1998). However, none of the methods has performed exceptionally well, particularly recently. Our purpose in this study was to improve the accuracy of preseason forecasts of sockeye salmon returns to Bristol Bay by selecting the most appropriate set of independent variables for forecasting. In addition, we wanted a reliable estimate of the uncertainty of such forecasts, a goal that may be even more important for some purposes.

We used cross-validation to select among several candidate forecasting models and to estimate the probable error in forecasting (Efron and Tibshirani 1993). Cross-validation estimates the error in forecasting by repeatedly fitting a model to subsets of the data and using these model fits to forecast the left-out data (the validation data). Because the parameters of the model are chosen as if the validation data were not yet known, forecasting these data is analogous to forecasting future observations. Thus, the errors in forecasting the validation data should be of similar magnitude to those of future forecasts.
We constructed forecasts and confidence intervals for sockeye salmon returns to each of the nine principal Bristol Bay drainages 1 to 4 years in the future. We used cross-validation to select among a wide class of models (Adkison et al. 1996) that could include as independent variables the number of spawners, sibling returns, air and sea surface temperatures, and the previous year’s deviation from the expected return. We found that no combination of predictor variables provided highly accurate forecasts. A typical 80% confidence interval for predicting returns to a drainage 1 year in advance spanned a four-fold range. Confidence intervals for forecasts 2-4 years in the future were even wider.

Using cross-validation to estimate the forecast error apparently resulted in an accurate representation of the uncertainty in future returns. The coverage probability of the confidence intervals about the forecasts was generally what it should have been. However, the returns in 1996, 1997, and 1998 were well below the forecast and outside of the 80% confidence intervals.

References


Comparison of Methods for Detecting Climate-Induced Changes in Productivity of Pacific Salmon Stocks

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Extended Abstract

Recent research has shown that Pacific salmon populations can experience abrupt and persistent changes in mean productivity that appear to be closely related to climatic changes. However, it is difficult to forecast such non-stationarity in salmon productivity because of large uncertainties about mechanisms that link climatic changes, freshwater and oceanographic conditions, and salmon. Furthermore, inseason monitoring of salmon abundance and changes in regulations have not usually been able to make up for such errors in forecasts when attempting to meet management objectives. Therefore, management agencies need methods to reliably detect and respond to such changes in productivity in a timely manner to avoid costly, suboptimal harvests or depletion of stocks. The purpose of our research was to compare the effectiveness of various parameter estimation methods at tracking such changes in a timely, accurate, and precise manner.

To meet this objective, we evaluated the relative effectiveness of several methods of annually updating estimates of parameters of Ricker stock-recruitment relationships: standard regression, Walters’ (1990) bias correction to that regression, and a Kalman filter. The latter is a method often used by electrical engineers to more accurately estimate the underlying signal amidst noise. However, with a few exceptions, this method has rarely been used in fisheries. We used Monte Carlo simulations in which we hypothesized a wide range of possible future climate-induced changes in productivity of a salmon stock. We represented such changes by a time-varying $a$ parameter in the Ricker model because Adkison et al. (1996) documented that this parameter, rather than the Ricker $b$, showed
consistent changes across Bristol Bay sockeye salmon stocks in the 1970s in response to major climatic changes. We analyzed three types of scenarios in a: a sine wave with a 60-year period, a “step” function with a 60-year period, and an autoregressive a.

We then used each parameter estimation method on the stochastic simulated stock-and-recruitment data to estimate the population’s parameters each year and set escapement targets and harvest goals accordingly. Because errors in parameter estimates translate into deviation from the true optimal escapement, we compared parameter estimation methods in terms of their resulting cumulative harvests and their accuracy and precision. We compared these methods to a fixed harvest rate policy that has been advocated previously for such nonstationary situations (Walters and Parma 1996). We also compared the resulting harvests to what could be obtained if there had been perfect knowledge of the true a parameter each year (i.e., expected value of perfect information).

The Kalman filter resulted in greater catch than the standard least squares approach for the scenarios that used an underlying 60-year sine wave or step function in the Ricker a parameter. However, for the scenario with an autoregressive a, these two methods gave roughly the same catches. Walters’ (1990) bias correction method consistently performed more poorly than the Kalman filter and least squares methods. All of these methods also generated greater catch than the best fixed-harvest-rate strategy.

The results above were derived from analyses where the model assumed “perfect control,” i.e., if a particular escapement goal was estimated, it was achieved exactly as long as recruitment was greater than that goal, and catch was simply the excess of recruitment over the goal. When recruitment was too low, catch was zero. However, this assumption of perfect control generated catches that were almost as large as the expected value of perfect information. Therefore, in a second set of analyses, we assumed “implementation error,” whereby the target was never achieved exactly, which reflects the field situation in which preseason and inseason knowledge of abundance is imperfect, as is control over harvest rate. When implementation error was added, the cumulative catches from all parameter estimation methods dropped dramatically and there was a smaller difference between catches from different parameter estimation methods.

The Kalman filter did better than least squares in some scenarios because it generally had more precise parameter estimates and therefore more estimated target escapements fell near the true optimum than with least squares. Analogously, Walters’ (1990) bias correction method did not perform as well as the other approaches because, although its parameter estimates were less biased, they were also less precise (Korman et al. 1995), which caused estimated optimal escapements to deviate further from the true optimum than with the other two approaches. However, the potential advantage of a Kalman filter in tracking changes in productivity can only be realized if there also is drastic reduction in implementation error.
References


Influence of Physical Processes on the Early Life History Stages of Walleye (*Stizostedion vitreum*) in Western Lake Erie

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**Abstract**

Physical processes create the environmental settings in which biological processes occur. Therefore, physical processes can have strong effects on fish populations, especially during vulnerable early life history stages. Much of the variability in recruitment of Lake Erie walleye is thought to be caused by variable survival during the egg and larval stages. Recent research on Lake Erie walleye indicates that density-independent physical processes directly affect the vital rates of these early life history stages. In western Lake Erie, large scale storm events in spring were related to high mortality of walleye eggs and larvae on reefs and subsequently produced poor recruitment. In addition, variability in environmental conditions (e.g., water warming rate) prolongs life history stage durations over which high mortality rates operate. Slower water warming rates in western Lake Erie prolonged walleye egg incubation and pelagic larval stages extending the
period of vulnerability to disease and predation for these early life history stages and negatively impact year-class strength. Physical processes rarely function independently but facilitate the underlying ecological mechanisms that drive fish population dynamics. Therefore, it is essential to examine physical processes in relation to biological processes in order to gain a more complete understanding of the linkages between them. By doing so, we gain a stronger basis for predicting the response of fish populations to environmental variability.

Introduction

Physical processes and other abiotic factors can have powerful, although usually indirect, effects on fish population and community dynamics by creating the environmental conditions in which many important biological processes operate (Dunson and Travis 1991). While many physical processes are difficult to predict (e.g., weather), we can gain insight into the response of fish populations to such factors by understanding how physical processes influence fish and their habitat. Therefore, it is important to identify and understand the various physical processes that structure fish populations and determine how physical processes influence the biological processes involved in fish population dynamics.

Lake Erie supports the world's largest naturally reproducing population of walleye (*Stizostedion vitreum*), producing valuable sport and commercial fisheries in the United States and Canada. Like most natural populations, Lake Erie walleye have exhibited significant variation in year-class strength over the past 20 years. The abundance of age-2 fish entering the stock has fluctuated nearly 60-fold since 1977 (Fig. 1) and the causes of this recruitment variability have been unclear (Henderson and Neepszy 1994, Madenjian et al. 1996). Recent field research in western Lake Erie, however, reveals the importance of density-independent physical processes in walleye year-class formation with the strongest year classes occurring in years with fast water warming rates and few storm events during egg incubation and larval dispersal periods (Mion 1996, Roseman et al. 1996). These studies concluded that variability in environmental conditions influenced the timing of life history events and caused differential survival rates during the egg and larval stages which translated into variability in recruitment to the adult stock. The goal of this paper is to review the effects of physical processes occurring in western Lake Erie on the vital rates (development, growth, and survival) of the egg and larval stages of walleye to gain a better understanding of how these processes temper the environmental setting for year-class development.

Because walleye are the dominant predator in Lake Erie and support important sport and commercial fisheries, fluctuations in their population size and structure can have direct implications for the entire Lake Erie ecosystem and local economies. For example, Knight and Vondracek (1993) found that increases in the abundance of walleye in the late 1970s played
a major role in the decline in abundance of soft-rayed species such as emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius*), and alewife (*Alosa pseudoharengus*). They concluded that management goals focusing primarily on walleye affected not only the targeted species but the entire fish community of western Lake Erie. During this same time period, abundant walleye populations attracted interest throughout the midwestern United States and led to the development of a substantial sportfishing industry in the states bordering the lake as well as a rejuv- nated commercial gillnet fishery in Canada. Consequently, fluctuations in the walleye population have resulted in direct economic consequences to businesses and families relying on these fisheries (Knight 1997, Lichtkoppler 1997).

*Figure 1. Number of age-2 walleye entering the Lake Erie stock as determined by Ohio Division of Wildlife fall gillnet surveys (Turner et al. 1998).*
Walleye Life History

Walleye are the dominant predator in the western basin of Lake Erie and are supported by a prey base of gizzard shad (Dorosoma cepedianum), alewife, shiners, white perch (Morone americana), white bass (Morone chrysops), and yellow perch (Perca flavescens) (Knight and Vondracek 1993). Walleye spawn on mid-lake reefs in the western basin as well as in tributaries such as the Maumee and Sandusky rivers (Fig. 2). Spawning typically begins shortly after ice-out and peaks around the middle of April (Baker and Manz 1971, Roseman et al. 1996). Walleye broadcast their eggs over hard substrates and provide no direct parental protection. Eggs typically hatch in 7-15 days depending on water temperature (Hurley 1972, Nepszy et al. 1991, Roseman et al. 1996). Small interstitial spaces in the substrate provide the benthic eggs protection from predation and displacement but eggs remain vulnerable to physical processes such as water warming rate, wind-induced wave and current action, and sedimentation that can influence the duration of the egg stage and subsequently their survival (Fig. 3) (Roseman et al. 1996).

In Lake Erie, walleye larvae emerge from the substrate immediately upon hatching and rely on lake currents for transport to nursery areas (Nepszy et al. 1991). The yolk sac is usually absorbed after 3-5 days depending on temperature when the larvae are about 9.5 mm total length (TL). The duration of the pelagic larval stage is temperature-dependent and typically lasts from 3 to 4 weeks until the young fish become demersal at about 30 mm TL (McElman and Balon 1979). Due to their small size, limited mobility, and delicate nature, larval walleye are susceptible to the influence of a variety of direct and indirect influence from physical processes like water temperature and wind-generated currents that can influence the timing and magnitude of larval development, growth, and survival (Fig. 3).

Physical Processes Influencing the Early Life History Stages of Walleye

Water temperature has been shown to be one of the most influential physical factors in walleye egg development and survival (Allbaugh and Manz 1964, Hurley 1972). Laboratory experiments have demonstrated that optimal egg survival occurs when water temperatures increase from 5°C at a rate of 1°C per day (Smith and Koenst 1975). Incubation periods are lengthened when waters warm more slowly, thereby increasing the time eggs are exposed to predation, disease, and severe wind events (Wolfert et al. 1975, Roseman et al. 1996). In western Lake Erie, Busch et al. (1975) and Roseman et al. (1996) found a positive relationship between water warming rate and walleye year-class strength. The index of fall walleye abundance never exceeded 5 fish per hour of trawling when waters warmed at a rate less than 0.2°C per day but greatly exceeded that number at higher warming
Figure 2. Map of Lake Erie detailing the western basin. Dotted ellipse represents mid-lake reef complex.
Figure 3. Conceptual model of physical and biological processes that influence walleye early life history stages.
rates (Fig. 4), indicating that 0.2°C per day may be a critical minimum threshold warming rate for walleye egg survival in western Lake Erie.

