CHAPTER 10. THE MARINE ENVIRONMENT

"Some might be tempted to attribute all changes in salmon abundance to changes in ocean conditions and to conclude that management related to rivers is therefore unimportant. However, because all human effects on salmon are reductions in the total production that environment allows, management interventions are more important when the ocean environment reduces natural production than when ocean conditions are more favorable."

National Research Council. 1996. Upstream: Salmon and Society in the Pacific Northwest. Report on the Committee on Protection and Management of Pacific Northwest Anadromous Salmonids for the National Research Council of the National Academy of Sciences. National Academy Press, Washington D. C. (p. 361).

The Columbia River Estuary

Transition from river to ocean

Pacific salmon undertake extensive migrations extending from headwater streams hundreds of kilometers inland to distant oceanic rearing areas. Twice during their migrations salmon must undergo extensive physiological changes to make the transition between radically different environments: when they migrate from freshwater to saltwater as juveniles and the reverse as adults. The estuary is where that transition between salt and freshwater takes place and the estuary is part of the salmon's ecosystem that, in general, has received little attention (Simenstad et al. 1982).

By standing at a critical transitional stage in the anadromous salmonid's life history, the estuary can be a key regulator of overall survival and year-to-year variation in abundance. The ecological state of the Columbia River estuary has been compromised by extensive habitat alteration from human activities in the estuary itself and in upriver areas. Many of those changes are of potential importance to salmon production. Because the estuary is the terminus of the river, it is where the cumulative impacts of upriver actions all have focused (Simenstad et al. 1992), including potential adverse effects from pollution, changes in biological and non-biological input and alteration of seasonal flow patterns. The estuary is critical habitat that can constrain total salmon production, particularly of the more estuarine dependent species such as chinook salmon.

Earlier in this report (Chapters 3 and 5), salmon habitat was equated to beads on a string. Beads were the places where salmon carried out important parts of their life cycle such as spawning, rearing, holding or avoiding predation; and the string was equated to migration corridors giving salmon access to those places. The estuary is a critical part of the string, a migratory corridor connecting riverine and oceanic habitats, and a place (bead) where some juvenile salmon may rear for extended periods prior to their migration to the sea.

Estuarine influence on salmonid life histories

Salmon have evolved a variety of strategies to utilize the estuary and move between freshwater and marine areas. Juvenile sockeye and coho generally spend a limited time in the estuary and move quickly from the riverine to the marine environment (Groot and Margolis 1991; Pearcy 1992). Pink and chum use the estuary for spawning as well as an early rearing phase that may last from days to weeks (Pearcy 1992). Chinook salmon display a variety of estuarine strategies. Reimers (1973) identified five different juvenile chinook life history strategies in the Sixes River based on size and timing of entry into the estuary. Schluchter and Lichatowich (1977) observed seven patterns in the use of the estuary by juvenile chinook in the Rogue River.

In the Columbia River, utilization of the estuary by juvenile chinook salmon has received little attention. However, differences in estuarine strategies can be distinguished at least at the level of the two major life history types. Sub-yearling or ocean-type chinook salmon enter the estuary gradually as part of their protracted downstream rearing and growth phase. They spend several weeks to months in the estuary prior to a long marine migration (Bottom et al. 1984; Healey 1991). The yearling or stream-type life history, on the other hand, appear to spend little time in the estuary (Healey 1991; Pearcy 1992). Given the variety of estuarine strategies displayed by juvenile chinook salmon in the Sixes and Rogue rivers and the variety of freshwater habitats in the Columbia River, it seems likely that the actual number of strategies for estuarine utilization in the Columbia River far exceeds the general, ocean- or stream-type life histories.

Estuarine habitats

Simenstad et al. (1982) hypothesized three important functions for estuaries which enhance the growth and survival of Pacific salmon:

- Physiological Transition Zone Salmonids undergoing physiological change may benefit from the gradual change from fresh to salt water within the estuary.
- Predator Avoidance Although the abundance of predators is higher in the estuary, juvenile salmon may disperse into habitats that offer protection from predators. In addition, during the period of juvenile residence in estuaries turbidity is higher, reducing the efficiency of predators.

