

June 1993

# OCEAN CARRYING CAPACITY

Recovery Issues for Threatened and Endangered Snake River Salmon  
Technical Report 6 of 11

Technical Report 1993



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Environment, Fish and Wildlife Division  
P.O. Box 3621  
905 N.E. 11th Avenue  
Portland, OR 97208-3621

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# OCEAN CARRYING CAPACITY

## Recovery Issues for Threatened and Endangered Snake River Salmon Technical Report 6 of 11

Prepared by

**Jim Lichatowich 1**

under subcontract to

**S.P. Cramer & Associates, Inc.  
Gresham, OR**

Prepared for

**U.S. Department of Energy  
Bonneville Power Administration  
Division of Fish and Wildlife  
P.O. Box 3621  
Portland, OR 97208-3621**

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**1 Mobrand Biometrics, Inc., Vashon Island, WA**

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Deborah Watkins served as Project Manager for Bonneville Power Administration.

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## EXECUTIVE SUMMARY

The northeast Pacific is comprised of four fishery production domains: The gulf of Alaska, a coastal downwelling zone, a coastal upwelling zone and a transition zone. Salmon from the Columbia River enter the sea in the upwelling zone. Marine survival of coho salmon in the Oregon Production Index area (southwest Washington, Oregon and California) has been the subject of extensive study. A major part of that work focused on the question: has the extensive hatchery program exceeded the carrying capacity of oceanic habitat? The question is still not resolved.

Variability in marine survival of coho salmon appears to be determined in the first month at sea while the fish are still in local marine areas in the upwelling zone. There is little evidence for food limitation or starvation as the primary agent of mortality. There is stronger evidence that upwelling might influence vulnerability to predation. A third hypothesis regarding marine mortality recognizes a complex relationship between growth and predation. Mortality factors during the first month at sea are an important area of continuing research.

A broader ecosystem view which considers salmon as a member of a complex marine community offers additional insight and raises new questions regarding the marine mortality of salmon. The pelagic fish community in the upwelling zone has undergone dramatic change in the last 50 years. That change is consistent with the historical record, however, the system has not completed a full cycle of change (as it has in the past) since the stocks have been subjected to intense commercial and sport exploitation. Salmon seem to be responding to shifts in productivity in the coastal upwelling zone. Changes in the pelagic fish community raise important questions regarding the additive or multiplicative effects of the degradation of freshwater habitats.

# OCEAN CARRYING CAPACITY

## 1. INTRODUCCION

### 1.1 PURPOSE, SCOPE AND METHODS

The term carrying capacity applied to salmon in freshwater, estuarine and marine habitats often carries with it the image of a fixed limit on the production of salmon. However, the concept of a fixed capacity is misleading. The carrying capacity of an ecosystem is the outcome of the interaction of the system's biotic and abiotic components. It represents the theoretical upper limit of the system's productivity -- the outcome of a favorable combination of the biotic and abiotic interactions. Capacity naturally changes and evolves and the trajectory of that evolution can be altered by human activities. Since the capacity of a system is the product of a large number of interactions, it can rarely, if ever, be measured directly. However, during the planning of restoration programs there is value in even a qualitative assessment of the salient features of capacity, particularly the identification of important changes in the ecosystem that alter the trajectory of the natural evolution of the system's capacity.

Although capacity is usually not measured, it can be indexed by the performance of specific components of the ecosystem. Performance is that part of the system's capacity that is measured in terms of interest. For example, fishery managers might be interested in the performance (production) of a salmon stock or important predators or prey of salmon.

A complete review of the factors influencing salmon performance (production and survival) in the ocean is beyond the time constraints of this project. The purpose of this report is to review selected literature on the marine production and survival of Pacific salmon, particularly coho salmon in the coastal upwelling zone. In addition, I have expanded the scope of earlier investigations by including a consideration of the literature on non-salmon components of the upwelling zone.

### 1.2 UNCERTAINTY IN THE OCEAN LIFE HISTORY OF SALMON

Even though the level of studies directed at salmonids is unparalleled in the fish literature (Miller and Brannon 1981), relatively little is known about the life history and habitat interactions of salmon during ocean residence (Percy 1992). Planning for salmon enhancement largely treats the ocean as an uncertainty; a "black box" that salmon enter as smolts and return from as mature adults. Although salmon are harvested in the ocean, the basis for ocean production and survival does not enter into the equations and models of enhancement planners in a meaningful way.

Hilbom (1992) identified three types of uncertainty in fisheries management: Noise, state of nature and surprise. The first two are relevant to oceanic capacity and performance as discussed in this report. Noise describes the annual variability in performance and results from variation in factors such as climate over which we have little control. Given a data series over a sufficient

number of years, noise can be statistically characterized and incorporated into the design of monitoring and evaluation projects.

However, even with statistical documentation, noise can make it difficult to detect changes in a stock's performance (Lichatowich and Cramer 1979). Noise in abundance data of Pacific salmon limits the detection of statistically significant trends. Bledsoe et al. (1989) suggested that 40 years of data collection is a reasonable objective in order to detect a 50% change in run size. Lichatowich and Cramer (1979) suggested it may take 20 to 30 years of data to produce a 80% chance of detecting a 50% change in adult abundance.

The need to monitor adult abundance for several years or decades to make a statistical determination of a population's status can have severe consequences to salmon populations that are potential candidates for listing under the Endangered Species Act. Severe depletion of a salmon population can occur in a relatively few years. For example, Gunsolus (1977) described the lower Columbia River coho populations in this way: *"The number of coho salmon returning to the Columbia River rose sharply in the 1960's, primarily because of increased hatchery production resulting from improved hatchery diet and techniques. Since then the run size has fluctuated considerably from year to year Coho are primarily of lower-river origin. populations are generally in good condition. and a good run is predicted in 1976"* (emphasis added).

Sixteen years later Johnson et al. (1991) in their review of the status of lower Columbia River coho populations concluded: *"Commercial exploitation of coho salmon and degradation of salmon spawning habitat reduced coho salmon numbers to near extinction around the middle of this century. The advent of artificial propagation of the species in hatcheries has 'rebuilt' the runs to at or above historic levels. However, this process has changed the coho salmon runs in the lower Columbia River from predominately natural spawning fish to predominately hatchery-maintained fish. Native runs, if they persist, would exist only as small remnant populations"* (emphasis added). The wild coho populations in the lower Columbia River went from healthy to extinction or remnant populations in the space of 16 years.

A change in the state of nature is a fundamental change in capacity as measured by the performance of specific components of an ecosystem. For example, Ware and Thomson (1991) identified a 40-60 year productivity cycle in the upwelling zone of the northeast Pacific. The difference between the peak and trough of a long-term ocean productivity cycle reflects a change in the state of nature and it can have important consequences to the performance of economically important species and their management. Changes in the state of nature are less frequent than noise so they may not be amendable to statistical characterization. They are evaluated through hypothesis testing (Hilbom 1992).

When considering capacity of oceanic habitats in recovery plans it is important to distinguish between noise and a change in the state of nature. The former may limit the ability to detect recovery; the latter may limit the scope of recovery objectives or make it difficult to attribute an increasing population to the recovery activities.