Water temperature mediates larval walleye activity including metabolism, feeding rate, growth rate, and ultimately, survival (Hokanson and Koenst 1986, Santucci and Wahl 1993, Mion 1996, Roseman 1997). Hokanson and Koenst (1986) reported that larval and juvenile walleye exhibited optimum growth in laboratory experiments at temperatures between 22º and 28ºC. Growth rate and development of sac fry is temperature-dependent, as temperature determines the rate of yolk absorption (McElman and Balon 1979) while post-sac-fry larval walleye growth is a function of food consumption and metabolism, both of which are temperature-regulated (McElman and Balon 1979, Johnston and Mathias 1994). Warmer water temperatures also benefit production of plankton (Wetzel 1975), which translates to increased walleye growth. Zooplankton are important prey for larval walleye in western Lake Erie and ichthyoplankton become important as the young walleye grow, especially after they become demersal (Paulus 1969, Roseman 1997).

Low-intensity winds (<15 km per hour) serve to mix lake waters and create low-velocity currents important for distributing oxygen and nutrients throughout the water column (Bowden 1983). Higher-intensity winds over western Lake Erie can cause more extensive mixing of lake waters, which retards water warming and may create currents that dislodge walleye eggs from shallow reef substrates and deposit them in areas unsuitable for incubation (Busch et al. 1975, Roseman et al. 1996). Roseman et al. (1996) documented that the cumulative effect of 21 days of intense wind events in 1995, especially winds from the east-northeast which have long fetches, contributed to slow water warming rates and created strong currents and wave action that displaced walleye eggs from reefs.

Although the effects of moderate wind events may be cumulative, short-term high-velocity wind events may have catastrophic consequences for egg survival. In early April of 1998, Roseman (Unpubl. data) documented the removal of over 80% of walleye eggs from reefs in western Lake Erie by wave and current action generated during a single intense storm (Fig. 5). This storm originated from the northeast and produced 36 hours of gale-force winds and wave heights in excess of 4 m in western Lake Erie. They hypothesized that displaced eggs were likely deposited in deeper waters where silt substrates and reduced bottom dissolved-oxygen levels (<3.0 ppm) suffocated the embryos (Seifert and Spoor 1974, Balon et al. 1977, McMahon et al. 1984).

As described earlier, winds create waves and current patterns that have both positive and negative effects on early life history stages of walleye. Prolonged strong wind events create wave and current conditions that can transport fish large distances (Martin et al. 1992) as well as cause damage to delicate larvae (Cordone and Kelley 1961). Further, heavy wave action is known to stir up sediments causing increased turbidity associated with sediment transport (Gedney and Lick 1972). Increased turbidity
Figure 4. Relationship between spring water warming rate and abundance of age-0 walleye collected in Ohio Division of Wildlife bottom trawls. Data from Busch et al. (1975), Roseman (1997), and Ohio Division of Wildlife (1997).

Figure 5. Numbers of walleye eggs collected per 2-minute tow on reefs in western Lake Erie in spring of 1998 showing removal of eggs caused by 8-9 April storm. From Roseman et al. (1999, In prep.).
reduces the phototrophic zone thereby reducing primary productivity (Wetzel 1975).

Pelagic walleye larvae are poor swimmers (Houde 1969) and consequently are subject to transport by water currents, which is the mechanism by which larvae move from spawning areas to nursery areas both in rivers and on reefs (Houde and Forney 1970, Mion 1996, Roseman 1997). Walleye spawned on reefs in western Lake Erie rely on current patterns in the spring to transport the larvae to the warmer and more productive nearshore nursery habitats (Roseman 1997). Ichthyoplankton samples collected from 1994 through 1998 showed high densities of walleye larvae and other ichthyoplankton in nearshore areas of western Lake Erie, suggesting that current patterns during this time of year act to transport pelagic larvae in these areas (Mion 1996; Roseman 1997; E.F. Roseman, Unpubl. data). These nearshore areas warm quickly in the spring and are known to have higher densities of prey than offshore areas (Roseman 1997) providing habitat conditions favorable to larval walleye growth and survival.

**Conclusions**

In this paper we have identified specific factors and mechanisms that influence the vital rates of egg and larval stages of walleye, providing insight to the ecological functions mediated by physical processes. While we do not propose that physical processes are more important than biological processes in determining the vital rates of walleye eggs and larvae or structuring year-class strength, we do contend that physical processes create

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<td>7,230</td>
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<td>8.1</td>
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<td>1.9</td>
<td>28.3</td>
<td>11.4</td>
<td>–</td>
</tr>
</tbody>
</table>

Data from Roseman et al. (1996, 1998), Roseman (1997), and Turner et al. (1998).
the environment in which biological processes occur. Further, we agree with Walters and Collie (1988) that research efforts should not focus solely on examining physical processes but rather should involve multidisciplinary approaches that examine the ecological linkages through which environmental variability influences the vital rates of fish populations.

Both episodic events (weather-related events) and subtle variability (temperature-dependent development) in early life history vital rates can significantly affect recruitment of walleye in western Lake Erie (Busch et al. 1975; Mion 1996; Roseman et al. 1996, 1998). Episodic events are usually catastrophic in nature, removing large numbers of individuals from the population (Houde 1989). Such events may relieve survivors of density-dependent regulatory mechanisms (i.e., competition) and shorten the duration of vulnerable early life history stages allowing good growth and survival of the remaining cohort. Conversely, decelerated development and larval growth rates precipitated by unfavorable temperatures can lead to substantially longer early life history stage durations over which high mortality rates can operate (Houde 1987), resulting in fewer recruits.

Walleye in western Lake Erie are recruited from two different spawning stocks: those that spawn in tributaries and those that spawn on the mid-lake reefs. Because walleye life stages most vulnerable to storm effects overlap in time (larvae in rivers, eggs on reefs), spring storms may ultimately drive survival in both habitats. This hypothesis is consistent with previous observations of synchrony of fish year-class strengths over large geographic areas in freshwater (Koonce et al. 1977) and marine (Ruzecki et al. 1976, Koslow 1984) systems as generated by large-scale climatic events. Linkage in survival between river- and reef-spawned fish should produce greater variability in total walleye recruitment than if survival was determined independently in the two habitats.

While we can modify the physical habitat in which fish populations exist, we do not have the capabilities to manage or manipulate most physical processes. For example, we can construct artificial reefs with deep crevices to shelter eggs from strong wave and current action, but we cannot alter the actual wave and current action to any appreciable degree that would benefit egg survival. Instead, we must rely on developing a sound understanding of the linkages between physical processes and the ecological processes that regulate fish production and recruitment. By doing so, we will be able to better predict the response of fish populations to variability in their habitat and respond with appropriate management strategies.

Acknowledgments

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References


Managing the Baltic Sea Cod (Gadus morhua): Stable Catches in an Unstable Environment

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Extended Abstract

Overcapacity is one of the most serious problems in the world fisheries, frequently resulting in overfishing (FAO 1995). The risk of attaining an overcapacity is particularly large in fisheries for fluctuating species (Ludwig et al. 1993). Constant harvest rate strategies, with catches proportional to the target species abundance, stimulate investments when stock sizes are large which can result in overcapacity. Constant catch strategies, on the other hand, lack this incentive. Therefore we explored the possibility of a management strategy based on constant catches by modeling the eastern Baltic Sea cod (Gadus morhua) population. The eastern Baltic cod stock is naturally fluctuating due to highly varying spawning conditions in the brackish Baltic Sea (Ojaveer et al. 1981, Bagge et al. 1994, Nissling 1994).

The model used is single species and cohort based, with mortality caused by the fishery, cannibalism, and “other causes.” To model cod recruitment, we used the empirical relationship between year-class strength, spawning volume (the volume of water with an oxygen content > 2 mL/L and salinity > 11 PSU), and spawning stock biomass found by Sparholt (1996). A Monte Carlo model with actual data from 1966 to 1992 simulates the variation in spawning conditions.

The risk of overfishing within 5, 20, and 50 years for different constant catch levels was calculated. If we do not accept any risk of overfishing within 50 years the long-term yield will, according to the model, be less than half the yield resulting from the constant harvest rate strategy which corresponds to the maximum sustainable yield. To increase the long-term yield we have to accept a higher risk of overfishing.

To avoid the low long-term yield and the high risk of overfishing resulting from the strict constant catch strategy, we developed a more dynamic constant catch strategy (the DCC strategy) based on alternative constant catches and two overfishing criteria. Normal catches were allowed
when the spawning stock biomass was above a certain level. When the spawning stock biomass was below this level, catches were reduced by 50%. If the spawning stock biomass fell below a second and lower threshold, fishing was stopped totally. According to the model, the long-term yield with the DCC strategy was almost as large as the long-term yield with the constant harvest rate strategy. The DCC approach had the advantage of smaller variation in catches between years and a better degree of utilization of the fishery capacity.

In conclusion, we find the DCC approach to be an interesting and competitive management strategy, probably able to decrease the problems of overcapitalization and overfishing for long-lived and highly fluctuating species like the Baltic Sea cod.

References
Retrospective Projection Using Monte Carlo Simulation: An Application of a Length-Based Model to Kachemak Bay Pink Shrimp

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Abstract
Pink shrimp (*Pandalis borealis*), the formerly abundant and commercially important species in Kachemak Bay, Alaska, has declined in population abundance since the mid-1980s. No sign of population recovery has been detected in recent years. This paper is a retrospective look at what the risk to a population would have been under various levels of harvest rate, incorporating uncertainty in natural mortality and recruitment. A length-based population dynamics model (Quinn et al., In press) was employed and Monte Carlo simulation was conducted to estimate the probabilities that various harvest strategies would have caused the shrimp population to fall below a threshold. Our results indicated that natural mortality was the most important factor controlling population dynamics, and the increasing trend in natural mortality in the 1980s resulted in the population crash. Because the pink shrimp population had a very high background risk of extinction, all harvest strategies led to a similar population decline. More effort should be expended in studying the relationship between pink shrimp and its predators. The common assumption of constant natural mortality in stock assessment and population projection should be revisited for forage species like pink shrimp.

Introduction
Traditional fish stock assessment focuses on point estimates of population parameters such as recruitment and fishing intensity with a common assumption of constant and known natural mortality. This assumption is
vital in that it often leads to underestimation of uncertainty in population dynamics and, most important, in the risk of population collapse. Risk, according to Burgman et al. (1993), is the potential or probability of an adverse event, e.g., population abundance going below some defined level. For many fish populations there exist threshold levels below which the population will have difficulty in recovering (Quinn et al. 1990, Zheng et al. 1993). This is especially true for some crustacean populations such as pink shrimp, in which copulation is necessary in the reproduction process. Animal populations that live in a highly variable and unpredictable environment can go extinct at some point even free from human disturbance. This is termed the “Background Risk of Extinction” (Burgman et al. 1993). Human activities such as harvesting can increase this risk of extinction. The impacts on population dynamics from natural and fishing mortality should be translated into the language of risk for proper understanding.

Pink shrimp (*Pandalus borealis* Krøyer), also known as northern shrimp or northern pink shrimp, was once a commercially important species in Kachemak Bay, constituting more than half of the harvests in the pandalid fishery (Davis 1982). While landings of pandalid shrimp from the otter trawl fisheries in Alaska have declined dramatically since the record high yield of 58,600 metric tons (t) in 1976, trawl catches in Kachemak Bay were relatively constant from 1970 to 1983. One important reason for the sustained yields is that conservative management of seasons and guideline harvest levels had been carried out based on the survey estimation of population biomass. Despite this conservative management, the catch during 1983 decreased to nearly 1/10 of that in 1980 due to reduced population abundance. The fishery was closed after 1986 due to continued low stock size (Gustafson 1994) and has not reopened.

The depletion of pandalid shrimp populations in Alaska was synchronous with the collapses of many other crustacean stocks. After simultaneously examining historical data from several populations, Orensanz et al. (1998) concluded that the sequential patterns of rise-peak-demise in total catch shown by many crustacean fisheries represented a serial depletion of resources. The serial depletion cannot be explained simply as a result of overfishing. Some lightly or seldom-fished pink shrimp populations experienced similar population declines (Anderson 1991). As proposed by Orensanz et al. (1998), climate change may have reduced reproductive success and increased natural mortality.