- <u>Optimum Foraging Conditions</u>   The size, distribution and density of many prey organisms in the estuary appear to be optimal for juvenile salmon.

The Columbia River plume, which is the freshwater lens that extends into the nearshore ocean, could be considered an extension of the estuary. The plume may provide extended estuarine rearing or possibly a refuge for juvenile salmon. Changes in the hydrograph of the Columbia River have altered the size and structure of the plume during the spring and summer when many juvenile salmonids are entering the ocean (Pearcy 1992). More research is needed on the ecological importance of the Columbia River plume in the life history of juvenile salmonids.

Given the number of potential predators in the estuary and in the nearshore ocean, the optimal foraging conditions found in the natural estuarine food webs may be the most important function of the estuaries. Rapid growth in the estuary allows the juvenile salmon to grow out of their vulnerability to predators (Simenstad et al. 1982). For that reason, changes in the estuary that impact the food web for juvenile pacific salmon could represent an important constraint on production.

Changes in the estuary that affect the quality of habitat for salmonids come from two principal sources:

- <u>Within the estuary</u>, for example, diking that separates marshes from the main channel,
- <u>Outside the estuary</u>, for example, dams and storage reservoirs that alter the flow regime through the estuary.

Human influences

Changes in the extent and nature of the Columbia River estuary result from a combination of natural and human-caused factors. Natural aging of the estuary results from the interplay between accretion of sediments derived from upriver areas, and the gradual rise in sea level since the last glaciation (Day et al. 1989). The process of estuary filling is accelerated by attached vegetation that acts to trap and stabilize sediments (Day et al. 1989). In the Columbia River estuary, the most important plant species in this regard is Lyngby's Sedge (*Carex lyngbei*) an emergent grass (Thomas, 1983). This grass is common in shallow brackish or freshwater embayments in the estuary and acts to trap sediments.

Accretion of sediment causes a gradual uplifting of the estuary that is countered to some extent by the continuing increase in sea level since the last glaciation. As the estuary builds up, marsh is gradually converted to willow and spruce swamp. Swamp dominated floodplain is the end product of the estuarine process in the Columbia River (Thomas 1983).

In addition to the slow filling of the estuary over time, natural processes act to move and modify the estuary continuously, often in a very rapid and dramatic fashion. The result is a

continuously changing and dynamic physical structure. Sherwood et al. (1990) analyzed early navigational charts and noted profound changes in the river entrance from year to year. The pre-development river mouth was characterized by shifting shoals, sandbars and channels forming ebb and flood tidal deltas. Prior to dredging and maintenance, the navigable channel over the tidal delta varied from a single, relatively deep channel in some years to two or more shallow channels in other years (Sherwood et al. 1990).

Although the process of erosion and deposition is ongoing and often dramatic, the overall rate of estuarine change due to natural aging is generally slow. Relative to the rate of change caused by human actions, natural aging of the estuary is likely insignificant over the last century (Thomas 1983). Most of the human alteration of the estuary results from attempts to stabilize and simplify a naturally dynamic and complex environment.

Early activities in the estuary attempted to stabilize the navigation channel. Jetties were constructed on the north and south shores of the river to hold a channel in place, while a regular dredging program deepened the channel (Sherwood et al. 1990). Material dredged from the main channel was deposited in shallow water areas. Many of these areas were subsequently diked and removed from the estuary.

Dredging, filling and diking resulted in important changes in the morphology of the estuary (Thomas 1983; Sherwood et al. 1990). Total volume of the estuary inside the entrance has declined by about 12 percent since 1868 (Sherwood et al. 1990). Thomas (1983) estimated that 40 percent of the original estuarine area has been converted to developed floodplain by diking and filling. Overall, development since the mid-19th century has resulted in a loss of 77 percent of the tidal swamps, 62 percent of the tidal marshes and 7 percent of the tidal flats (Thomas 1983). Flow patterns were drastically altered in the mid-1970s changing the seasonal input of freshwater to the estuary. Other human induced changes in the Columbia Estuary are either too recent or have not had sufficient study to demonstrate linkages to the status of Pacific salmon.