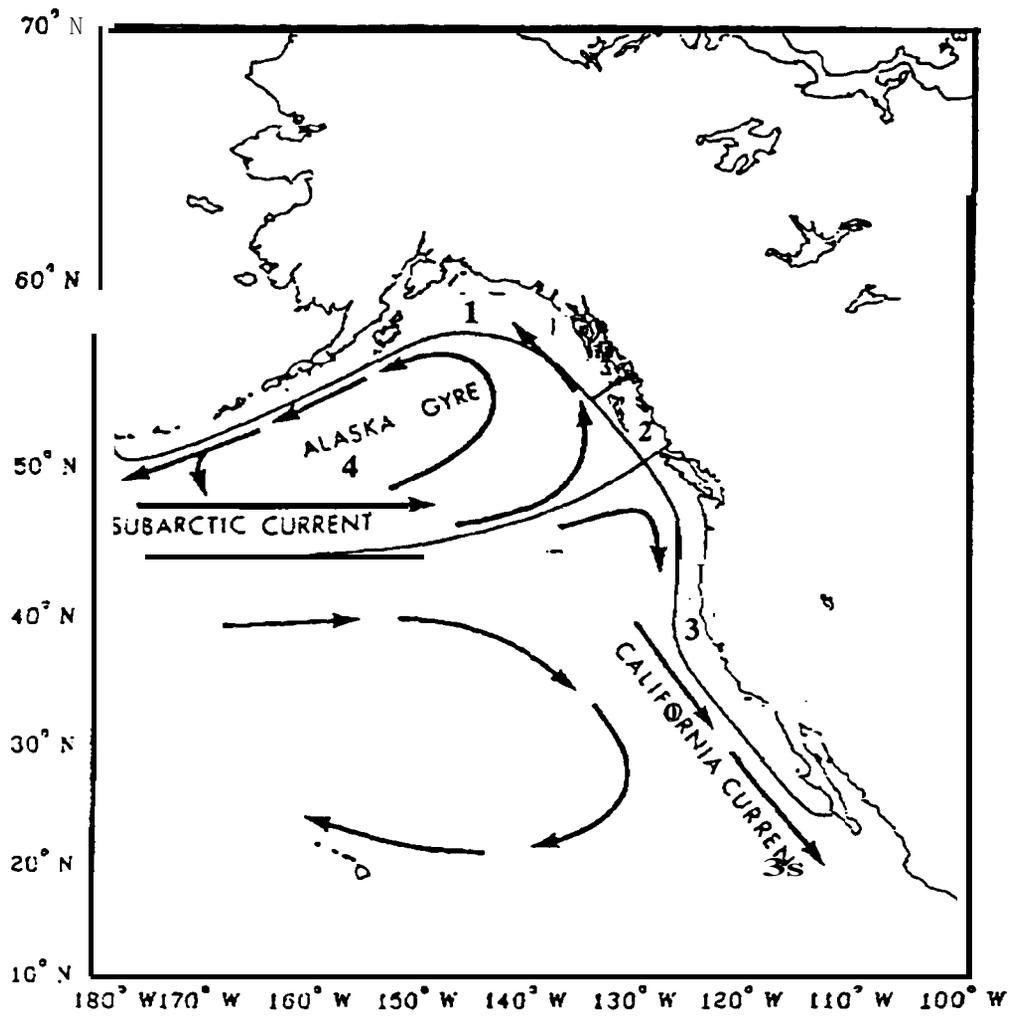
## 2. THE PHYSICAL SYSTEM

Ware and McFarlane (1989 cited in Ware and Thomson 1991) described three fisheries production domains and a transition zone in the northeast Pacific Ocean (Figure 1). Hartt (1980) identified salmon from the Columbia River in samples collected in the Gulf of Alaska. Those fish had migrated through or reared in more than one of the production domains. The movement between zones can be rapid; juvenile salmon migrate as much as 1,000 miles during the salmon's first summer at sea (Hartt 1980). Extensive migration through more than one production domain could severely complicate the evaluation of the salmon's performance in the marine environment. However, Percy (1992) concluded that juvenile chinook and coho salmon from Oregon and Washington remain in local coastal waters during their first summer at sea. Furthermore, year class strength of coho salmon in the Oregon Production Index<sup>1</sup> (OPI) is determined by mortality factors operating during the first month juvenile salmon are at sea (Percy 1992). Those observations suggest that this study focus on the upwelling zone off Oregon and Washington (Figure 1)

Northwesterly winds during spring and summer induce upwelling of cold nutrient-rich water along the coast. Several authors have shown a positive relationship between the intensity of upwelling at the time smolts enter the sea and subsequent adult production (see section 3.2.1). However, upwelling along the California, Oregon and Washington coast is not the only oceanographic feature that influences salmon production and survival. El Nino events that transport warm, low salinity water northward can reduce growth and survival of salmon (Percy 1992 and Johnson 1984). In addition, periodic, southward transport of subarctic water enhances productivity in the California current (Bottom et al. 1986).

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<sup>1</sup> The Oregon Production Index is comprised of coho salmon that enter the ocean from California, Oregon and the Washington coast north to Willapa Bay.



**NE Pacific Ocean**

- |   |
|---|
| <p><i>1 Coastal Downwelling</i></p> <p><i>2 Transition Zone</i></p> <p><i>3 Coastal Upwelling</i></p> <p><i>4 Central Subarctic</i></p> |
|---|

Figure 1. Fishery production domains.  
(From Ware and Thomson, 1991)

### **3. PERFORMANCE OF PACIFIC SALMON IN THE OCEAN**

#### **3.1 COHO SALMON PERFORMANCE IN THE UPWELLING AREA**

Marine life history and production of coho salmon in the OPI area were the subject of extensive study following the collapse of the fishery in 1977. Survival of hatchery reared coho salmon in the OPI was high in the late 1960's and early 1970's following development of better disease control, more nutritious feeds and improved release practices. The increase in survival following the improvement in hatchery technology led managers to conclude they could circumvent freshwater production bottlenecks and maintain high levels of production (Lichatowich and McIntyre 1987). Because managers believed they had successfully circumvented the freshwater habitat, the collapse of the fishery in 1977 immediately focused attention on the ocean for an explanation.' Although we have learned a great deal about coho in coastal waters, we have not learned enough to answer the fundamental questions that emerged shortly after the collapse of the coho fishery. What we do know about marine survival and production of coho salmon in the OPI area generally comes from two sources: (a) studies of historical records of catch, escapement and upwelling and (b) direct sampling of salmon in the nearshore environment.

##### **3.1.1 Analysis of Historical Data**

Following the collapse of the coho fishery in 1977, several managers and researchers published analyses of historical records of smolt production and subsequent marine survival. Most of the resulting papers addressed some aspect of the question: Have hatchery releases of coho smolts exceeded the carrying capacity of the marine habitat? Six of the nine papers discussed in this section specifically addressed that question. Three of the six give support to the hypothesis that marine mortality is density dependent (smolt releases exceed carrying capacity) and three support the hypothesis that marine survival is density independent (smolt releases do not exceed carrying capacity). Since those studies used the same data, but in different models, the debate will probably continue until experiments specifically designed to test the hypotheses of density dependence are carried out.