The serial depletion of crustacean populations in Alaska regardless of fishing pressure underlines the necessity of seriously considering temporal variations in both recruitment and natural mortality. One of the purposes in this study is to understand what roles recruitment and natural mortality played in the collapse of pink shrimp population in Kachemak Bay using estimates of recruitment and natural mortality trends from a length-based model (Quinn et al., In press) in conjunction with other as-
sumptions. We also use retrospective analysis to examine how different harvest rates might have altered the population's fate. Monte Carlo simulation together with probabilistic risk analysis provide the essential tools for accomplishing these goals. This approach not only captures variability present in real population fluctuations but also presents results in terms of risks, which are useful in decision-making. Finally, we discuss the possibility of incorporating major environmental factors such as predator abundance into population projection and harvest recommendations.

Methods

Data

For doing retrospective simulations, two components are important: i.e., parameters, some of which are random variables, and a model to describe the population in a mathematical language. To obtain population parameters, historical data need to be analyzed. Data utilized in this study come from the commercial fishery and research surveys. Annual commercial yield data from the shrimp fishery in Kachemak Bay between 1971 and 1986 were provided by the Alaska Department of Fish and Game (ADF&G). A trawl survey for pandalid shrimp in Kachemak Bay was initiated by the National Marine Fisheries Service (NMFS) in 1971, and continued once every year in May until 1974 using a 66-foot Nordby trawl net with assumed 50% net efficiency. From 1975 to 1990, the trawl survey was conducted twice every year (October and May) by ADF&G using 61-foot NMFS-designed net with assumed 100% net efficiency. Since 1991, the survey has been conducted only once every 2 years in May due to a depressed shrimp population. Data available from spring surveys include absolute biomass estimates from 1971 to 1991 and length frequency data during the same period with data missing from 1975 to 1977. For the purpose of doing simulations, we filled in length frequencies for the 3 years using those observed from 1971 to 1973 to stabilize the estimation. Survey data after 1991 are not yet available due to processing lags. During fall surveys (mid-October), females are nearly 100% ovigerous, which makes identifying sex easy. Female proportion at length was therefore calculated from length frequency data obtained in fall surveys.

Model and Parameter Estimation

A length-based age-structured population model (Quinn et al., In press) was applied to the population to obtain parameter estimates. This model follows individual cohorts through time and has flexibility to incorporate general forms of selectivity and natural mortality (Appendix 1). Parameter estimation was accomplished using the software Autodif Model Builder (ADMB) which estimates parameters in a step-by-step fashion, known as a multi-phase procedure (Otter Research Ltd. 1996). Parameters estimated include growth parameters: $L_\infty, \kappa, \sigma, \sigma_r$ and mean length at recruitment $\mu_{r,t}$. 
annual recruitments $R_t$ and $\alpha, \beta,$ and $\phi$ in the spawner-recruitment (S-R) relationship (described in Appendix 1); full recruitment fishing mortality $F_t$ and selectivity parameters $\gamma$ and $L_{50\%}$; and natural mortality $M_t$. Interannual variation of $M_t$ was modeled as a time series structure of a random walk $\ln(M_t) = \ln(M_{t-1}) + \delta_t$, where $\delta_t$ is a normal error term. The initial value of natural mortality was set at 0.2 per year for 1970, which gives a better fit than larger values. Parameters were estimated by minimizing an objective function (Appendix 1).

**Retrospective Projection Procedure**

**Examining the Impact of $M$ and $R$**

To reduce the complexity of the retrospective projection procedure, we only took account of the uncertainties in recruitment and post-recruitment natural death. All other parameters were fixed at the estimated values from the parameter estimation procedure. Temporal variations in both recruitment ($R_t$) and natural mortality ($M_t$) were simulated with log-normal error: $\Theta' = \Theta e^{\text{cv}(\Theta)Z}$, where $\Theta'$ is the random value of $M$ or $R$, $\Theta$ is the deterministic value, and $Z \sim N(0,1)$.

To carry out the projection, we employed three ways of generating a deterministic $M$ for each year. First, because traditional methods of stock assessment and population projection often make the assumption of a constant and known survival rate over time, we investigated the validity of this assumption and its effect on the population analyses. The constant mean was assumed to be 0.2 per year. Second, the estimates of $M$ from the model were simulated with lognormal errors of equal variability across years. Third, a linearly increasing trend in $M$ was also imposed for years between 1980 and 1990 together with a constant $M$ of 0.2 per year for the years before 1980. Parameters for this linear function were obtained from a linear regression of estimated $M$ for years between 1980 and 1990 versus year so that the linear function would approximate the estimated $M$. The intercept and slope were $-10.559$ and $0.134$, respectively. We assumed a coefficient of variation (cv) of 30% in $M$ for all the $M$ sets.

Temporal variation in $R$ has been the focus of considering uncertainties in population projections (Francis 1992). Four ways were used to generate deterministic recruitment for the projections because the Beverton-Holt (B-H) model with autocorrelated errors fitted the estimated recruitment best, this relationship was first considered for projecting. The S-R parameters were obtained from the parameter estimation procedure (Table 1). Second, because density-independent S-R models are more conservative and therefore desirable when the population level is low (Ferson 1993), a linear increasing function of spawners and recruitment with autocorrelation was also applied. The slope for the linear S-R function was estimated to be 0.228 by linearly regressing the estimated $R$ versus $S$ through the origin. Third, the common assumption of constant $R$ was considered with the constant mean calculated as the average value of the
Fourth, for gaining a better understanding of recruitment impact on population dynamics, the estimated values of $R$ were utilized. The cv for $R$ was chosen as 20%, which was close to the average cv of 12% estimated from the model.

Combinations of each $M$ and $R$ model gave rise to 12 scenarios. For each of these 12 scenarios, annual $F$ was fixed at the estimated value from the model in order to examine the effects on projection of uncertainties in $M$ and recruitment $R$. Each scenario used the same random seeds, and 5,000 replicates were implemented.

Projection was initiated using the estimated abundance at ages and lengths in 1971 from the parameter estimation procedure and continued through 1991, covering the period when historical survey indices for biomass were available. The projection procedure produced estimates of population biomass, yield, and probabilities of going below the quasi-extinction threshold level (Ferson et al. 1989) over years. The quasi-extinction threshold level was arbitrarily defined as 10% of the maximum historical biomass from the surveys.

### Evaluating Harvest Strategies

To examine how alternative fishery management might have affected the pink shrimp population, nine different harvest strategies relative to the estimated fishing mortality ($F_{est}$) were investigated. They were $0$, $0.25F_{est}$, $0.5F_{est}$, $0.75F_{est}$, $F_{est}$, $1.5F_{est}$, and $F_{est}$ with earlier fishery closures in 1980, 1982, and 1984.

For these analyses the scenario with the estimated $M$ and a B-H spawner-recruitment relationship was employed. The comparison criteria among various harvest strategies were cumulative yield over the entire fishing

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<td>$S-R \phi$</td>
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Results

Model Parameter Estimation
Estimated scalar parameters had relatively small values of cv except for the S-R relationship parameters (Table 1). Estimated recruitment displayed a dramatic drop in 1978 and stayed relatively low until a peak occurred in 1984 and 1985 (Fig. 1). Field observations did indicate a rebound of biomass in 1985 and 1986, but mainly with small male shrimp (Gustafson 1994) which is in concordance with our recruitment estimates. No strong spawner-recruitment relationship was discernable (Fig. 2). In some years, low spawner biomass resulted in high recruitment, for instance, 1984 and 1985, while in some other years, such as 1978 and 1981, spawner biomass of median size did not produce reasonable recruitment as we would expect. Anderson (1991) found with a pink shrimp population in Pavlof Bay that a relatively small spawning stock may give rise to an outstandingly large year class in some years, with the majority of years conforming to a Ricker relationship. For our estimated spawners and recruitment, the B-H model with autocorrelation resulted in a better fit.

The estimates of $M$ displayed an increasing trend, which started in 1980 (Fig. 3). In accordance with the change in $M$ over time, there was an increasing trend in the relative abundance of Pacific cod, considered to be the major predator, in the late 1980s and through the 1990s (Bechtol 1997). The mean frequencies of occurrence for Pacific cod were obtained during shrimp trawl surveys in Kachemak Bay. In contrast, estimated $F$ was relatively stable except for that in 1983, when the fishery was partially closed, and in 1986, the last year with a fishery operation.

The overall fit of biomass and yield from the parameter estimation procedure was good after 1979. However, there were some discrepancies between the predicted and observed values in the 1970s (Fig. 4), which might partially be due to the missing length frequency data from 1975 to 1977.

Comparison of Projections with Different Models of $M$ and $R$
Monte Carlo simulations produced 5,000 replicates from which statistical summaries and the probabilities of extreme events were drawn. We used the scenario with the estimated $M$ and $R$ to illustrate the possible ways of summarizing results. Although each individual trajectory from the 5,000 replicates has a different path, 50% of the projected biomass values fall into the range between the 25th and 75th percentiles (Fig. 5). This range followed the pattern of the observed biomass trend. The mean line of the trajectories appeared to be a good representative of the observed bio-
mass. Therefore, we chose the trajectory mean to demonstrate the impact of $M$ and $R$ models on population projections.

Comparisons were made among the $R$ models with each set of $M$. With constant $M$, the trajectory means were driven by the fluctuations in $R$ and $F$. No matter what recruitment scenario was examined, there were big discrepancies between the projections and the observations after 1983 when $F$ began to decrease, and they got particularly larger after 1986, when the fishery was completely closed (Fig. 6). This discrepancy between the observed decline in biomass and a projected increasing trend in biomass indicated that $M$ was greatly understated in the 1980s with the constant $M$ model. In addition, there was one biomass peak in 1976 when the estimated $R$ was used, which may have resulted from a combination of high recruitment anomalies in 1972, 1973, and 1975, and a peak $M$ in 1975 (Fig. 3).

In contrast, when we used the estimated $M$ values as the deterministic mean, all $R$ models resulted in a population decline similar to what was actually observed (Fig. 7). The best projection came from the scenario with the estimated $R$. Once again the underestimation of biomass for years with peak biomass may have resulted from high recruitment anomalies. One prominent result from this exercise was that a constant $R$ did not project the population any worse than the B-H or linear model did. Precise prediction of recruitment anomalies would help the projection, but for most years, recruitment predicted from general models is likely to be adequate.
The approximation of $M$ to the estimated values by using the linearly increasing function resulted in projections consistent with the observed biomass values in the 1980s, similar to what were obtained from the scenario with the estimated $M$ (Fig. 8). This also implies that the natural mortality must have had some increasing trend in the 1980s, in order for the pink shrimp population to crash. In conclusion, an increasing trend in $M$ appears to be the most likely explanation of the decline of the pink shrimp population in Kachemak Bay. Recruitment did not seem to be as critical in this case.

**Comparison of Harvest Strategies**

Harvest strategies are commonly evaluated in terms of fishery or economic gain and their impact on the exploited populations as well. We compared the consequences of different harvest strategies based on the scenario with the estimated $M$ and B-H $R$. The best harvest level was 75% of the $F_{est}$ which resulted in not only the highest cumulative yield, but
Figure 3. Estimated natural mortality (±1 SE) from 1970 to 1990 and fishing mortality estimates from 1970 to 1986 from the length-based model and relative frequencies of occurrence of Pacific cod obtained from the same shrimp trawl surveys.

Figure 4. Comparisons between observed and predicted biomass and yield from the length-based model.
Figure 5. Projected biomass at the mean level and 25th and 75th percentiles from the scenario with estimated natural mortality and recruitment.

Figure 6. Comparisons of biomass projections among four recruitment models: B-H, linear, constant R, and estimated R using constant natural mortality.
Figure 7. Comparisons of biomass projections among four recruitment models: B-H, linear, constant R, and estimated R using estimated natural mortality.

Figure 8. Comparisons of biomass projections among four recruitment models: B-H, linear, constant R, and estimated R using constant natural mortality before 1980, and a linearly increasing function for years after 1980.
also a lower risk of quasi-extinction compared with those under harvest levels of $F_{est}$ or 50% of the $F_{est}$ (Table 2).