The strength of the spring freshet was appreciably diminished when upriver storage projects were used to shift water into the winter (Figure 10.1). The result has been a general flattening of the seasonal hydrograph. In addition, the timing of the spring freshet has been moved forward about one month. The biological impacts of these changes have not been studied, however, changes in physical parameters with potential biological impacts have been significant. Changes in estuarine bathymetry and flow have altered the extent and pattern of salinity intrusions into the river and have increased stratification and reduced mixing (Sherwood et al. 1990). Ebbesmeyer and Tangborn (1992) present evidence that the shift of spring flow into the winter has altered sea surface salinities along a large part of the North American coast.

Development has changed the circulation patterns and increased the shoaling rates in the estuary. Sediment input to the estuary has declined due to the altered hydrograph but the estuary is now a more effective sediment trap. Although the Columbia river is characterized as a highly energetic system, it has been changing as a result of development and is now similar to more developed and less energetic estuaries throughout the world (Sherwood et al. 1990). More research on the possible linkages between changes in the estuary and the Pacific salmon is needed.
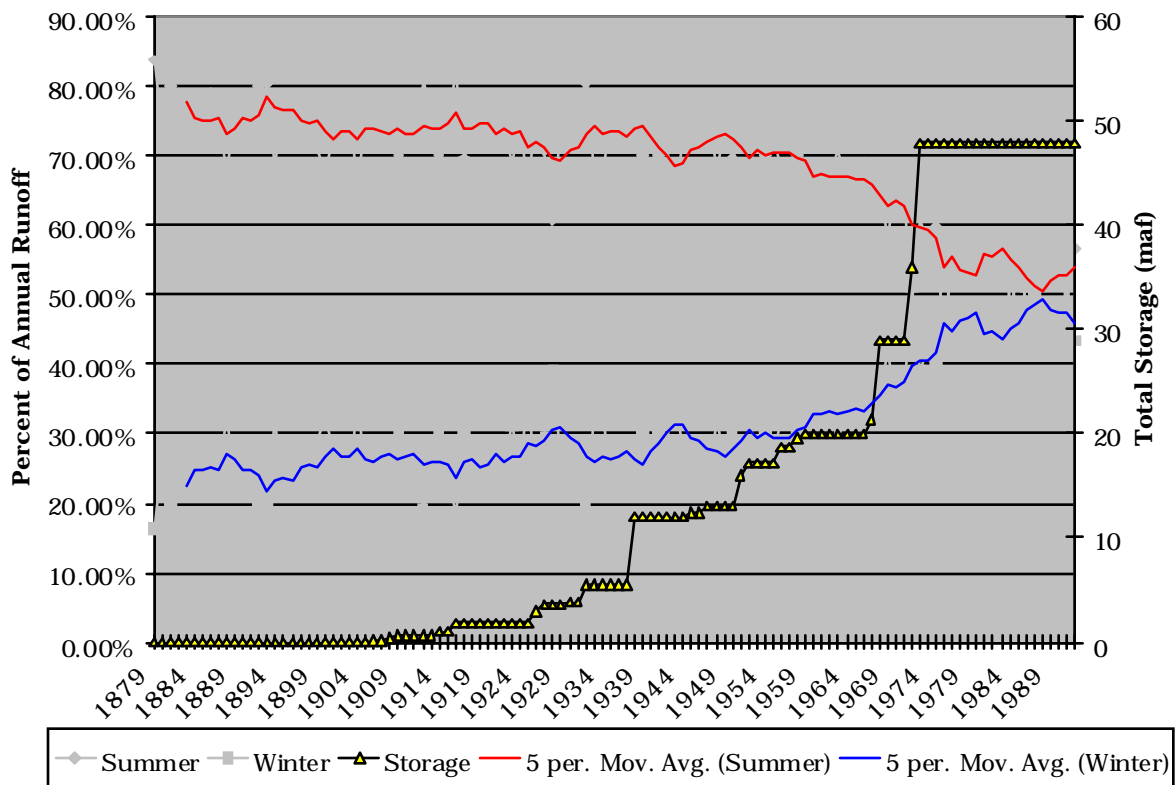

Figure 10.1. Changes in the Columbia River hydrograph as percent of annual runoff at the Dalles, Oregon. 1979-1992.