##### **3.1.1.1 Gunsolus (1978)**

Gunsolus (1978) was one of the first to suggest that the hatchery program for coho salmon might have exceeded the carrying capacity of the ocean. Gunsolus (1978) developed multiple working hypotheses to explain the decline in marine survival of coho salmon after 1976. His hypotheses were largely tested through graphical analysis of several data sets. He listed 20 conclusions that to a large degree framed the context for much of the subsequent work. His paper still provides the basic description of the problems associated with coho management in the OPI, however, Lawson (1992) recently made an important addition to that framework. The more relevant conclusions from Gunsolus (1978) are:

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<sup>2</sup> Pearcy (1992) noted that spring chinook from the Mid Columbia River also declined sharply after the 1975 smolt migration.

***Factors responsible for the fluctuations and leveling off trend of the numbers of adult coho produced after 1967 asserted their influence during the first few months of ocean life of coho smolts.***

***Predation on juvenile coho occurs in the ocean; it is possibly a major influence on survival in years of poor upwelling.***

***Upwellings in the Oregon Index area are strongly related to the survival of juvenile coho in their 1st year in the ocean and the ultimate size of the adults present that same year. Survival rates and growth are best with high upwellings.***

***Numbers of adult coho produced are dependent more on upwelling intensity than numbers of smolts released (at releases of over 20-25 million smolts in the Oregon Index area).***

***It is very unlikely that the numbers of adult coho produced could be noticeably increased by the addition of more smolts unless the relationships of present parameters controlling survival are changed or otherwise overcome***

***The escapement of wild coho to natural spawning areas is presently inadequate to sustain wild stocks.***

### **3.1.1.2 Oregon Department of Fish and Wildlife (1982)**

Oregon's coastwide plan for the management of coho salmon (Oregon Department of Fish and Wildlife 1982) was prepared, in part, in response to the depressed coho production following 1976. The plan identified and evaluated several working hypotheses in an attempt to determine the cause of the depressed coho fishery. The planners were unable to conclusively eliminate any of the hypotheses although some of the probable causes emerged as more likely than others. Gunsolus (1978) provided a framework for describing the overall management problem. ODFW (1982) went one step further and focused attention on the question: Is ocean mortality of coho a result of density dependent or density independent factors? The former would imply that carrying capacity had been reached and exceeded by the growing hatchery program. Although the coho plan did not resolve this question, it did stimulate the work of several researchers.

### **3.1.1.3 Clark and McCarl (1983)**

Clark and McCarl (1983) used five regression models to investigate the relationship between hatchery smolts released and subsequent adult production. They concluded that upwelling is an important parameter in models that attempt to predict adult returns from hatchery releases. The regression models they used which were capable of demonstrating density dependence did so, but weakly; the parameters were not statistically significant. As a result, Clark and McCarl (1983) could not conclude that a specific release policy for hatcheries was warranted i. e., that the

number of hatchery *smolts* released was exceeding carrying capacity. Their analysis suggested that the maximum release of smolts probably ranged somewhere between 32 and 180 million smolts.

#### **3.1.1.4 McCarl and Rettig (1983)**

McCarl and Rettig (1983) used a different model attributed to Pope and Just (1978 and 1979 cited in McCarl and Rettig 1983) to analyze the marine survival of aggregated hatchery and wild smolts. This paper concluded that survival of coho was density dependent. McCarl and Rettig (1983) also showed that the standard deviation of adult abundance increased with the square of the number of smolts released from hatcheries. They also suggested that upwelling was not a statistically significant parameter in determining standard error. Because variability increased with the square of the number of smolts, they concluded hatchery releases should be limited, if stability of the fishery was an important goal.

#### **3.1.1.5 Nickelson and Lichatowich (1983)**

Nickelson and Lichatowich (1983) showed a relationship between upwelling and marine survival of coho released from public hatcheries in the OPI area. They concluded that the number of smolts released within high and low upwelling periods did not appear to influence survival--density dependent mortality was not significant. Nickelson and Lichatowich (1983) incorporated information on shoreline development, standing stocks of herring and anchovies, coho production trends from other regions and spawning behavior of non-salmonid fishes into their analysis.

#### **3.1.1.6 McGie (1983)**

McGie (1983) provided a commentary and alternative analysis to Nickelson and Lichatowich (1983). He combined public and private hatchery smolts and an estimate of wild smolts in his analysis. McGie (1983) observed a nonlinear (density dependent) relationship between smolts and adults during periods of low upwelling which were the result of either compensatory mortality or a high degree of variability or a combination of both. Since low upwelling had been recorded in 74% of the years between 1946 and 1983, McGie (1983) cautioned fishery managers that they faced a difficult economic choice when attempting to enhance coho salmon in the OPI area with expensive hatchery programs.

#### **3.1.1.7 Nickelson (1986)**

Nickelson (1986) analyzed the components of production (private and public hatchery and wild smolts) separately and in combination for both strong and weak upwelling years. The relationship between smolts and subsequent adult production was linear in all analyses except the combined hatchery and wild population in weak upwelling years and when all years (high and low upwelling) were combined. Nickelson (1986) explained how the combined hatchery-wild population could exhibit a nonlinear relationship as an artifact of the relative abundance and

differential survival between hatchery and wild fish. He concluded that population regulation after entry into the ocean was density independent. He also suggested some mechanisms to explain the difference in survival between weak and strong upwelling years.

### **3.1.1.8 Peterman and Routledge (1983) and Peterman (1989)**

Peterman (1989) analyzed the power of the test employed by Nickelson (1986) and concluded that power was below 0.19 for all the tests involving components of coho production in the OPI. Those results indicated there was at least an 81% chance of making a Type II error i. e., incorrectly accepting the null hypothesis of density independent marine survival. Given this level of uncertainty Peterman (1989) cautioned managers about increasing smolt releases strictly on the evidence presented in Nickelson (1986). In an earlier paper, Peterman and Routledge (1983) explored the design of an experiment to test density dependent marine mortality. They concluded that a release size of 88 million smolts would be required to achieve a reasonable level of statistical power in the experiment.

### **3.1.1.9 Emlen et al. (1990)**

Emlen et al. (1990) is the latest in the series of papers examining the question: Is marine survival of coho salmon in the OPI density dependent? In the earlier papers, simple empirical expressions were used, however, Emlen et al. (1990) constructed alternative models based on biological criteria and different biological assumptions designed specifically for the question being addressed. They concluded there was weak statistical support for density feedback on survival and that the question of density dependence remains open. The question that several researchers have attempted to answer since ODFW (1982) is yet to be resolved.

## **3.1.2 Direct Sampling of Juvenile Salmon in the Ocean**

Data from juvenile salmonids sampled by purse seine from 1956-1970 in the eastern north Pacific and Bering Sea were summarized by Hartt (1980). All of the sampling along the northwest coastal area was conducted in or north of the Strait of Juan de Fuca so juvenile salmonids from the Columbia River did not enter the sampling area until after they had travelled a considerable distance.