The population had a high background risk of quasi-extinction in 1991 (56%). The risk of quasi-extinction in 1991 became larger as fishing mortality got higher or the fishery closure was implemented later. Nevertheless, the difference among the different harvest strategies was not large in terms of the risk of quasi-extinction. The risk of going below various biomass levels under fishing mortality of $F_{est}$ and no fishing mortality had great similarity (Fig. 9), which implies that the population decline was unavoidable.

The projected mean biomass under no fishing mortality was extremely high during the early 1980s (Fig. 10). However, there was a dramatic decline after that peak, which brought the population down to a level similar to the observed. A fishery closure in 1980 temporarily brought the population to a very high level (Fig. 11), which was also followed by a dramatic decline. Overall, it appears that the fate of the pink shrimp population to collapse could not have been altered by lessening fishing or executing early fishery closures.

**Discussion**

Because of parameter confounding, measurement error, and/or process error, the accuracy of $M$ and $R$ estimates is unknown. Nevertheless, the retrospective simulation with various sets of $M$ and $R$ values indicated that the conclusion from the simulation is robust to the assumed $M$ or $R$ patterns. That is, $M$ is the most important factor controlling the population dynamics and $R$ does not seem to be as critical in this case.

Both parameter estimation and simulations indicated that an increasing trend in natural mortality in the 1980s had led the pink shrimp population to collapse. The serial depletion of other crustacean stocks in Alaska is likely due to the same reason: high natural mortality.

Because the abundance of forage fishes is highly correlated with that of predators, a major part of $M$ for forage species may come from predation mortality. The dramatic increase in the abundance of shrimp predators, such as Pacific cod and walleye pollock, may have directly resulted in the increase in shrimp natural death in Kachemak Bay. Therefore, the assumption of constant post-recruitment $M$ will inevitably bias population analyses under the circumstances of dramatic change in predator abundance.

Owing to the high correlation between natural death of forage species and their predator abundance, the temporal variation in $M$ is likely to be more visible and therefore easier to study than that in $R$, which is generally driven by many physical environmental factors. This study leads us to conclude that more effort is desirable to investigate dynamics of predator populations in order to obtain more realistic population analyses and projections for forage species. Applying this conclusion to other pink
Table 2. **Projected total yield and risk of quasi-extinction using estimated M and B-H R.**

<table>
<thead>
<tr>
<th>Scenario</th>
<th>$F$</th>
<th>Total yield</th>
<th>1987 riska</th>
<th>1991 riska</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>0.0</td>
<td>5.38%</td>
<td>56.02%</td>
</tr>
<tr>
<td>2</td>
<td>0.25 $F_{est}$</td>
<td>31.66</td>
<td>11.90%</td>
<td>60.22%</td>
</tr>
<tr>
<td>3</td>
<td>0.5 $F_{est}$</td>
<td>43.14</td>
<td>24.58%</td>
<td>75.26%</td>
</tr>
<tr>
<td>4</td>
<td>0.75 $F_{est}$</td>
<td>45.90</td>
<td>43.04%</td>
<td>71.68%</td>
</tr>
<tr>
<td>5</td>
<td>$F_{est}$</td>
<td>44.86</td>
<td>66.40%</td>
<td>78.34%</td>
</tr>
<tr>
<td>6</td>
<td>1.5 $F_{est}$</td>
<td>38.95</td>
<td>96.68%</td>
<td>89.84%</td>
</tr>
<tr>
<td>7</td>
<td>Closure 1980</td>
<td>31.60</td>
<td>6.90%</td>
<td>57.08%</td>
</tr>
<tr>
<td>8</td>
<td>Closure 1982</td>
<td>39.64</td>
<td>11.32%</td>
<td>60.88%</td>
</tr>
<tr>
<td>9</td>
<td>Closure 1984</td>
<td>43.19</td>
<td>25.08%</td>
<td>67.74%</td>
</tr>
</tbody>
</table>

a Risk is measured by the percentage of simulations in which biomass is less than 10% of the historical maximum.

*Figure 9. Comparisons between the background risk of biomass going below various levels and the risk when fishing at level $F_{est}$, using the scenario with the estimated $M$ and predicted recruitment from the B-H model with autocorrelation in 1991.*
Figure 10. Comparisons of biomass projections under fishing mortality $F = 0$, $0.5 F_{est}$, $F_{est}$, and $1.5 F_{est}$ using the scenario with estimated natural mortality and predicted recruitment from B-H model with autocorrelation.

Figure 11. Comparisons of biomass projections under fishery closure in 1980, 1982, and 1984 using the scenario with estimated natural mortality and predicted recruitment from B-H model with autocorrelation.
shrimp populations, particularly those that are still under commercial fishing, prudent study of $M$ is important. Models incorporating the relationship between $M$ and the abundance of predators should be helpful for projecting the dynamics of forage species.

**Acknowledgments**

We appreciate the comments and support of Dr. Gordon Kruse, Alaska Department of Fish and Game. This publication is the result of research sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration, Office of Sea Grant, Department of Commerce, under grant number NA90AA-D-SG066, project numbers R/07-21 and R/31-03, from the University of Alaska with funds appropriated by the State of Alaska. The U.S. Government is authorized to produce and distribute reprints for government purposes, notwithstanding any copyright notation that may appear hereon.

**References**


Appendix 1. Details of the Length-Based Model

Assume that the length frequency distribution of shrimp population at recruitment, before entering the fishery, is a simple discrete normal. The probability density function (PDF) for the lengths $x$ at recruiting age $r$ and time $t$ is:

$$f_{r,t}(x) \sim N_D(\mu_{r,t}, \sigma_r^2) = \frac{1}{\sqrt{2\pi \sigma_r^2}} e^{-\frac{(x - \mu_{r,t})^2}{2\sigma_r^2}}, \text{ where } \xi_{r,t} = \sum_x e^{-\frac{(x - \mu_{r,t})^2}{2\sigma_r^2}}.$$

The abundance of the newly recruited shrimp at length $x$ is:

$$N_{r,t}(x) = N_{r,t} \times f_{r,t}(x).$$

To obtain abundance $N_{a+1, t+1}(x)$ from abundance $N_{a,t}(x)$ at age $a$ (starting at age $r$) and time $t$, the process of growth was modeled first followed by mortality. The standard von Bertalanffy growth model is utilized to express the growth pattern from one age to next, assuming that growth is constant over time:

$$L_{a+1} = L_a(1 - \rho) + \rho L_a + \epsilon, \text{ where } \rho = e^{-\alpha},$$

is the Brody coefficient, and $\epsilon \sim N(0, \sigma^2)$.

The expected length and variance at age $a+1$ for an individual of length $x$ at age $a$ are from Cohen and Fishman (1980):

$$\mu_{a+1}(x) = L_a(1 - \rho) + \rho x, \text{ and } \sigma_{a+1}^2 = \sigma_r^2 \frac{1 - \rho^2}{1 - \rho^2} + \rho^2 \sigma_r^2.$$ 

After one growth increment, the relative distribution of lengths $p_{a+1,t}(L)$ is:

$$p_{a+1,t}(L) = \sum_x f_{a,t}(x) e^{-\frac{1}{2\sigma_{a+1}^2}(L - \mu_{a+1,t+1}(x))^2}.$$ 

Assume full recruitment fishing mortality at time $t$ is proportional to the ratio of observed yield and estimated biomass from the survey at time $t$ with a deviation term $e^{\nu t}$:

$$F_t = \frac{Y_{t,obs}}{B_{t,obs}} e^{\nu t}.$$ 

The selectivity function follows the common assumption of a logistic curve:
\[ S_x = \frac{1}{1 + e^{-\gamma(x - L_{50\%})}} \]

where \( \gamma \) is the shape parameter and \( L_{50\%} \) is the length at which 50\% of the individuals are vulnerable to fishing.

Absolute abundance, \( N_{a+; t+1}(L) \), at the start of time \( t+1 \) after fishing mortality \( F_t S_x \) and natural mortality \( M_t \) is:

\[ N_{a+; t+1}(L) = N_{a; t} p_{a+; t+1}(L) e^{-(M_t + F_t S_x)}, \]

where \( M_t + F_t S_x = Z_{t,x} \) is the total mortality at time \( t \), and natural mortality \( M_t \) is assumed to be constant for all length intervals after recruitment.

Abundance is summed over all ages for length \( L \) at time \( t \) to get length distributions of the population at time \( t \):

\[ N_{t,x} = \sum_a N_{a,t,x}. \]

Length frequency distributions in the sample at time \( t \) are:

\[ LF_{t,x} = n_t \frac{N_{t,x} S_x}{\sum_x N_{t,x} S_x}, \]

where \( n_t \) is the sample size for measuring length.

The expected survey biomass at time \( t \) is:

\[ B_t = \sum_x N_{t,x} S_x W_x, \]

where weight at length is modeled as the allometric relationship: \( W_x = \alpha^* x^{\beta^*} \). The parameters \( \alpha^* \) and \( \beta^* \) were obtained independently from the survey conducted in spring 1997, the same time of year when survey biomass indices and length frequency distributions were collected. We assume the length-weight relationship has no interannual variation. Estimated yield from the model at time \( t \) is:

\[ Y_t = \sum_x N_{t,x} \frac{F_{t,x}}{Z_{t,x}} (1 - e^{-Z_{t,x}}) W_x. \]

Expected female abundance at time \( t \) and length \( x \) is: \( FN_{t,x} = N_{t,x} \chi_{t,x} \), where \( \chi_{t,x} \) is the female proportion at length \( x \) and time \( t \). This proportion is modeled as a logistic function:
\[ \chi_x = \frac{1}{1 + e^{-\delta(x - p_{50\%})}}, \]

where \( p_{50\%} \) is the length at which 50\% individuals are composed of females. Note that the female proportion parameters were estimated from the survey data outside the model to avoid complications.

Parameters were estimated by minimizing the objective function:

\[
f = \lambda_B \sum_t (\sqrt{B_t'} - \sqrt{B_t})^2 + \lambda_L \sum_t \sum_{i,t'} (\sqrt{LF_{i,t,t'}'} - \sqrt{LF_{i,t,t'}})^2 + \lambda_Y \sum_t (\sqrt{Y_t'} - \sqrt{Y_t})^2 \\
+ \lambda_R \sum_t [\ln(R_t') - \ln(R_t)]^2 + \lambda_M \sum_t \delta_t^2,
\]

where variables \( B_t', LF_t', \) and \( Y_t'; \) denote observed values, while those without primes denote corresponding predicted values. Square root transformation of data is more desirable than a logarithm transformation (Quinn et al., In press). The component \( \lambda_R \sum_t [\ln(R_t') - \ln(R_t)]^2 \) is for estimating the spawner-recruitment parameters \( \alpha, \beta \) and \( \phi \) in the Beverton-Holt (B-H) S-R relationship with first-order autocorrelation, which fitted the recruitment estimates best:

\[
\ln(R_t') = \ln(\alpha S_{t-1}') - \ln(1 + \beta S_{t-1}') + \phi e_{t-1} + v_t = \ln(R_t) + v_t,
\]

where \( R_t' \) are observed values, \( \phi e_{t-1} \) is the first-order autocorrelated error term, and \( v_t \sim N(0, \sigma^2) \). The last part of the objective function, \( \lambda_M \sum_t \delta_t^2 \), is a penalty term controlling the degree of variability in the time series of \( M \) from year to year.

The weighting factors \( \lambda \)'s for the observations were determined based on their accuracy and variance ratio (\( \lambda_B = \lambda_Y = 1 \), \( \lambda_L \) (1971 to 1974 and 1978 to 1991) = 4, and \( \lambda_L \) (1975 to 1977) = 1). Weights \( \lambda_R \) and \( \lambda_M \) were determined based on the assumptions on the variation in the spawner-recruitment parameters and \( M \) (\( \lambda_R = 5 \), and \( \lambda_M = 10 \)).
Variations in Abundance of Year Classes of Threadfin Hakeling (*Laemonema longipes*, Moridae) in the Northwestern Pacific Corresponding to Oceanographic Conditions

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Pacific Scientific Research Fisheries Centre (TINRO-Centre), Vladivostok, Russia

**Extended Abstract**

This paper gives data on the biology of threadfin hakeling (*Laemonema longipes*) and compares year-class abundance and subarctic water regimes at 149°E for the period 1965-1990. A quasi-seven-year period, caused by the “pole” tide, is present in the variations of threadfin hakeling year-class abundance and the subarctic water regime. It is assumed that high year-class abundance of threadfin hakeling will occur in the late 1990s and early 2000s.