The estuarine food web

These changes internal to the estuary and in the watershed above it have altered the food web in ways that are detrimental to Pacific salmon. The estuarine food webs that support juvenile salmon are apparently detritus-based (Bottom et al. 1984; Salo 1991), and in the

Columbia Estuary, the detritus-based food web has undergone an important shift in response to development. Macrodetritus derived from emergent marsh vegetation has undergone a dramatic reduction due to the loss of shallow water habitat. The loss of those production areas reduced emergent plant production by 82 percent (Sherwood et al. 1990). Sherwood et al. (1990) estimate that, prior to development, the standing crop of organisms that feed on the macrodetritus would have been 12 times the current standing crop. Since those organisms are prominent prey of juvenile salmonids, it is not unreasonable to assume that a reduction in the food web supported by macrodetritus has had a negative impact on the Pacific salmon. However, Sherwood et al. (1990) could not provide empirical evidence of a linkage between the food web and the status of salmon in the Columbia Basin.

Bottom et al. (1984) found that the index of feeding intensity (IFI) was lower in subyearling chinook salmon from the Columbia estuary compared to the IFI for chinook salmon in either the Fraser (British Columbia) or Sixes (Oregon) estuaries. The IFI is the total weight of the stomach contents expressed as a percent of the fish's total weight.

The food web based on macrodetritus, which is characterized by shallow water, benthic consumers has largely been replaced by a food web composed of deep water, benthic and pelagic consumers. Apparently, primary production of pelagic algae has increased in the impounded stretches of the mainstem Columbia and Snake rivers and the resulting microdetritus input to the estuary is nearly equivalent to the macrodetritus cut off from the estuary by diking the wetlands (Sherwood et al., 1990). The new food web is favored by fishes such as Pacific herring, smelts and the nonnative American shad (Sherwood et al., 1990). The American shad is one of the dominant species in the Columbia estuary (Bottom and Jones 1990). It should be noted that American shad have been increasing in abundance whereas chinook salmon have been declining.

Influences of hatchery stocks

The extensive use of artificial propagation to maintain salmon production in the Columbia River, has altered the patterns of use and movement through the estuary in ways that tend to reduce survival of juvenile salmonids. The release of large numbers of hatchery reared fish over a short time interval could create a density barrier in the river (Royal 1972) or the estuary and near shore ocean (Oregon Department of Fish and Wildlife 1982).

The relationship between massive hatchery releases and a density dependent limitation in the survival of juvenile coho salmon in the near shore ocean and estuary has been the subject of at least ten studies (Gunsolus 1978; Oregon Department of Fish and Wildlife 1982; Clark and McCarl 1983; McCarl and Rettig 1983; McGie 1983; Nickelson and Lichatowich 1983; Peterman and Routledge 1983; Nickelson 1986; Peterman 1989; Emlen et al. 1990). The studies produced contradictory findings, so the issue is still not resolved (Lichatowich 1993).

Hatchery releases and subsequent downstream migration of juveniles often differ from the natural emigration of wild Pacific salmon. Some of those differences include the mass releases from hatcheries instead of the sequential movement of juveniles from individual tributaries, the pulsed movement of hatchery fish (all fish from a hatchery released at the same time) compared to the natural migration over a longer time interval, and hatchery juveniles that are usually larger than their wild counterparts. Hatchery fish may be the wrong size or they may arrive at the wrong time to exploit the food resources of the estuary (Simenstad et al. 1982). For example, wild chinook salmon from the Lewis River, Washington are in healthy condition (Washington Department of Fisheries and Washington Department of Wildlife 1993) and it is one of the largest and most stable populations in the Columbia Basin (McIsaac 1990). One of the reasons for the success of this stock might be the timing of juvenile migration through the estuary. The migration of fall chinook salmon from Lewis River peaks two months after all other salmonids and is later than the other subyearling fall chinook stocks (McIsaac 1990).