Since sockeye, chum and pink salmon were rare in offshore areas during their first summer at sea, Hartt (1980) concluded that those species remained in coastal waters. In contrast, some chinook, coho and steelhead exhibited offshore movement. However, substantial numbers of chinook and coho also remained in nearshore waters. The majority of steelhead appear to migrate rapidly from the coastal waters into the open sea (Hartt 1980). Juvenile coho, chinook and steelhead captured, tagged and released in the northeastern Gulf of Alaska were recovered in Oregon and California coastal streams and the Columbia River. Based on limited tag returns (54 coho, 3 chinook and 1 steelhead), Hartt (1980) suggested that a large proportion of the coho from that region migrate north during their first summer of ocean residence. However, based on his

sampling of those stocks, Pearcy (1992) concluded that many juvenile salmon in the OPI area remain in the local coastal waters of Oregon and Washington during their first summer at sea. The different conclusions of Hartt (1980) and Pearcy (1992) could have resulted from different oceanographic conditions (Pearcy 1992).

A positive relationship between coho jacks and the number of adults from the same brood that return the following year implies that most of the variability in marine survival of coho occurs within the first four to six months at sea (Gunsolus **1978**). Fisher and Pearcy (1988) found a relationship between an index of jack survival and their catch of juvenile coho in the ocean in June. Since the peak outmigration of coho smolts from the Columbia River peaks in May, their data narrowed the critical survival period to the first month at sea (Pearcy 1992). As indicated in the previous paragraph, Pearcy (1992) concluded that juvenile coho remained in local coastal areas during their first summer at sea. This means that the coastal upwelling zone of Oregon and Washington is the critical habitat--the place where coho year class strength is determined.

Although both coho survival and zooplankton abundance have been positively correlated with upwelling, Pearcy (1992) noted little evidence for food limitation of juvenile coho in the nearshore marine habitats of Oregon and Washington. He based his conclusion on a review of the literature and his own work. The two principal observations are described below:

- The biomass of prey consumed by coho is small compared to the biomass of prey potentially available. Walters et al. (1978) also concluded that ocean limitation on production was unlikely unless the biomass of zooplankton is largely unavailable to the salmon and Honkalehto (1984) reached a similar conclusion. A possible exception to these observations occurs during periods of low upwelling when prey abundance is reduced and additional competitors such as mackerels move north with the warmer water. Pearcy (1992) did note that coho have a large number of competitors for the same prey organisms.

If the relationship between marine survival and upwelling (Nickelson 1986) is a function of prey abundance, i. e., low upwelling reduces prey abundance leading to reduced growth and starvation of coho, we should expect a positive relationship between upwelling and coho growth during their first month at sea. However, growth of juvenile coho salmon from Oregon coastal streams estimated from the spacing of scale circuli laid down after ocean entrance did not show a positive relationship with upwelling (Bottom 1985 and Pearcy 1992). Variation in annual survival of coho is greater than the variation in growth determined from scales of surviving adults (Bottom 1985).

Pearcy (1992) also evaluated the hypothesis that upwelling influenced smolt transport in marine waters making the juvenile coho more or less available to predators. He presented evidence from the literature that adult salmon preyed on juvenile salmon, as well as, evidence of predation by other species including marine birds. However, in his own sampling Pearcy (1992) did not obtain direct evidence of heavy predation on juvenile salmonids by adult salmonids and other predators.

Pearcy (1992) suggested that survival of coho during the critical first month at sea is determined by functional responses of predators to coho smolts and alternative prey. The abundance of alternative prey and the dispersal of coho is mediated by upwelling. In high upwelling years more alternative prey is available to predators of juvenile salmon and the coho are more dispersed. Pearcy (1992) also discussed evidence that Pacific herring buffered predation on juvenile coho salmon. Smolt to adult survival rates of coho from Carnation Creek, British Columbia increased during years when herring were abundant (Holtby 1988 cited in Pearcy 1992). Pearcy (1992) concluded that the cause of mortality of juvenile coho salmon during the first critical month at sea is still speculative.

Pearcy (1992) evaluated the food limitation and predation hypotheses as though they were independent events. There is support for combining the two hypotheses. Based on a model of minimum sustainable biomasses of marine ecological groups along the northwest coast, Laevastu and Favorite (1977) concluded that predation rates in the nearshore habitat are high. They concluded that ecosystem internal consumption was much higher than the catch i.e., the marine ecosystem was consuming itself at rates much higher than the commercial and sport harvest. Laevastu and Favorite (1977) suggested that the high turnover rates indicate partial starvation might be common at sea. Partial starvation combined with high predation pressure could explain the relationship between upwelling and survival of juvenile coho during the critical first month at sea. This explanation is supported by Iles (1980) who proposed a hypothesis of preprogrammed growth rate which he summarized this way:

***The high zygote production by teleosts results in intense density dependent mortality at the larval - post larval stage. The mortality agency is "programmed growth": the need to maintain a minimum genetically determined growth rate The motto for teleost larva is "grow, or die!"***

The failure to show growth differences in juvenile coho between low and high upwelling years (Bottom 1985 and Pearcy 1992) could be interpreted as support for Iles's (1980) hypotheses rather than rejection of the hypothesis of food limitation and starvation. There was no evident difference in growth of coho between high and low upwelling years because the juveniles that failed to grow at the minimum rate were consumed by the intense predation. Bottom (1985) did show better than average growth for the one brood of coho that entered the sea during the El Nino event of 1983. That year class exhibited poor survival (Johnson 1984). Improved growth in years of poor survival also supports Iles's hypothesis in that he suggested better than average growth in fish with a preprogrammed growth rate will only be observed when the habitat is not fully seeded because of a brood failure.

I suggest that Iles's hypothesis can be extended to the Pacific salmon during the first critical month at sea. This implies that there is a high degree of interaction between Pearcy's productivity

growth and predation hypotheses. High predation rates in the sea will overtake and consume the slower growers. Growth might be influenced by reduced food availability, poor physiological condition (specifically in hatchery reared fish) and stress from poor passage conditions at mainstem dams.

## 4. PERFORMANCE OF THE NON-SALMON PELAGIC FISHERIES

### 4.1 HISTORICAL PERFORMANCE

Most of the work on marine mortality of Pacific salmon described so far in this report has given little consideration to other fishes in the upwelling zone. Salmon have generally been treated as though they had little or no interaction with the rest of the marine community. In this section, selected biological features of the pelagic fish community in the upwelling zone will be reviewed. The purpose of this section is to examine salmon in the marine habitat from a different point of view to see if a different set of questions or hypotheses emerge.

Soutar and Isaacs (1974) were able to estimate the abundance of pelagic fishes in the California current from scales found in cores of anaerobic marine sediments. Their data permitted estimates of biomass for an extended time series--1785 to 1970 (Smith 1978). Baumgartner et al. (1992) extended estimates of sardine biomass to a 1,700 year period. The pelagic fish community in the upwelling zone has been dominated by three species (California sardine, hake and anchovy) for the past 200 years (Smith 1978) (Figure 2). The time series of combined biomasses for those species show three important features: 1) The years from 1895 to 1915 were a period of exceptional productivity unequaled in the 200 years of record; 2) the period of exceptional productivity was followed by a precipitous decline; and 3) the decline after 1925 was deeper than any of the troughs in the previous 150 years and it appeared to coincide with intensified exploitation of marine fisheries and a strong relaxation of wind induced upwelling between 1916 and 1942 (Ware and Thomson 1991). A well known consequence of the decline in the first half of this century was the collapse of the northern subpopulation of the California sardine. Overall the biomass in the California current declined from about 25 million tons in 1905 to 4.5 million tons by 1950 and has remained well below its historic levels (Ware and Thomson 1991).