The threadfin hakeling is an important commercial bathyal fish of the northwest Pacific. It was first mentioned by Taranets (1937) and described by Shmidt (1938). Matsubara (1938) also described threadfin hakeling. Significant aggregations of threadfin hakeling were found during the 1974 TINRO expedition to Alaid Hollow (Okhotsk coast of Paramushir Island) and waters off the east coast of Honshu. Russian fishermen began harvesting it in the same year. In the late 1980s and early 1990s the threadfin hakeling catch ranged between 17,000 t and 87,000 t, composing 66-88% of the general world catch of all species of Moridae for that time (FAO 1995).

The amount of water with temperatures less than 5°C at 149°E longitude between 43° and 33°N latitude at 0-1,000 m of depth during the summer is used as an indicator of interannual fluctuations of the water regime. Threadfin hakeling year-class abundance was estimated by adding
the number of fish of the same year class caught in different years from one unit of effort.

Threadfin hakeling inhabit the continental slope and mesopelagial of the northwestern Pacific to the north of 33ºN, the Sea of Okhotsk, the Bering Sea, and the Gulf of Alaska, but are most abundant near Japan and the Kuril Islands (Shmidt 1950, Rass 1954, Pautov 1980, Kodolov and Pautov 1986, Savin 1993). Catching threadfin hakeling near eastern Kamchatka, in the Bering Sea, and the Gulf of Alaska is rare and those regions are zones of its emigration paths. Such vast threadfin hakeling areas with different habitation conditions are caused by the presence of well-expressed seasonal and yearly migrations.

Temperature and salinity characteristics of threadfin hakeling habitat correspond in most cases to the warm intermediate layer of the subarctic water mass structure. According to Burkov and Arsenyev (1958) and Moroshkin (1964), temperature and salinity of this layer increase from 0.8ºC and 33.3‰ in the Sea of Okhotsk to 4-6ºC and 34.5‰ in the spawning area near southeastern Honshu (Fig. 1). The peak of threadfin hakeling density is usually observed at 400-800 m of depth.

On the basis of data obtained, the migration cycle of threadfin hakeling is presented in the following description (Savin 1993). In spring adult threadfin hakeling from the spawning grounds off the Idzu Archipelago migrate along the continental slope to the north at the foraging areas near Hokkaido and the Kuril Islands. In autumn after foraging they migrate back to the south and reach the spawning grounds in midwinter, completing the yearly migration cycle (Fig. 2).

After spawning, eggs and larvae are transported to the north in the northeastern branch of the Kuroshio that includes several gyres of an anticyclonic character—the peculiar “vortex” track. In their second year juveniles enter the Sea of Okhotsk and feed there until 3 years of age. They then enter through deepwater straits to the oceanic side of the Kuril Ridge and as they mature they migrate south toward Japan, recruiting to the spawning stock.

Spawning grounds of the threadfin hakeling are located near the southeastern coast of Honshu in the regions of the Boso Peninsula and the Idzu Archipelago (Fig. 3). They localize at depths of 400-800 m between the coast and the Kuroshio current (Yasui et al. 1979, Savin 1993). The Kuroshio, moving along Honshu, agitates the upwelling of relatively cold and low-salinity deep waters enriched by organic elements near the coast. Consequently, an environment favorable for threadfin hakeling spawning is created. The higher temperatures in the intermediate layers, compared with other areas, are apparently a required condition for final maturing and spawning. The Kuroshio, that carries more warm water masses from the south, limits the entrance of *L. longipes* to the south and southwest along the continental slope of the Idzu Archipelago and Honshu.
It is obvious that variability in position of the Kuroshio and Oyashio currents has considerable effect on threadfin hakeling year-class abundance.

Threadfin hakeling is a fluctuating species. As investigations have shown, relatively high abundance of year classes of threadfin hakeling occurred in 1963, 1971, and 1978. Trawl survey data for 1984-1991 showed high abundance for the 1987 year class (Fig. 4). Judging from the amount of water of temperatures less than 5°C at 149°E during these years, the subarctic waters expanded to the east from Japan (Fig. 4). Moreover, from data for 1965-1990 the absolute maximum was observed in 1987. In spring 1963 a distinct cooling of the water near the southeastern coast of Honshu was observed as a consequence of the extreme southerly position of the coastal Oyashio branch (Fujimori 1964). As an analysis showed, a quasi-seven-year period, caused by the “pole” tide (Maximov 1970), is present in the variations of threadfin hakeling year-class abundance and subarctic water regimes. In addition, data resulting from spectrum analysis show the presence of a similar cycle in interannual dynamics of the Kuroshio.
Figure 2. Scheme of threadfin hakeling distributions and migrations.
Distributions: 1 – spawning grounds; 2 – mature females; 3 – mature males; 4 – region of primary gravid females and larvae; 5 – region of juvenile habitat; 6 – zone of emigration paths.
Migrations: 7 – postspawning; 8 – prespawning; 9 – juvenile; 10 – first maturing young; 11 – emigration; 12 – direction of juvenile transport. Roman numerals show the number of months of adult occupancy.
Figure 3. Distribution of threadfin hakeling eggs in March 1975.
1 – regions of threadfin hakeling removal
2 – Kuroshio axis
3 – egg station
Egg catch per one set (Yasui et al. 1979):
4 – 1-10 eggs
5 – 10-100 eggs
6 – >100 eggs
cyclonic meander between 135° and 140°E where a powerfully productive zone is formed (Pavlychev 1980).

Penetration of subarctic waters increases the suitability for threadfin hakeling spawning in this area and also has a favorable influence on the survival of early life stages.

The correlation between threadfin hakeling year-class abundance and subarctic water regime has great forecast importance, making it possible to predict threadfin hakeling year-class abundance. We predict that high abundance of year classes of threadfin hakeling will occur in the late 1990s and early 2000s.

References


Monitoring Changes in Oceanographic Forcing Using the Carbon and Nitrogen Isotopic Composition of Prince William Sound Pelagic Biota

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Abstract

Changes in the physical environment known to affect phytoplankton and zooplankton production can be linked to fish production through carbon and nitrogen stable isotope natural abundance measurements. Stable isotopic analyses of herbivorous copepods and juvenile fishes from Prince William Sound (PWS) and the northern Gulf of Alaska (GOA) were conducted as part of the Sound Ecosystem Assessment (SEA) project, a comprehensive multidisciplinary ecosystem study. The advective regime connecting the GOA with PWS was postulated by SEA to affect recruitment and nutritional processes in juvenile fishes. Herbivorous zooplankton, an indicator for pelagic production sources, had distinctive carbon isotope signatures when sampled in the GOA compared to those from PWS. PWS carbon had consistent spring bloom carbon isotopic signatures during 1994-1996 while GOA carbon differed in 1996. Nevertheless, PWS carbon was always distinctive from GOA carbon. This variation suggested that interannual fluctuations occurring at the food chain base are driven by processes in the gulf.

Analyses of nitrogen isotope ratios and C/N ratios of juvenile fishes were used to normalize their carbon isotope ratios, enabling determination of their relative affinity for GOA or PWS carbon. The data suggest a large affinity range, changing on annual time scales, consistent with observed oceanographic phenomena. For example, there was a shift to a greater dependency on GOA carbon in 1995 compared with 1994 and 1996. A parallel shift to increased GOA-originating copepods undergoing diapause (resting phase) in 1995 suggesting an influx of GOA zooplankton,
provided a second line of evidence. Thus herring and other fishes partially dependent on GOA carbon are subject to vagaries of carbon flow that fall under the domain of physical oceanographic processes connecting the GOA with PWS as well as processes occurring on the GOA continental shelf adjacent to PWS.

**Introduction**

Cycles in the size of fish and shellfish populations have had dramatic effects on Gulf of Alaska coastal fisheries of Alaska (McDowell et al. 1989). Variations in natural stable isotope abundance provide evidence that the advective regime connecting the northern Gulf of Alaska (GOA) with Prince William Sound (PWS) can alter nutritional processes in PWS pelagic food webs (Kline 1999). Gradients of stable isotope ratios of carbon in the PWS study area serve as effective tracers of energy supply due to conservative transfer of carbon isotope ratios between the lower trophic levels (phytoplankton to zooplankton to forage fishes, etc.) up to the top consumers. Fishes acquire these isotope ratios in response to the importance of the food in bulk body tissues (muscle and fat). Isotope ratio analysis of these tissues can provide insight into the effects of fluctuations of GOA carbon sources on PWS fish populations (Kline 1999).

The large interzonal herbivorous copepods of the genus *Neocalanus*, which comprise the bulk of the zooplankton during vernal zooplankton blooms, have a yearly life history pattern. They undergo a prolonged stage copepodite-V diapause at depth following termination of feeding at the end of the bloom. The diapaused copepods provide the “seed” for the following generation since reproduction takes place at depth in late winter. A portion of PWS has depths great enough to accommodate the *Neocalanus* diapause stage; i.e., depths > 400 m (Kline 1999). The offspring of *Neocalanus* diapausing in PWS form a source of primary consumers of the PWS spring bloom. A secondary source of *Neocalanus* are populations diapausing beyond the continental shelf in the GOA. The Alaska Coastal Current flow in PWS may transport *Neocalanus* into PWS while feeding or during ontogenetic migrations in the water column (Kline 1999).

Diapausing samples were analyzed for $^{13}C/^{12}C$ for comparison with the regional isotope gradient obtained during the bloom to assess input of GOA copepods after feeding is complete. Concomitant shifts in the $^{13}C/^{12}C$ content of diapausing copepods and fishes in PWS during the 1994-1996 study period suggested a common system-wide cause.

**Materials and Methods**

Copepods were collected at the terminal feeding stage (Copepodite IV and V) throughout PWS and stations in the northern GOA and during diapause (Copepodite V and VI) at stations located in suitable habitat in PWS (Kline
Juvenile Pacific herring and walleye pollock were collected throughout PWS during 1994-1997 from multivessel broad-scale surveys (Kline 1999). Laboratory handling procedures, isotopic analysis preparation, and data analysis were as described by Paul et al. (1998) and Kline (1999).

Normalization for lipid (DeNiro and Epstein 1977) and trophic level effects on $\delta^{13}C$ values of fish enabled “fingerprinting” of their carbon source (Kline 1997, 1999). The McConnaughey and McRoy (1979) lipid normalization based upon the C/N ratio using a $C/N = 4$ as the base level was used. The Kline (1997) method for the normalization for trophic level effects used: (1) the $\delta^{15}N$ value of the herbivore, N. cristatus, as the trophic level baseline (Vander Zanden et al. 1997); and (2) an assumed constant N and C trophic fractionation factor ratio of 3.4:1. In general, normalization reduces sources of $^{13}C$ variability, enabling comparisons among species without the confounding effects of trophic level and lipid content (Kline 1997). Thus, normalized $^{13}C/^{12}C$ content of fishes could be compared directly with N. cristatus at a consistent lipid storage level (Kline 1999).

The expressions $\delta^{13}C$, $\delta^{13}C'$, $\delta^{13}C_{TL}$, or $\delta^{13}C'_{TL}$ denote $^{13}C/^{12}C$ abundance in relation to the international standard (Vienna PDB), normalized for lipid content, normalized for trophic level, and normalized for lipid content and trophic level, respectively, using conventional delta notation (the per mil [%] deviation from the international standard). Whereas $\delta^{13}C'$, $\delta^{13}C_{TL}$, and $\delta^{13}C'_{TL}$ are used in accordance to a particular data analysis context, “$^{13}C$” is used to reflect generic $^{13}C/^{12}C$ isotopic trends irrespective of normalization. Similarly, $^{15}N/^{14}N$ abundance is expressed relative to air $N_2$ as $\delta^{15}N$ values.