Conclusions

Conclusions (and Levels of Proof)

1. Development in the estuary and in the river have altered the historical estuarine food webs in a way that is likely to have negative impacts on the survival and growth of juvenile salmonids (2).

2. Regional consideration of the biological impacts of flow modification in the Columbia River as being limited to areas above Bonneville Dam ignore the potential impact of these alterations on the physical and biological nature of the estuary (2).

3. Other changes in the physical estuarine processes may influence salmon production, but additional research is needed to document the linkages (3).

4. Hatchery operations may have altered the patterns of estuary usage by salmonids and further reduced their survival and growth (3).

The Pacific Basin: Patterns and Processes Influencing Columbia River Salmon

The decline of Pacific salmon stocks extends well beyond the boundaries of the Columbia River basin. Loss of coastal as well as interior populations is widespread throughout the southern edge of the range of Pacific salmon species in Washington, Oregon, and California (Nehlsen et al. 1991). This coherent pattern suggests a systemic problem rather than just a series of localized

effects. Recent studies reveal large-scale changes in oceanic and atmospheric conditions across the entire Pacific Ocean Basin that may regulate temporal patterns of variation in salmon and could be a factor in regional patterns of salmon decline. Although the specific mechanisms are poorly understood, the results underscore the importance of the larger oceanic and atmospheric system within which the Columbia River Basin and its migratory stocks of salmon are embedded.

Relevance of the Ocean Environment to Salmon Production

       Until recently, changes in salmon abundance were attributed primarily to poor habitat conditions in freshwater. These ideas were formalized in theoretical population models, which emphasized the role of density-dependent mortality during egg and early juvenile stages, and in hatchery programs, which assumed that annual production would be increased by eliminating various causes of freshwater mortality (Lichatowich et al. 1996; Bottom 1997). The first serious challenge to these assumptions came after 1976 when abundance of Oregon coho salmon (*Oncorhynchus kisutch*) precipitously declined despite continued increases in the production of hatchery smolts (Bottom et al. 1986). This poor performance offered convincing arguments that annual production of salmon adults could be regulated by conditions in the marine environment (Jeffries 1975). The successful prediction of adult returns from the previous year's run of precocious males (jacks) provided compelling evidence that survival of juvenile coho salmon sometime within their first six months in the ocean could determine production of adults for an entire year class (Gunsolus 1978).

       In the last several decades, oceanographers have described dramatic changes in marine fish assemblages and food chains that have important implications for salmon conservation. From analysis of fish scales deposited in anaerobic marine sediments off Southern California, researchers documented large fluctuations in abundance and shifts in the dominance of pelagic species that occurred well before intensive fisheries had any impact on fish stocks (Soutar and Isaacs 1969; Soutar and Isaacs 1974; Smith 1978). Regional fluctuations in fish populations have been linked to large-scale climatic changes. For example, strong El Nino conditions in the tropics have been associated with changes in marine fauna throughout the Northeast Pacific including northern range extensions for marine, fishes, birds, and plankton (McClain and Thomas 1983; Pearcy et al. 1985; Mysak 1986); reduced reproductive success of Oregon seabirds (Graybill and Hodder 1985); changes in the migration routes of adult sockeye salmon (*O. nerka*) returning to the Fraser River in British Columbia (Wickett 1967; McClain and Thomas 1983); and reduced size, fecundity, and survival of adult coho salmon off Oregon (Johnson 1988). Shifts in abundance of dominant species may reverberate throughout marine food chains with unpredictable effects on the abundance of associated species. For example, Sherman (1991) reported that overfishing on the northeast continental margin of the United States was

responsible for sudden flips in the biomass of dominant pelagic species with cascading effects on marine birds, mammals, and zooplankton. Coincidental declines in the abundance of several bird and marine mammal populations has raised similar concerns about the potential effects of intensive harvest of walleye pollock *Theragra chalcogramma* on pelagic food chains of the Bering Sea and Gulf of Alaska (Springer 1992). Although poorly understood, the risks of harvest-mediated effects on many marine ecosystems may be increasing. Pauly and Christensen (1995) estimate from 24 to 35 percent of the primary production of fresh water, upwelling, and continental shelf ecosystems of the world is required just to sustain current levels of fishery harvest.