Commercial salmon harvest also peaked between 1890 and 1915 in most areas of the northwest (Cobb 1930). When the Oregon commercial harvest of coho salmon is superimposed on the longer data set in Figure 2, the trend in coho catch appears to follow a pattern of abundance similar to hake, anchovy and California sardine. Nickelson (1986) also showed a correspondence between anchovy and coho abundance for more recent years. The information presented in Figure 2 suggest that the ecological processes driving the decline of pelagic fisheries through the first half of this century also had a strong influence on the production of coho salmon. The similarity in the patterns of decline after 1900 suggest that the species represented in Figure 2 shared similar environmental constraints on production. However, life history patterns of three of those species (coho, hake and sardine) also suggest a possible biological interaction.

Figures 3, 4, and 5 illustrate the migration patterns of Pacific hake, California sardine and coho salmon. Pacific hake migrate north from winter spawning grounds off California and northern Mexico reaching the northwest coast in July and August (Figure 3). The Pacific hake supports

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<sup>3</sup> Baumgartner et al. (1992) show nine collapses and recoveries of the California sardine over the past 1,700 years.

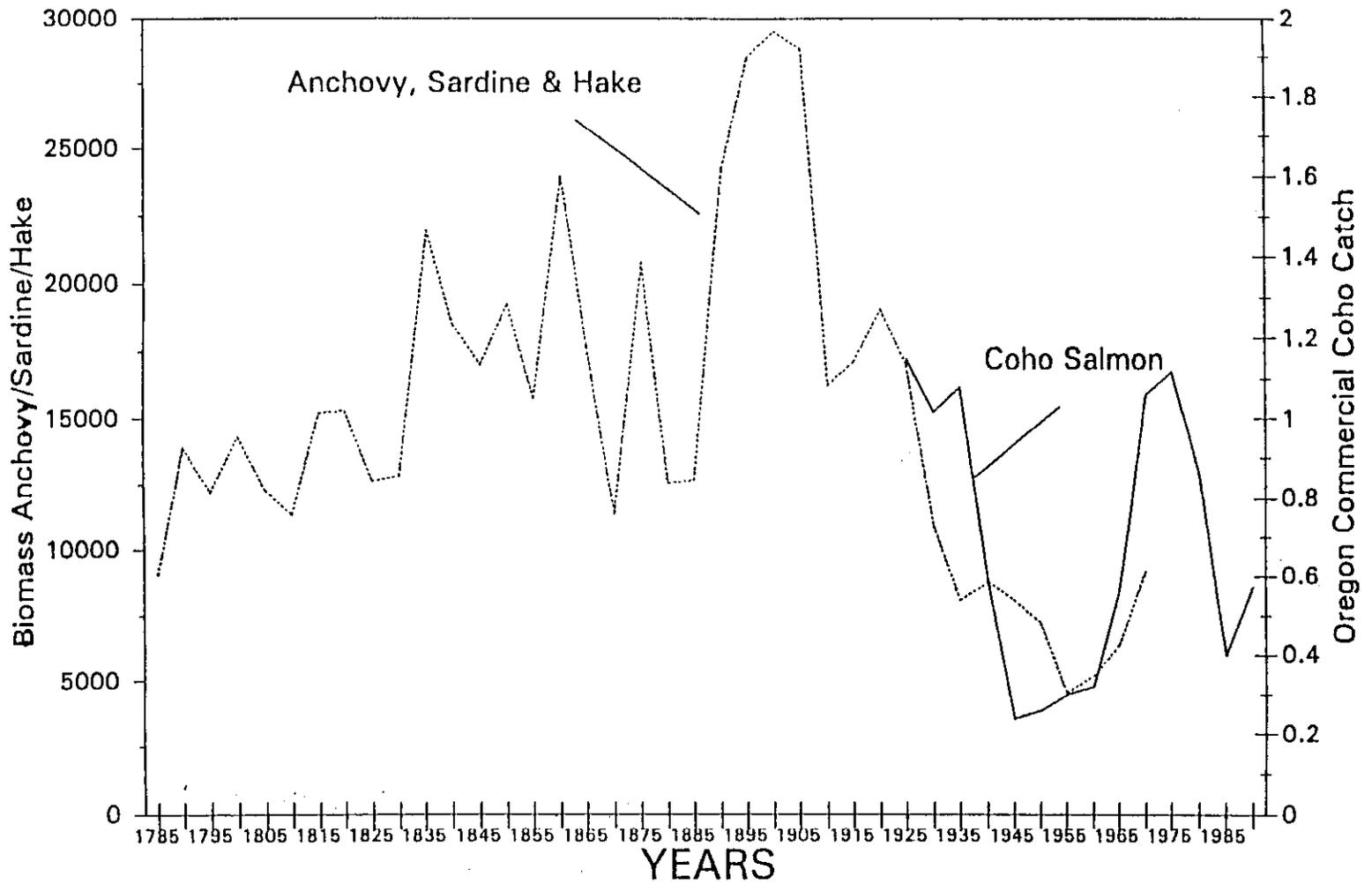


Figure 2. Total biomass of anchovy, sardine and hake in the California current in thousands of metric tons. Standing stock inferred from contemporary stock sizes and scale deposition rates in 18th and 19th Centuries (from Smith 1978). Commercial catch of coho salmon in million of fish (from International North Pacific Fisheries Commission, 1979, 1981a, 1981b, 1982, and 1986). Annual coho data averaged by five year intervals.