**Results**

*Neocalanus cristatus* sampled throughout the PWS and GOA were consistently different (Kline 1999). The mean values plotted versus time show a consistency for PWS carbon $\delta^{13}C'$ of $-19$ to $-20\%$ (Fig. 1). GOA carbon was usually $^{13}C$-depleted having $\delta^{13}C'$ values of $-22$ to $-23.5\%$. However, in 1996, *Neocalanus cristatus* (as well as other *Neocalanus* species) shifted to an anomalous high $\delta^{13}C'$ of $\sim -17.5\%$ (Fig. 1).

The isotopic composition of *Neocalanus cristatus* diapausing in PWS include those with signatures consistent with those feeding in PWS (upward arrows, Fig. 2) and those feeding in the GOA (downward arrows, Fig. 2). While mean $\delta^{15}N$ was consistently $\sim +8\%$ each year, the relative proportion of high and low $\delta^{13}C'$ varied (Fig. 2.). While the contribution of PWS and GOA copepods was approximately the same in 1994, most of those in 1995 and 1996 originated from the GOA.

Juvenile herring and pollock < 100 mm long shifted in $\delta^{13}C'_{TL}$ content in concert during 1994-1997 (Fig. 3). The lowest $\delta^{13}C'_{TL}$ values measured in juvenile fishes in 1995 coincided with low $\delta^{13}C'_{TL}$ in diapausing *Neocalanus cristatus* (Fig. 2).
Figure 1. Time series of $\delta^{13}C'$ measured in feeding Neocalanus cristatus from Prince William Sound (PWS) and the Gulf of Alaska (GOA), 1994-1996. Points indicate mean values, standard deviations were 0.5-1‰. PWS and GOA values were consistently statistically different (t-test $P < 0.05$). (1) Mean values inferred from diapaused population modes. (2) Mean values of terminal feeding stages sampled with 0.5 m diameter plankton net. (3) Mean values of terminal feeding stages sampled with MOCNESS sampler. (4) Mean values inferred from diapaused population modes (Fig. 2: 1996).
Figure 2. The δ¹³C' composition of Neocalanus cristatus diapausing in Prince William Sound (PWS) from three cohorts. The upward-pointing arrows indicate δ¹³C' values of Neocalanus cristatus originating in PWS which were inferred from mode values (1994) or measured in spring sampling (1995 and 1996; Fig. 1). The downward-pointing arrows indicate δ¹³C' values of Neocalanus cristatus originating in the Gulf of Alaska which were inferred from mode values (1994 and −22.5 value in 1996) or measured in spring sampling (1995 and −17.5 value; Fig. 1). The isotopic shifts indicate a greater extent of zooplankton transport into PWS in 1995 than 1994 and 1996.
Figure 3. Shift in $\delta^{13}C_{TL}$ for Prince William Sound Pacific herring and walleye pollock < 100 mm long in 1994-1997; sample sizes as indicated. The distributions of values are shown as box and whisker plots that denote the 10th, 25th, 50th, 75th, and 90th percentiles. There was a large shift to greater Gulf of Alaska carbon dependency in 1995 for both species as indicated by the low $\delta^{13}C_{TL}$ values.
Discussion

Regional Isotopic Gradient and Interannual Variability

There was a consistent isotopic gradient between PWS and GOA in the 1994-1996 period except for May 1996 when the gradient reversed owing to a large magnitude change in the GOA signature (Fig. 2). Whereas PWS mean $\delta^{13}C'$ values ranged within 1‰, and the difference between PWS and GOA averaged 3‰, the GOA mean value shifted in spring 1996 by 5‰. This large shift probably reflected a change in phytoplankon fractionation during uptake of CO$_2$ which varies as a function of growth rate (Laws et al. 1995). Thus the productivity pattern during the spring bloom of 1996 was markedly different from other times. These isotopic values corroborate model predictions made for spring 1996 that suggest poor GOA primary and zooplankton productivity (Eslinger and Cooney 1997). If fluctuations in GOA productivity are typical, they could affect year-to-year inconsistencies in food availability for consumers. Thus the question arises: Are fluctuations in GOA spring bloom $\delta^{13}C'$, and inferred growth rate changes (Laws et al. 1995), typical?

Juvenile Fish Carbon Source Dependencies

A change in carbon source dependency for fishes can be inferred from their $\delta^{13}C'_{TL}$ shifts (Fig. 3). Juvenile herring and pollock are the dominant pelagic fishes in PWS and both consume zooplankton. Juvenile herring and pollock from PWS shifted in $\delta^{13}C'_{TL}$ content during this study from which a change in carbon source dependency can be inferred (Fig. 1). Although both species shifted in concert to lower $\delta^{13}C'_{TL}$ suggesting a greater GOA dependency in 1995 than 1994, pollock were generally 0-1‰ more positive in $\delta^{13}C'_{TL}$ suggesting a lower dependency on GOA carbon. Juvenile pollock and herring occupy different levels in the water column, have different schooling behavior, and recruit from the larval stage at different times, effecting access to a different forage base as confirmed by differences in the data. This difference may not be reflected in the species composition of diet, but instead, the where and when of the production cycle as integrated into the isotopic signature (Kline 1999), which reflects the assimilated carbon pool of the fish. The greater reliance on GOA-derived carbon in herring may reflect their dependence on carbon generated later in the season during the time when advection of GOA production was nearly the sole carbon source in 1995 (Kline 1999).

Significance of Parallel Isotopic Shifts

The concordant shift to greater GOA dependency by both fish species throughout PWS in 1995 implied that system-scale oceanographic process-driven bottom-up effects permeated PWS. Furthermore, Neocalanus cristatus diapausing in fall 1995 principally came from the GOA. A common process that explains these observations is the physical transport of
water containing zooplankton (both copepods entering diapause and zooplankton fish forage) into PWS from the GOA sometime after the spring bloom via the Alaska Coastal Current or deepwater renewal (Kline 1999). The greater degree of GOA carbon dependency by fishes and the greater proportion of GOA copepods in diapause in 1995 than other years suggests that the influx of GOA water was stronger that year. Variations in zooplankton transport into PWS among years are thus evidenced. Such system-wide changes suggest that there are year-to-year inconsistencies in the food web base and fish production potential for PWS and thus should be a concern for management of exploited populations.

Ecosystem Considerations for Management

Fishes living in PWS but dependent on GOA carbon are subject to changes in carbon flow that result from physical oceanographic processes (e.g., currents and gradients of temperature and salinity) that connect the GOA with PWS. It is conjectured that affinities range from total dependency on PWS carbon to significant input of carbon from the GOA. Fishes wholly dependent on PWS are more likely to be directly affected by internal PWS processes. Increased competition for PWS carbon by all species, however, may occur if GOA carbon is less available to those that normally use it. Shifting to increased dependency on PWS carbon by species with normal affinity for GOA carbon during years of poor GOA carbon availability would provide evidence of competition for a limited carbon supply by the increasing overlap in their $^{13}$C/$^{12}$C signature. Increased competition for PWS carbon by all species, however, may occur if GOA carbon is less available to those that normally use it. Time-series measurements of natural stable isotope abundance in fishes combined with data on fish populations and cogent oceanographic measurements will enable a new understanding of how basic environmental processes affect fish recruitment and interaction.

Acknowledgments

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References


Marine Survival of Puget Sound Coho Salmon: Deciphering the Climate Signal

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Abstract

Each year the State of Washington forecasts the number of adult coho salmon (*Oncorhynchus kisutch*) that will return to Washington waters. The abundance forecast is conducted jointly by the Washington Department of Fisheries and Wildlife (WDFW) and the Northwest Indian Fisheries Commission in January and February of each year to aid the Pacific Fisheries Management Council in West Coast salmon allocation. This forecast relies on accurate predictions of marine survival combined with hatchery and wild smolt abundance estimates. Historical estimates of the number of hatchery and wild smolts have been quite accurate, whereas marine survival for Puget Sound hatchery coho has been underestimated in the recent past.

Recent studies have implicated localized oceanographic conditions at the time of ocean entry as the critical phase of marine survival for Pacific salmon (*Oncorhynchus*) species. Coded wire tag (CWT) data are used to calculate time series of coho salmon marine survival for Puget Sound, the Washington coast, west coast of Vancouver Island, and the Strait of Georgia. Several climatic variables related to Puget Sound's freshwater input are analyzed by principal component analysis.

A conceptual model is presented to visualize how interannual climatic variability affects marine survival of coho salmon in Puget Sound. Changes in climatic variables coincide with changes in marine survival at the decadal scale. The Strait of Georgia and Puget Sound show different patterns in marine survival of hatchery coho salmon due to differences in the freshwater input to volume ratio of these two estuarine systems.
Introduction

The Pacific Fishery Management Council conducts salmon fishery management off the coasts of Washington, Oregon, and California. This complicated and epic task relies upon preseason estimates of abundance provided by state-level fishery management agencies. Every year the Washington Department of Fish and Wildlife (WDFW) and the Northwest Indian Fisheries Commission jointly forecast the abundance of both natural and hatchery adult coho salmon (*Oncorhynchus kisutch*) that will return to Washington coastal waters and Puget Sound.

The current Puget Sound forecast methodology makes separate forecasts for wild and hatchery fish. Wild forecasts are separated into four management units (Skagit, Stillaguamish-Snohomish, South Sound, and Hood Canal), each with its own forecast methodology. The 1997 (1994 brood year) forecast of wild marine survival incorporated an average wild marine survival from the brood years 1985-1992 (Seiler 1997); 1997 hatchery returns were forecast in a similar manner, but using the hatchery average of the 1988-1992 (brood years) marine survival estimates. The weakness in the forecast is the application of the 5-year average of marine survival because it under-forecasts large runs and over-forecasts low runs. Recent forecasts (1990-1995) have over-forecasted preseason natural coho salmon abundance by more than 250% in some river systems (PFMC 1997), due to over-estimating marine survival.

Spatial and temporal variations exist at the regional scale in coho salmon marine survival, a measure of salmon productivity. Coronado-Hernandez (1995) calculated marine survival from smolt to adult of hatchery coho salmon from coded wire tag (CWT) data dating to 1971. Historically, coho salmon from the Strait of Georgia and Puget Sound (long-term average ≈ 8.5%) had much higher marine survival than their coastal counterparts (long-term average ≈ 3.9%), the west coast of Vancouver Island and the Washington coast. Puget Sound coho salmon marine survival peaked at 17% in 1984 and Strait of Georgia coho salmon marine survival peaked at 26% in 1973. In addition, Coronado-Hernandez (1995) found no relationship between length of hatchery operation and marine survival of coho salmon.

An internal memo from the WDFW states “presently, no correlation with ocean environmental conditions has been found to explain the observed inter-annual variation in [Puget Sound] marine survival” (Seiler 1997). It is hoped that by carefully examining the oceanography and interannual climate variability in Puget Sound that a robust relationship between marine survival and ocean conditions will be found. Hatchery fish are chosen because of large release numbers (approximately 35 million smolts per year), and a long time series (1971-1995) stored in an easily accessible database (Pacific States Marine Fisheries Commission, Regional Mark Information System). Wild and hatchery coho salmon from the same system show remarkable similarity in patterns of marine survival, although wild survival is typically much higher than hatchery survival (Fig. 1).
Marine survival, a measure of salmon production, is established during early marine residency (Hare and Francis 1995). Evidence from the Oregon coast suggests that the majority of marine mortality occurs in the first 3 months of ocean residency (Pers. comm., William Pearcy, Oregon State University, Corvallis, OR 97331, February 1997). Beamish et al. (1995) found synchronous timing of an increase in mean temperature of the Strait of Georgia and marine survival of hatchery-reared chinook salmon (*O. tshawytscha*) released into the Strait of Georgia. Francis and Hare (1994) found a relation between a climate index and subsequent returns of salmon in Alaska, adjusted for year of entry. This evidence suggests that the effects of climate variability on salmon are manifested in the first 3 months of ocean residency.