Variability in marine ecosystems raise fundamental issues for salmon conservation. First, although fishery managers cannot control environmental variations in the ocean, this does not mean that they can afford to ignore them. For example, in the 1960s and early 1970s, the assumption that hatcheries were responsible for increases in adult returns led to continued growth in hatchery programs and in ocean fisheries during a period of unusually favorable conditions for marine survival of salmon. As noted above, abundance of salmon later collapsed along with the overinflated fishery after the return to less productive ocean conditions. But by this time, overharvest of wild populations had already reduced escapement and stock diversity in Northwest rivers and compromised the capacity of coho salmon to withstand subsequent environmental fluctuations (Bottom et al. 1986). The failure to account for natural variability may lead to faulty conclusions about the response (or lack of response) of salmon to hatchery practices, fishery quotas, habitat restoration efforts, or other management prescriptions (Lawson 1993). To avoid choices that undermine conservation, restoration programs in the Columbia River basin must account for the "background" of environmental change upon which management actions are superimposed.

Second, changes in the ocean environment raise important questions about the appropriate scales and indicators of biological response. Traditionally, management programs for salmon have emphasized year-to-year variations in adult abundance and, in studies of environmental factors, the spatial scales of freshwater habitats, stream reaches, or river systems (meters to tens of kilometers). But changes in salmon production involve processes that vary over periods of decades and longer and extend for distances greater than the thousands of kilometer migrations of individual fish. Unlike the well-defined and relatively restricted boundaries of streams and watersheds, oceans are highly "open" systems in which physical and biological properties are linked across vast distances. Short (days to years) and long-period signals (decades to centuries) propagate through the ocean and atmosphere and change (e.g., become amplified or dampened) through their interaction. Oceanic and atmospheric influences on salmon production therefore involve multiple spatial and temporal scales of variability. Decadal

or longer changes in ocean productivity may not be understood by simply tracking annual harvest and escapement. Furthermore, appropriate indicators of oceanic changes affecting salmon may include species other than salmon. Salmon are members of complex marine communities. Significant shifts in the distribution of predators or in the structure of food chains may be important factors in the dynamics of salmon populations, whose ocean distributions, physical environments, and biotic interactions are at least partially predetermined by the migratory route they must follow to and from their home streams.

Third, large-scale changes in ocean climate and current regime undermine simple distinctions between density-dependent and density-independent factors that may inhibit understanding of population regulation. Researchers have long debated without resolution, for example, whether the coastwide collapse of Oregon coho salmon was the result of density-dependent or density-independent effects (Lichatowich 1993). But if fluctuations in the ocean environment involve qualitative shifts in the structure of entire communities and in the physical distribution of species, food, and nutrients, how do we separate density-dependent from density-independent effects? Do we emphasize the proximate density-dependent influences of food limitation or predation? Or do we highlight the ultimate density-independent effects of an unstable ocean environment that may reset the successional clock after every storm, spring transition, or El Nino event, and, therefore, may regulate the specific array of biotic interactions at a particular place? Sinclair (1988) proposes that populations of marine fish can suffer losses via "spatial" processes that physically displace individuals from the appropriate area needed to sustain themselves or through energetics processes associated with starvation, predation, or disease. Both kinds of processes may involve density-dependent as well as density-independent causes. In the case of salmon, a changing background of current or upwelling conditions each year of smolt migration may create new sets of potential "winners" and "losers" among different salmon stocks based on when and where they enter the ocean and tend to migrate. More important than arbitrarily characterizing coastwide trends in salmon abundance as either density-dependent or density-independent is understanding how physical and biological processes interact to influence the relative performance of geographically discrete stocks over a shifting background of oceanic states.