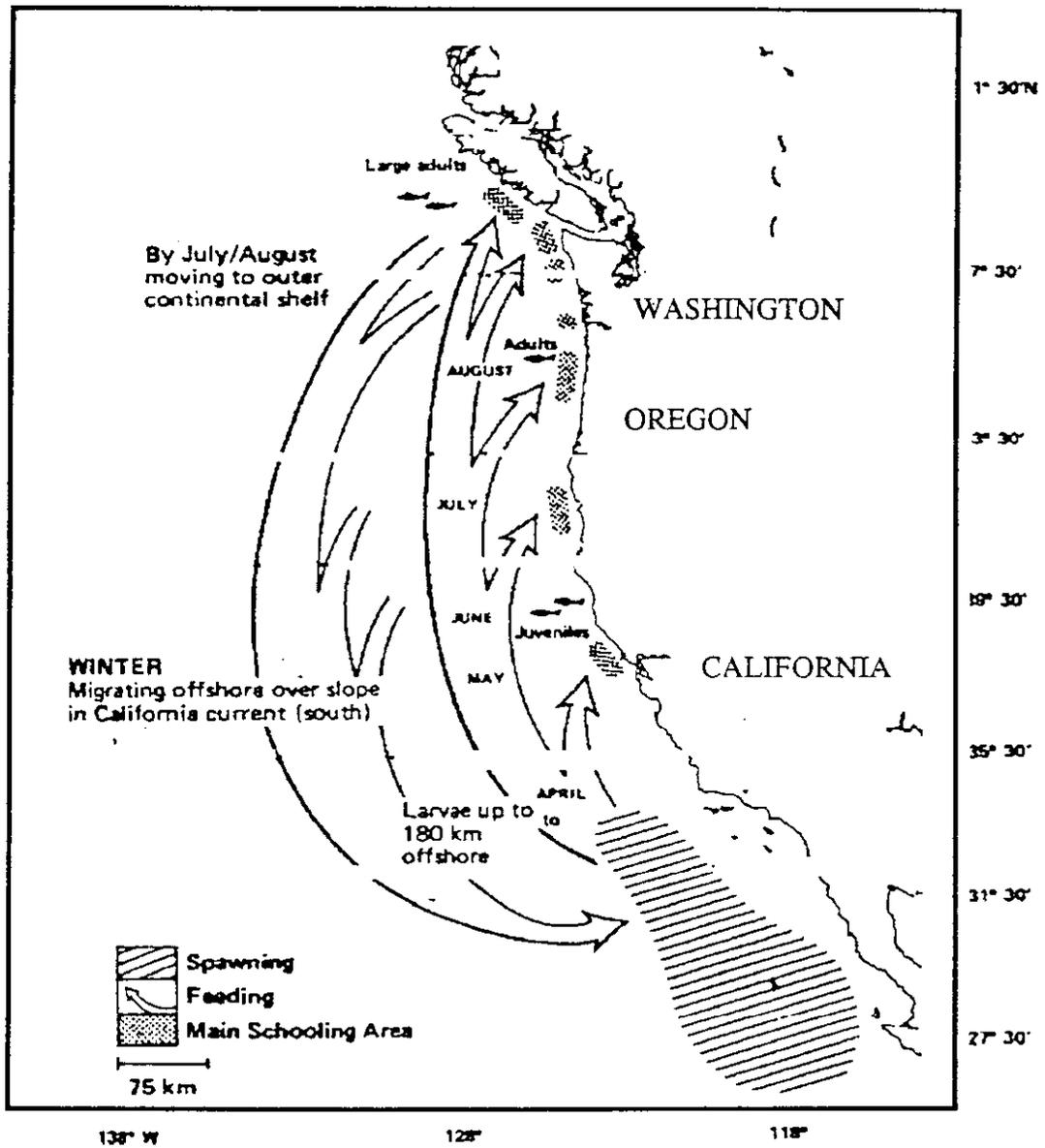


Figure 3. Life history and migration of Pacific Hake off the West Coast.  
(From Francis et al. 1984)

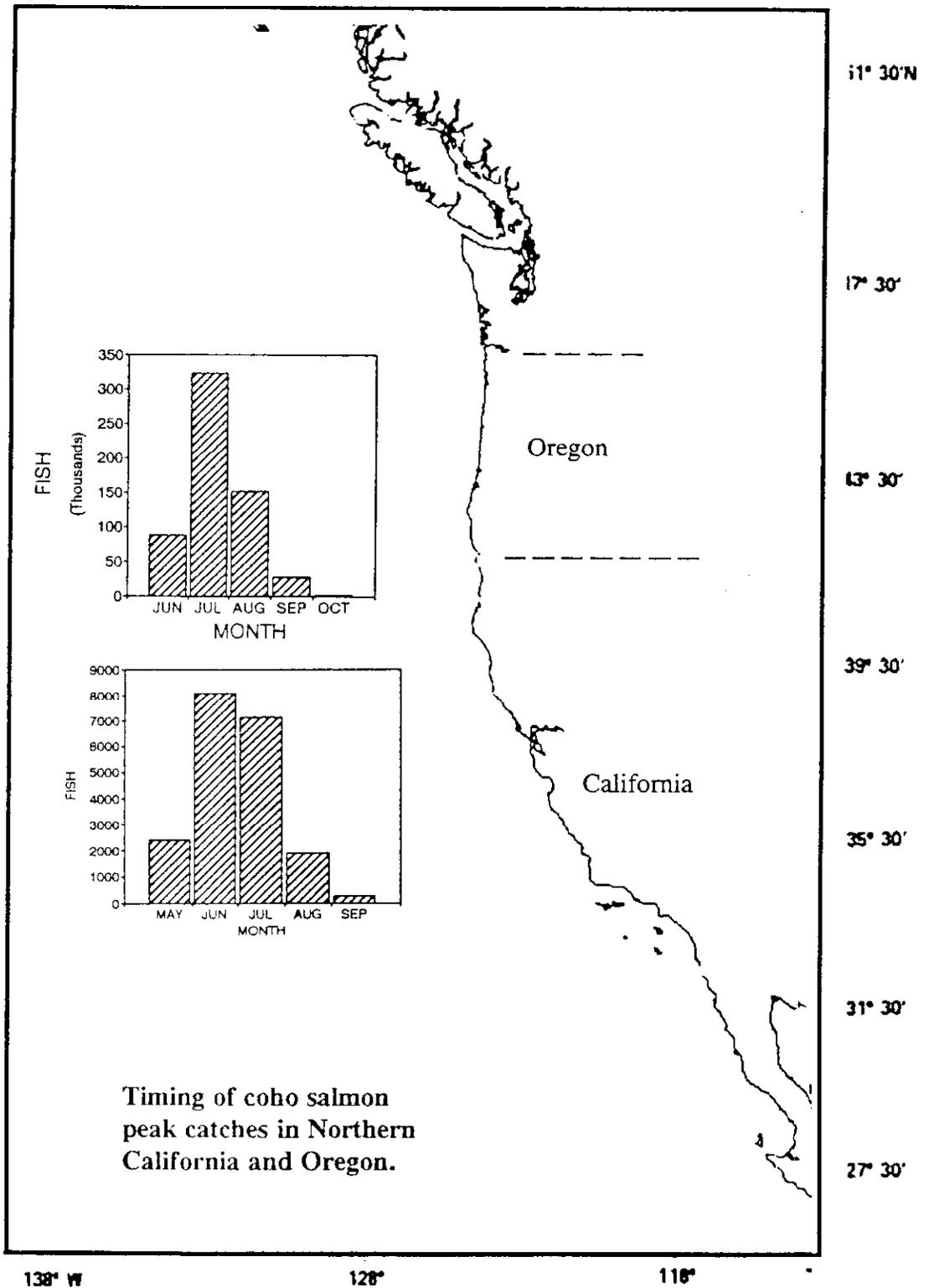


Figure 4. Timing of coho harvest in northern California and Oregon. Harvest peaks in California in June and in Oregon in July. Data are averaged harvest for the years 1952-1990. (From Oregon Department of Fish and Wildlife unpublished data)