Marine survival is thought to be a function of the ability of coho salmon smolts to outgrow the initial suite of predators, and therefore a function of growth rate. Holtby et al. (1990) found that growth during the first few months of life in the ocean, was well correlated with total marine survival. It is thought that growth is related to availability of food.

Gargett (1997) proposed a hypothesis that juvenile salmon pass through a "stability window" on their seaward migration. This mechanistic hypothesis attempts to explain the apparent oscillation in production of Pacific salmon between Alaska and the Pacific Northwest. If oceanic conditions create an optimal stability, then in theory, conditions favoring higher than average plankton production will ultimately benefit coho salmon in higher growth rates, marine survival, and production. On the other hand, if oceanic conditions are less than optimal then juvenile salmon
marine survival and production would be less than average. Thus a "bottom-up" response is proposed as the link between climate and salmon production, and is the basis of the North Pacific trophic model proposed by Francis et al. (1998).

Coho salmon from Puget Sound spend about 3 months in Puget Sound before entering the open ocean (Pers. comm., Bill Tweit, WDFW, Olympia, WA 98501, March 1997), so their critical period is entirely within Puget Sound. Gargett's (1997) hypothesis adapts nicely to Puget Sound, because Puget Sound is an estuarine system. Therefore, by examining the oceanographic components of Puget Sound we should gain a better understanding of the link between the physical forces of climate and the biology of coho salmon.

**Puget Sound Oceanography**

Exchange of water between Puget Sound and the Strait of Juan de Fuca is driven by the difference in density, or angle of the pycnocline (Ebbesmeyer et al. 1989). These different water masses (Puget Sound is estuarine and the Strait of Juan de Fuca is more oceanic) meet at Admiralty Inlet (Fig. 2). Differences in river runoff, changes in wind direction, and the gradient in temperature, regulate the density difference across Admiralty Inlet. Changes in the exchange and inflow depth of oceanic water are driven by decadal fluctuations (Fig. 3) in atmospheric circulation over the North Pacific Ocean (Ebbesmeyer et al. 1989). This atmospheric forcing, in turn, drives changes in climate over the North Pacific Ocean and Puget Sound.

The unique circulation properties of the main basin of Puget Sound regulate residence time and stratification properties of the sub-basins (Fig. 2). Residence time in the lower layer of the main basin is up to 3 weeks (Ebbesmeyer and Barnes 1980) but organisms riding the currents, such as plankton, may stay resident in Puget Sound much longer because of the recycling of surface waters that occurs at Admiralty Inlet. As much as 60% of the surface water is downwelled into the deeper waters of Puget Sound on every ebb tide (Strickland 1983:48).

Optimal conditions for phytoplankton blooms in Puget Sound occur when a balance between mixing (bringing nutrients to the surface), light, and stratification occurs (Strickland 1983:45). The coastal waters of Alaska are thought to be light limited (a function of stratification), whereas the coastal waters of the Pacific Northwest are thought to be mixing (and nutrient) limited (Gargett 1997). Mixing is important for bringing nutrients to the surface, and stratification is important for keeping phytoplankton near energy from the sun. Optimal phytoplankton conditions in Puget Sound lie somewhere between Ebbesmeyer et al.’s (1989) two different regimes of velocity profiles (Fig. 3), and therefore between heavily mixed and highly stratified.

This paper answers a number of specific questions. Does marine survival of hatchery coho salmon in Puget Sound show regime-like steps in
Figure 2. Sub-basins of Puget Sound.
mean levels, and do these steps coincide with steps in climatic variables? What mechanisms may account for differences in patterns of marine survival between adjacent regions that experience similar climatic conditions (i.e., Puget Sound and the Strait of Georgia)? How can this information aid the management process?

Data and Methods

Coded wire tag data were obtained from the Pacific States Marine Fisheries Commission Regional Mark Processing Center. The processing center houses information pertaining to the mark, release, and catch of Pacific salmonids throughout the Pacific region involving the CWT marking project. Data exist from 1971. Each release group of smolts has a unique tag code. A hatchery in a given year may have a number of tag codes. Because coho salmon return as adults at different ages, it is necessary to standardize marine survival to one age class.

Marine survival by tag code is calculated as the ratio between the standardized number of tags recovered and the total number of smolts released with tags (equation 1). Tag recoveries are standardized to age 3

\[
\text{Marine survival} = \frac{N_3}{N_{\text{released}}} 
\]

(1)

\[
N_3 = C_1s_1s_2 + C_2s_2 + C_3 + \frac{C_4}{s_4} + \frac{C_5}{s_4s_5} + \frac{C_6}{s_4s_5s_6} + \frac{C_7}{s_4s_5s_6s_7} 
\]

(2)

where

- \( N_3 \): number of fish that would be alive if they were not caught, or spawned at an age different than age 3.
- \( C_t \): number of fish recovered (caught + spawned [escaped]) at age \( t \)
- \( S_t \): survival rate from age \( t-1 \) to \( t \), 0.5 for all ages except age 3, which has no \( S \) component (Hilborn and Hare 1992).

The survival rates used in calculation of of numbers alive at age 3, do not make a large difference in the result of \( N_3 \) because over 90% of returning coho salmon are age 3 (Hilborn and Coronado 1997). The percent age composition of Puget Sound coho salmon from Coronado-Hernandez (1995) is: age 1, 0.01%; age 2, 6.68%; age 3, 91.20%; age 4, 1.91%; age 5, 0.17%; and age 6, 0.02%.

Yearly averages of marine survival estimates within Puget Sound were made for Hood Canal, South Sound, and Whidbey Basin (see Fig. 2). These sub-basins correspond to the management units in Puget Sound; the Skagit and Stillaguamish-Snohomish units both lie within Whidbey Basin. Standardized anomalies were computed for each sub-basin. Averages of the three sub-basin yearly standard anomalies were computed to form a Puget Sound marine survival average. Time series of marine survival were calculated for the Strait of Georgia, the west coast of Vancouver Island, and the Washington coast from CWT data.

**Coded Wire Tag Selection Criteria**

Coded wire tag codes were selected based on several quality and stock composition criteria. Tag codes were selected from hatcheries that are on or near marine waters. This was done to eliminate any freshwater influence that could possibly cloud the marine survival estimate. Survival estimates from these groups is thought to be representative of marine survival (Pers. comm., Bill Tweit, WDFW, Olympia, WA 98501, March 1997). Tag code notes were reviewed to eliminate any releases of fish that may have been diseased or impaired in any way that would inflate marine mortality. When possible, tag codes were selected for stocks of fish native to the region, because stocks of salmon are transported from their natal streams to be reared in hatcheries and released in non-natal waters. Hatchery managers in Puget Sound
have begun releasing coho salmon smolts late in the summer (July-September) to encourage residency in the sound to enhance the sport fishery. Late release (after 1 July) tag codes were not included in the analyses.

**Extended Coded Wire Tag Time Series**

The coded wire tag time series for Puget Sound extends back to brood year 1970. The tagging program was in its infancy at that time, and recoveries of tags may have been underestimated (producing low marine survival estimates). In order to validate early tag code estimates, and to extend the marine survival time series back in time, the literature was reviewed for estimates of marine survival prior to 1975. Olson (1978) analyzed factors contributing to Puget Sound hatchery-reared coho salmon. I used survival estimates for brood years 1966-1974 from his table of smolt-to-adult survival estimates for a number of hatcheries in Puget Sound. Standardized anomalies were computed within these 9 years and are not included in rest of time series statistics because the estimates do not include a large portion of catch.

The time series for each sub-basin was extended another 3 years using data presented in Mathews (1980). The long-term mean (calculated from the CWT data) was removed from Mathew's marine survival estimates and was divided by the long-term standard deviation. The inclusion of Mathew's and Olsen's data allowed me to create a marine survival time series from broods 1964-1993 (ocean entry years 1966-1995). Mathew's data (1980) covers ocean entry years 1968-1970. Olsen's data (1978) covers ocean entry years 1970-1976. Coded wire tag data cover ocean entry years 1972-1995. Where time series overlapped, yearly mean anomalies were calculated.

The extended Puget Sound coho salmon marine survival index was regressed against total Puget Sound coho salmon run size. Run size was obtained from WDFW’s run-reconstruction model (Pers. comm., Bill Tweit, WDFW, Olympia, WA 98501, March 1997).

**Climate Variables**

In this study a suite of variables, often used to describe the state of climate and the ocean, was examined. Each of the variables was summarized in terms of the water year (October of year \(t-1\) through September of year \(t\)). For example, water year 1995 is October 1994 through September 1995. Seven environmental variables were collected from various sources. Table 1 presents the data gathered and the sources. All variables were averaged over the winter (October-March) and the summer season (April-September).

The time series of winter and summer standardized anomalies of these variables were calculated and a principal component analysis (PCA) was performed on this suite of climatic variables. The PCA analysis extracts vectors that explain the largest amount of variance in the combined time series. The significance of the components was calculated following North
et al. (1982). The principal components represent the temporal structure of the variance of the combined time series while the loading vectors represent the spatial component, or contribution of each variable to the particular principal component.

**Intervention Analysis**

Intervention analysis (Francis and Hare 1994) was performed on the marine survival index and the first principal component of the climate variables. Principal component 1 was tested for the effects of interventions in the years 1942, 1977, and 1989, while the marine survival time series was tested for interventions in 1977 and 1989. Hare and Francis (1995) reported on major shifts in both climate and salmon stocks in the early 1940s and late 1970s, and Mantua et al. (1997) identified climatic shifts that occurred in 1925, 1942, and 1977. Recent changes in atmospheric circulation (Pers. comm., Tom Murphree, Naval Postgraduate School, Monterey, CA 93943, September 1998) and shifts in marine survival of Strait of Georgia coho salmon (Pers. comm., Richard Beamish, Pacific Biological Station, Nanaimo, B.C., Canada, V9R 5K6, June 1998) point toward significant biophysical shifts in 1989.

**Results**

**Coded Wire Tag Data**

The values of marine survival computed from coded wire tags, along with their associated standardized anomalies, are presented in Table 2. The extended Puget Sound coho salmon marine survival index expressed as standardized anomalies is presented in Fig. 4. Total Puget Sound coho salmon run size was plotted with the marine survival index (Fig. 5). The

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**Table 1. Monthly environmental variables collected and their sources.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Dates</th>
<th>Source</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature</td>
<td>1895-1997</td>
<td>NCDC&lt;sup&gt;a&lt;/sup&gt;</td>
<td>°F</td>
</tr>
<tr>
<td>Precipitation</td>
<td>1895-1997</td>
<td>NCDC</td>
<td>Inches</td>
</tr>
<tr>
<td>Sea surface</td>
<td>1950-1997</td>
<td>Neah Bay, SIO&lt;sup&gt;b&lt;/sup&gt;</td>
<td>°C</td>
</tr>
<tr>
<td>temperature</td>
<td>1921-1998</td>
<td>Race Rocks, IOS&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Snow pack</td>
<td>1926-1997</td>
<td>AWC, NWS&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Inches</td>
</tr>
<tr>
<td>Streamflow</td>
<td>1914-1997</td>
<td>USGS&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Ft³/s</td>
</tr>
</tbody>
</table>

<sup>a</sup> National Climatic Data Center, Division 3 (Puget Sound Lowlands).

<sup>b</sup> Scripps Institution of Oceanography, Shore Station Database.

<sup>c</sup> Institute of Ocean Sciences, Victoria, British Columbia.

<sup>d</sup> Avalanche Warning Center, National Weather Service, Seattle, Washington.

<sup>e</sup> United States Geological Survey.
Table 2.  Percent marine survival of Puget Sound hatchery coho salmon.