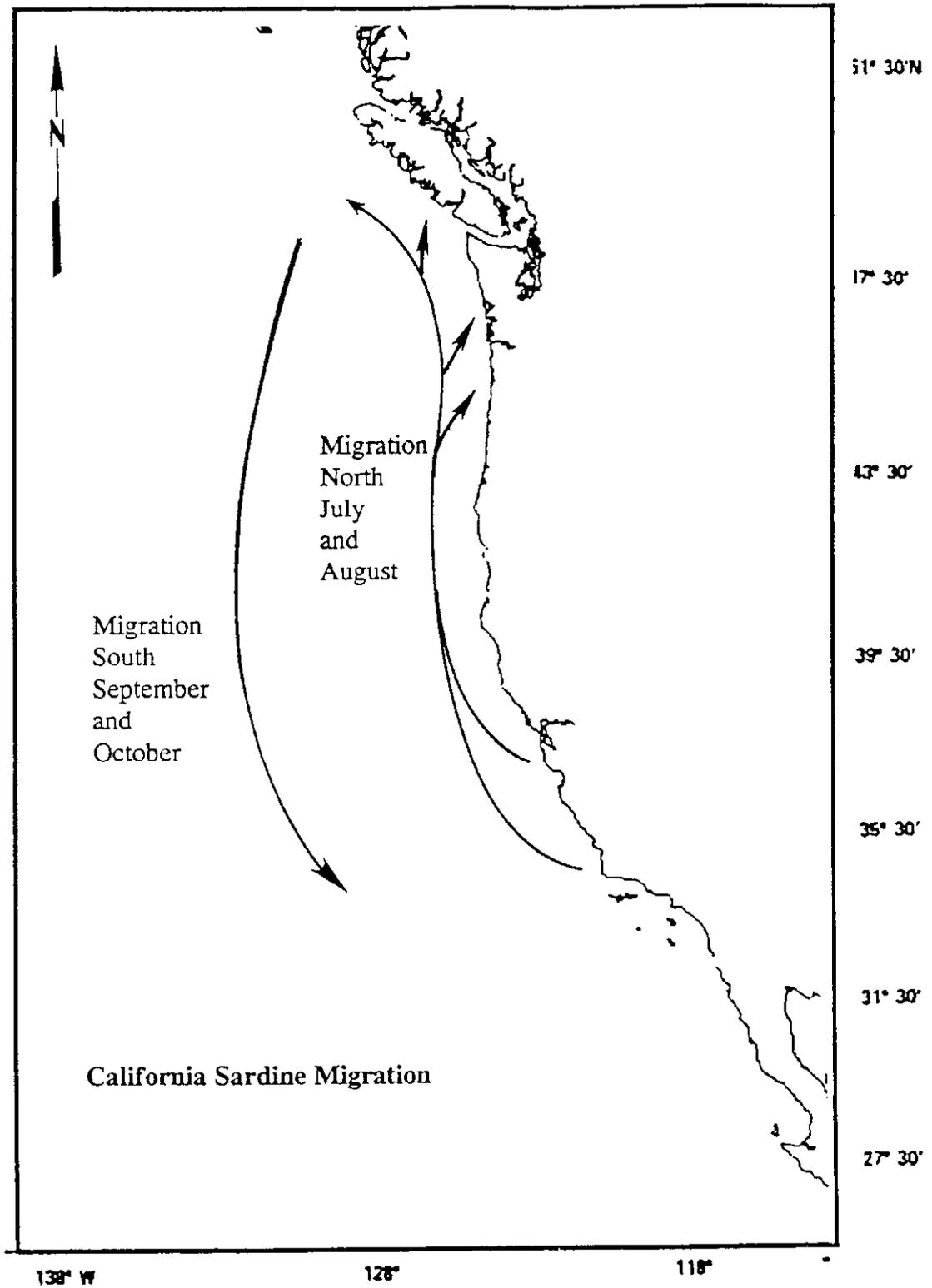


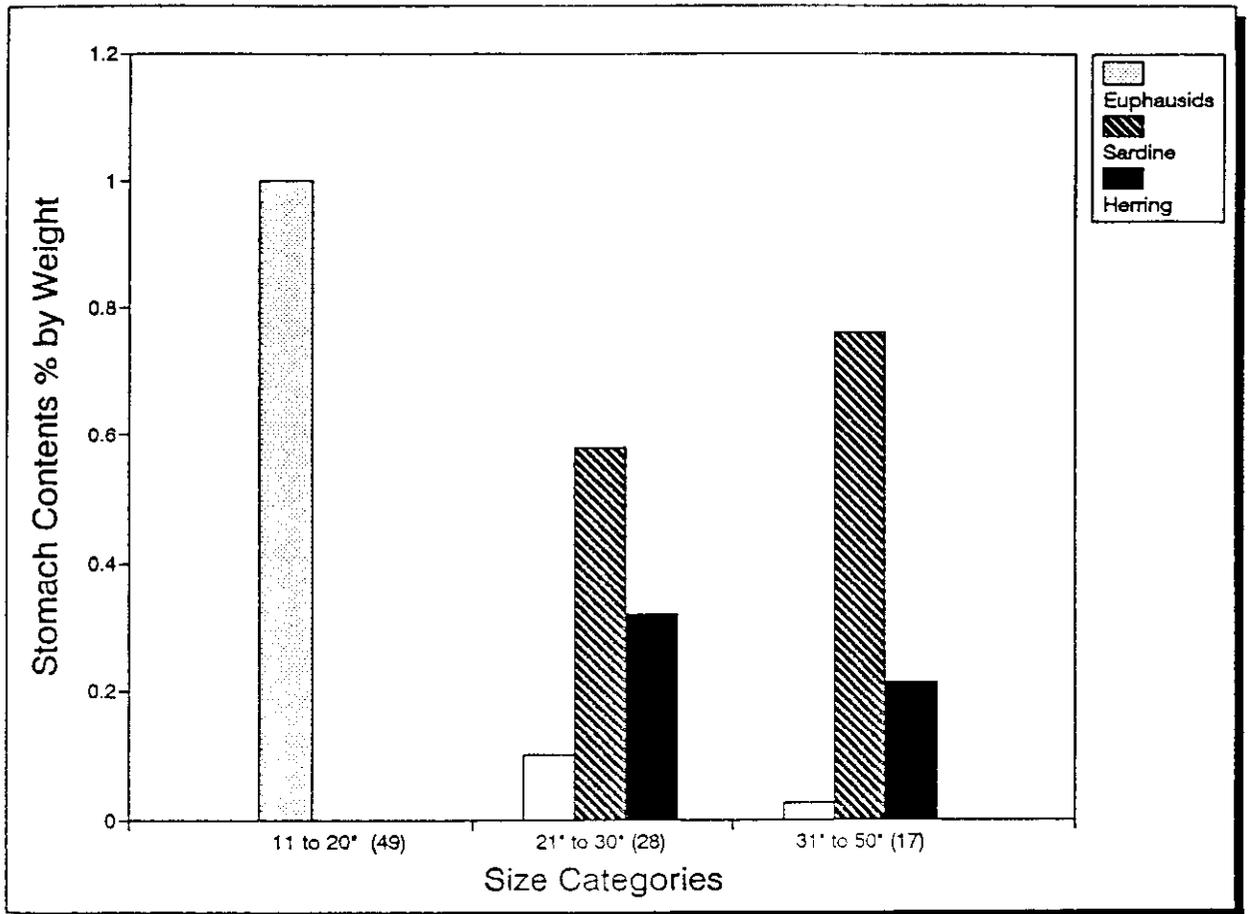
Figure 5. Migration of California sardine on the west coast. (From Murphy 1966)

the largest single species fisheries on the west coast and it is an important trophic link in the California current (Francis et al. 1984). Pearcy (1992) examined the stomach contents of 290 Pacific hake and found no juvenile salmon.

Before its collapse, the large northern subpopulation of the California sardine migrated north from spawning areas off Southern California reaching Oregon, Washington and the west coast of Vancouver Island in July and August (Figure 4). In addition to the large California fishery, the large migrating schools of sardines supported significant fisheries in Oregon, Washington and British Columbia peaking at 26,000 tons/year in Oregon and Washington and 88,000 tons/year in British Columbia (Murphy 1966). The northwest fishery on sardines collapsed after 1948.

Coho salmon migrate northward in their last summer at sea as evidenced by the timing of peak catches in the ocean fishery off California (June) and Oregon (July) (Figure 5). The timing of coho, sardine and hake movement along the west coast suggest a trophic connection; the possibility that coho and hake were feeding on sardines. I found only one study of the food habits of ocean caught coho and chinook salmon conducted before the collapse of the sardine. Chapman (1936) examined the food habits of ocean caught chinook and coho salmon from Westport and Neah Bay, Washington. The stomach contents of chinook salmon captured by purse seine on Swiftsure Bank (Neah Bay) are compared in Figure 6. Prey preference shifted with the length of the chinook (Figure 6). Fish between 11 and 20 inches feed almost entirely on euphausiids; between 21 and 30 inches the chinook shifted to sardines and herring with sardines being more important; and about 80% of the stomach contents in fish 31 to 50 inches in length were sardines. Sardines were also important prey of coho sampled at Westport in July and Neah Bay in August, however, Chapman (1936) did not report those stomach contents by weight.

This single study does not definitively verify the importance of sardines in the diet of adult salmon but it does suggest that sardines and salmon were linked trophically. Sardines may have been an exceptionally rich source of calories for salmon especially in the final months before entering rivers to spawn. While feeding off the northwest coast during the summer months, the oil content of the sardine increased dramatically from a low of about 14 gallons of oil/ton of fish in late July to 54 gallons of oil/ton of fish in early September (Chapman 1936). Sardines may have had another trophic linkage to salmon. The large schools of sardines may have served as a buffer against predation of juvenile salmon during their critical first summer at sea. The buffer may have acted in much the same way as the herring buffered predation of Carnation Creek coho discussed earlier in this report.



**Figure 6.** Stomach contents of three size categories of chinook salmon. Stomach contents are expressed as percentage by weight of the three important food items. Numbers in parenthesis are the number of fish sampled in that size category. The chinook salmon were captured by purse seine from swiftsure bank near Neah Bay, Washington on July 13 and 26, 1936. (From Chapman 1936)

The historical reconstruction of the biomass of sardine, hake and anchovy and the stomach contents of the salmon sampled in 1936 off the Washington coast suggest trophic linkages in the California current comprised, in part, of the migration of hake and coho salmon and possibly other predators following the migration of their prey (sardine) north to feeding grounds. Another species whose movement exhibits a trophic linkage to the species listed above is the California sea lion. Ainley et al. (1982) concluded that the movement of California sea lions were tied to the movement and availability of their principal prey the Pacific hake.

These observations do not pretend to exhaust the pertinent literature on the trophic structure of the upwelling zone where the Pacific salmon of the Columbia River spend their first critical month at sea. The observations are sufficient to frame new questions or hypotheses regarding a possible change in state of nature that could have important consequences to salmon management and restoration programs. Two of those questions are given here for the purpose of stimulating further discussion and research on the subject.

1. Did the most recent collapse of the California sardine trigger a trophic cascade in the California current characterized by standing stocks at depressed levels over the last 40 to 50 years? What are the management and recovery implications of productivity cycles in the upwelling zones?

The loss of the California sardine may have impacted trophic linkages including salmon. Anchovy staged a partial recovery in the 1970's but declined and hake also showed a modest recovery in the late 1940's but declined and appear to be trapped in a narrow production range of 1 to 2 million tons after 1960 (Ware and Thomson 1991). Sardines are currently characterized as recovering (Baumgartner et al. 1992). Those changes in standing stocks occurred as the California current moved into a low productivity phase of a 40 to 60 year productivity cycle. The north Oregon coast and Columbia River chum salmon went into decline after 1947 with a sharp decrease after 1954 (Nickelson et al. 1992). It could be argued that wild Oregon coast coho failed to fully recover from the low productivity cycle in the early part of this century and are now declining rapidly in the current productivity trough. Oregon coast chinook stocks were also severely depressed in the 1930 to 1960 period (Nicholas and Hankin (1989) and many of the coastal populations have recovered but not to historic levels of abundance (Lichatowich and Nicholas, in review). Changes in the California current were not limited to the hake, sardine and anchovy but include Pacific salmon. The implications of those changes to harvest management and freshwater habitat protection are not clear but deserve further attention.

2. Given the apparent changes in the biota of the California current, what are the additive or synergistic effects of freshwater habitat degradation on salmon production?

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4 Springer (1992) described a trophic cascade triggered by a decline in the biomass of juvenile walleye pollock in the Bering Sea and Gulf of Alaska.

Resource managers are being encouraged to incorporate a watershed perspective in their programs when dealing with production problems and conflicts in resource use (see for example, Naiman 1992). However, for salmon the watershed defined as a catchment basin is not adequate. The salmon's watershed includes oceanic rivers such as the California current. Thompson (1959) defined the home stream of salmon as a "chain of favorable environments connected within a definite season in time and place." He went on to speculate that the chain extends to the sea. Thompson (1959) suggested that we attach more importance to what we can see so the freshwater part of the chain assumes more importance. That is why solutions to salmon production problems have historically come from the familiar freshwater links in the chain, i.e., hatcheries, spawning escapements, stream habitats. The question posed above suggests we need to devote more effort evaluating the entire chain of life history-habitat linkages including the sea.

If the California current has undergone a "change in state" that influences salmon production then it follows that the state of the freshwater links in the chain may become more important. Healthy freshwater habitats may become more critical when oceanic productivities are lower and marine mortality higher. Our degradation of freshwater habitat combined with cyclic changes in ocean productivity and high harvest rates may have had the effect of "burning the candle at both ends." Cycles of ocean productivity can at the very least mask the effects of improvement in freshwater habitat or hatchery production or cause us to falsely attribute increased marine survival to restoration effects in freshwater. However, there may also be important additive or multiplicative consequences of freshwater habitat degradation in the troughs of ocean productivity cycles.

## **5. RECOMMENDATION**

There is a need for additional literature review and research on oceanic habitats and life history of salmon from the Columbia River. Additional work should be approached from an ecosystem point of view which should include emphasis on the pelagic fish community in the California current. Additional literature review and analysis should be implemented to formulate hypotheses and shape the design of any future data collection either directly in oceanic habitat or indirectly through analysis of tagging information, catch records and data sets from past sampling programs.

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