<table>
<thead>
<tr>
<th>Brood year</th>
<th>Hood Canal</th>
<th>South Sound</th>
<th>Whidbey Basin</th>
<th>Puget Sound average</th>
</tr>
</thead>
<tbody>
<tr>
<td>1971</td>
<td>3.50 (-1.30)</td>
<td>1.35 (-1.26)</td>
<td>6.67 (-0.63)</td>
<td>4.04 (-1.11)</td>
</tr>
<tr>
<td>1972</td>
<td>4.05 (-1.17)</td>
<td>N/A</td>
<td>8.60 (-0.08)</td>
<td>6.33 (-0.62)</td>
</tr>
<tr>
<td>1973</td>
<td>6.62 (-0.56)</td>
<td>6.30 (-0.11)</td>
<td>9.53 (0.18)</td>
<td>8.88 (-0.16)</td>
</tr>
<tr>
<td>1974</td>
<td>9.35 (0.10)</td>
<td>N/A</td>
<td>15.86 (1.98)</td>
<td>13.95 (1.03)</td>
</tr>
<tr>
<td>1975</td>
<td>N/A</td>
<td>N/A</td>
<td>3.57 (-1.51)</td>
<td>3.57 (-1.51)</td>
</tr>
<tr>
<td>1976</td>
<td>N/A</td>
<td>3.70 (-0.72)</td>
<td>6.40 (-0.71)</td>
<td>5.86 (-0.72)</td>
</tr>
<tr>
<td>1977</td>
<td>N/A</td>
<td>12.10 (1.24)</td>
<td>12.12 (0.92)</td>
<td>11.95 (1.08)</td>
</tr>
<tr>
<td>1978</td>
<td>11.50 (0.60)</td>
<td>12.40 (1.31)</td>
<td>8.10 (-0.22)</td>
<td>8.20 (0.56)</td>
</tr>
<tr>
<td>1979</td>
<td>8.00 (-0.23)</td>
<td>12.70 (1.38)</td>
<td>11.18 (0.65)</td>
<td>10.67 (0.60)</td>
</tr>
<tr>
<td>1980</td>
<td>8.00 (-0.23)</td>
<td>7.23 (0.11)</td>
<td>11.96 (0.87)</td>
<td>10.31 (0.25)</td>
</tr>
<tr>
<td>1981</td>
<td>12.57 (0.86)</td>
<td>12.33 (1.29)</td>
<td>8.86 (-0.01)</td>
<td>9.67 (0.72)</td>
</tr>
<tr>
<td>1982</td>
<td>11.13 (0.52)</td>
<td>9.75 (0.69)</td>
<td>8.89 (0.00)</td>
<td>9.65 (0.40)</td>
</tr>
<tr>
<td>1983</td>
<td>15.27 (1.51)</td>
<td>15.08 (1.93)</td>
<td>11.49 (0.74)</td>
<td>12.02 (1.39)</td>
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<tr>
<td>1984</td>
<td>19.47 (2.51)</td>
<td>6.73 (-0.01)</td>
<td>16.23 (2.09)</td>
<td>16.84 (1.53)</td>
</tr>
<tr>
<td>1985</td>
<td>11.00 (0.49)</td>
<td>2.90 (-0.90)</td>
<td>11.49 (0.74)</td>
<td>8.96 (0.11)</td>
</tr>
<tr>
<td>1986</td>
<td>9.98 (0.24)</td>
<td>5.48 (-0.30)</td>
<td>8.63 (-0.07)</td>
<td>7.63 (-0.04)</td>
</tr>
<tr>
<td>1987</td>
<td>10.68 (0.41)</td>
<td>8.44 (0.39)</td>
<td>11.98 (0.88)</td>
<td>9.10 (0.56)</td>
</tr>
<tr>
<td>1988</td>
<td>4.07 (-1.17)</td>
<td>5.35 (-0.33)</td>
<td>7.45 (-0.41)</td>
<td>5.76 (-0.64)</td>
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<tr>
<td>1989</td>
<td>9.37 (0.10)</td>
<td>2.93 (-0.89)</td>
<td>5.49 (-0.97)</td>
<td>5.26 (-0.58)</td>
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<tr>
<td>1990</td>
<td>4.20 (-1.14)</td>
<td>4.18 (-0.60)</td>
<td>8.30 (-0.17)</td>
<td>3.31 (-0.63)</td>
</tr>
<tr>
<td>1991</td>
<td>10.01 (0.25)</td>
<td>1.57 (-1.21)</td>
<td>8.61 (-0.08)</td>
<td>7.74 (-0.35)</td>
</tr>
<tr>
<td>1992</td>
<td>7.56 (-0.33)</td>
<td>3.06 (-0.86)</td>
<td>5.20 (-1.05)</td>
<td>5.32 (-0.75)</td>
</tr>
<tr>
<td>1993</td>
<td>2.72 (-1.49)</td>
<td>1.88 (-1.14)</td>
<td>1.92 (-1.98)</td>
<td>2.19 (-1.54)</td>
</tr>
</tbody>
</table>

Values in parentheses are standardized anomalies. Values in the Puget Sound Average column are averages of the yearly values of the subbasins.
Figure 4. Puget Sound marine survival index, ocean entry years 1966-1995. Y axis is standard deviations from the mean. Dashed vertical lines represent significant interventions. Solid horizontal lines are mean levels for each regime.

Figure 5. Puget Sound coho salmon run-size standard anomalies plotted with coded-wire-tag Puget Sound marine survival (MS) index. X axis is run-size year. Marine survival time series has been shifted forward 1 year to coincide with associated run size.
Figure 6. Regional patterns of marine survival standard anomalies computed from coded wire tag data. Y axis represents number of standard deviations. X-axis is ocean entry year.
marine survival index accounted for 86% of the variance \((p < 0.001)\) in total Puget Sound run size. Regional patterns in hatchery coho salmon marine survival are presented in Fig. 6.

**Principal Component Analysis**

The first two principal components are statistically significant and together account for 56.6% of the variance of the combined time series. Figure 7 presents the time series of the first two principal components and Fig. 8 presents the loading vectors of these components.

The first principal component (PC1) shows a strong interdecadal pattern similar to the Pacific inter-Decadal Oscillation (PDO, Mantua et al. 1997). The loading vector of PC1 suggests that the decadal pattern of climate in the Puget Sound region follows a warm-dry cold-wet pattern (Fig. 8, PC1). That is, when air and sea surface temperatures are warm, less rain and snowfall, making the region dry. In contrast when air and sea surface temperatures are cool, more precipitation falls and more snow accumulates.
Figure 8. Loading vectors of Puget Sound environmental variables for PC1 and PC2. On the X axis, Win and Sum signify winter and summer mean values, respectively. SST is sea surface temperature at Neah Bay, Washington. SSTr is sea surface temperature at Race Rocks, British Columbia. AT is air temperature. SFI is streamflow at Concrete, Washington, on the Skagit River. PPT is precipitation. SNO is snowpack at Paradise Meadows, Mount Rainier, Washington. Y axis represents magnitude of loading vector.
The loading vectors of PC2 suggest that on an interannual time scale, the Puget Sound region follows a warm-wet and cool-dry pattern. That is, when air and sea surface temperatures are warm more precipitation falls, and the converse holds true.

**Intervention Analysis**

The extended Puget Sound marine survival index had significant ($p < 0.001$) interventions in ocean entry years 1978 and 1989. This differs from the interventions found by Mantua et al. (1997), and other studies that have identified a climatic shift occurring in 1977.

Intervention analysis shows that the PC1 time series shows significant ($p < 0.001$) steps in its sign in 1942 and 1977 calendar years. This is consistent with the regime shift concept put forth by Hare and Francis (1995) and supported by the findings of Mantua et al. (1997).

**Discussion**

The time series of Puget Sound coho salmon marine survival shows significant steps in mean levels in 1978 and 1989. These roughly coincide with changes in Puget Sound climatic data. The first principal component of Puget Sound climatic data shows significant steps in 1942, 1977, and 1989. So why the discrepancy in the late 1970s shift? The answer is twofold. First, although the first principal component captures a significant shift in climate, 1977 was a particularly dry year with very low streamflow with values comparable to the early 1990s. Second, since plankton production in Puget Sound is nonlinear, low as well as high values of streamflow will lead to lower plankton production, and therefore lower marine survival. With higher streamflow stability is greatly weakened because of enhanced estuarine circulation, and with lower than average streamflow, stability is enhanced because of retarded estuarine flow. This may seem counter-intuitive, but is supported by Ebbesmeyer (1989).

Gargett's (1997) optimal stability window (Fig. 9) that links oceanographic properties and salmon production is supported by Puget Sound climatic data. In Puget Sound this optimal stability window hypothesis can be framed in terms of the PDO. The first principal component of Puget Sound climatic data, PC1, has shifts in its sign that coincide with shifts in the PDO.

During the negative PDO of 1942-1976 more precipitation fell, the snowpack was higher, and temperatures were cooler. This would shift the frame of the stability window in Puget Sound to the left of optimal conditions (Fig. 9). With increases in runoff there is more vertical mixing in Puget Sound because of enhanced estuarine flow and it follows that stability would break down. Thus the period prior to 1977 would be a period where the conditions in Puget Sound were not met for optimal growth of the phytoplankton pathway that supports coho salmon, as reflected in lower marine survival during this period.
During the positive PDO of 1977-1984, the stability window would be framed to the right of the optimal window because of reduced runoff and retarded estuarine flow (Fig. 9). The period from 1976 to 1989 was a time of near normal streamflow, and following the hypotheses of Gargett (1997) and Strickland (1983), would be a period of optimal conditions necessary for the fish-enhancing phytoplankton pathway in Puget Sound.

The climate conditions in Puget Sound since 1990 seem to be an enhancement of the positive PDO signal. Air and sea surface temperatures are much higher than normal during both the winter and summer and higher than the period 1977-1989. Snowpack has been much lower than normal and streamflow has been sharply reduced during the summer months. These changes could be due to increases in mean global temperatures (Mann et al. 1998), or changes in global atmospheric circulation (Pers. comm., Tom Murphree, Naval Postgraduate School, Monterey, CA 93943, September 1998). Regardless of the drivers of these changes, impacts on the marine ecosystem of Puget Sound have been significant.

Why do we see different patterns in coho salmon marine survival in neighboring (Puget Sound and Strait of Georgia) estuarine systems? This optimal stability window should hold true for the Strait of Georgia. It too

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Figure 9. Schematic of Gargett's (1997) optimal stability window hypothesis, as it applies to hypothesized Puget Sound plankton production.
is an estuarine system similar in many properties to Puget Sound. Beamish et al. (1994) found a relationship between Fraser River discharge and interannual salmon production in the Strait of Georgia, relating to freshwater input into this estuarine system. A potential answer to the different patterns lies in the amount of freshwater input to volume ratio.

Puget Sound has a freshwater input (m³/s) to volume (km³) ratio of 13.0, while the ratio for the Strait of Georgia is 5.5 (Pers. comm., Rick Keil, University of Washington, Seattle, WA 98195, February 1997). Thus Puget Sound has more than twice the amount of freshwater input per volume. So in order to get to the optimal window in the Strait of Georgia, it would require very high streamflow, precisely the conditions prior to 1977. This explains why Strait of Georgia marine survival was highest prior to 1977. These same climatic conditions in Puget Sound would deluge the system with water shifting away from optimal plankton conditions.

The optimal window hypothesis assumes that climate will force changes in absolute magnitude of plankton production. Brodeur (1990) showed that growth of Oregon coast coho salmon was related to plankton species assemblages and these assemblages were related to climatic conditions. The paucity of plankton data in Puget Sound prohibits testing either of these hypotheses at present. The optimal stability window is adequate in capturing the physical oceanography of Puget Sound, as supported by Ebbesmeyer's (1989) work. Comparing Puget Sound and Strait of Georgia coho salmon marine survival supported the optimal window hypothesis at least qualitatively.

How can fishery managers use this climate information to quantify coho salmon abundance? The impetus for this research was to improve the forecast of marine survival of Puget Sound coho salmon. This paper identified climate patterns of Puget Sound and presented a hypothesis on how these patterns alter the oceanography of this unique estuarine ecosystem. By examining regional differences and similarities in time series of marine survival, key components of the Puget Sound ecosystem (a linear combination of PC1 and PC2 which represents an index of freshwater input) were identified that were then used in a forecast model for Puget Sound. The description of the forecast model is reserved for a future publication.

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