Finally, variability in the ocean underscores the importance of life history diversity to productivity of salmon. Diverse life histories minimize the risk of brood failure in an uncertain ocean environment because not all individuals behave uniformly. Slightly different migration times, for example, may be advantageous in different years depending upon the exact timing of the shift in along-shore surface currents (e.g., the spring transition), the specific location of the Columbia River plume, the location and timing of upwelling events, or the distribution of predators along the coast. These and other conditions in the ocean can vary markedly between

years. The diversity of life history characteristics within and among populations, thus may determine the number of individuals that successfully make the transition from riverine to oceanic life. Moreover, this diversity is directly tied to the conditions that regulate salmon survival in the river and estuary. Habitat quality, flow conditions, or other factors that affect mortality during early life history may subsequently limit the range of sizes or times of emigration among surviving juveniles. Loss of life history diversity in the river may thus limit the capacity of salmon to survive variable conditions at sea.

In summary, the fact that salmon production may be regulated by conditions in the ocean argues for a broader management perspective incorporating the entire riverine-estuarine-marine habitat continuum of salmon life cycles. This perspective requires (1) an understanding of the relevant scales of variability influencing the physical and biological conditions of this extended salmon "ecosystem," and (2) an understanding of the relevant geographic discontinuities of the north Pacific Ocean that could affect the structure of salmon populations and regulate their relative production in a shifting ocean environment. This section reviews current understanding of oceanic and atmospheric processes relevant to salmon, their influence on large-scale patterns of salmon abundance, and the implications of these variations for conservation in the Columbia River Basin.

Scales of Ocean Processes

The harvest statistics routinely collected to manage salmon fisheries in the ocean generally provide indices of abundance over large management areas. Consequently, understanding of salmon variability is frequently based on indirect statistical correlations between coastwide trends in survival or production and selected indices of environmental conditions (Nickelson 1986). Fewer data are available regarding the effects of smaller or larger scale processes on salmon production. For example, other than the general surveys conducted in the early 1980s (Pearcy and Fisher 1990), relatively little is known about the stock-specific migrations of juvenile salmon from Washington and Oregon, conditions that might alter these movements, or the mechanisms that cause the loss of individuals from a population. Reported estimates of survival for freshwater and marine life-history stages of salmon species were reviewed by Bradford (1995). However, difficulties in accounting for smolt abundance, fishing mortality, and total escapement generally limit understanding of ocean survival of wild populations, and, therefore the specific mechanisms that might account for any local differences. At the other end of the spectrum, processes at scales much larger than the size of individual management jurisdictions have only recently been considered with regard to salmon production, and much of this research emphasizes stocks in the Gulf of Alaska (Beamish and Bouillon 1993; Francis et al. 1996).

This section of the science review focuses on three scales of processes that play an important role in regulating ocean survival of salmon: local upwelling events, which bring nutrient-rich water to the surface during the spring and summer months and involve periods of 1-10 days and distances of 5-200 kilometers (Barber and Smith 1981); currents that transport water seasonally along the entire Washington, Oregon, and California coast and determine the character of the water mass affecting salmon along a north-south gradient; and global oceanic and atmospheric changes that regulate both local and regional processes on interannual to interdecadal scales. By influencing survival and selecting migratory or other behaviors among local populations, geographic variations in the ocean environment may be important factors in the development of diverse salmon life histories.

Local Upwelling

When coho salmon production collapsed off Oregon in the late 1970s, biologists first considered whether upwelling conditions in nearshore coastal waters might explain variations in marine survival. The successful prediction of adult returns from the previous year's run of jacks implied that conditions during the first few months in the ocean were most critical. Researchers initially focused attention on the upwelling process along the Oregon coast; (Gunsolus 1978; Scarnecchia 1981), which was known to increase nutrient levels and biological productivity at about the time that salmon smolts entered the ocean. Nickelson (1986) found a positive correlation between the percent survival of hatchery coho salmon released in the Oregon Production Area and average upwelling conditions in the spring and summer. These results further suggested a threshold response to upwelling levels: In years of "strong" upwelling (greater than 625 units) survival of hatchery coho averaged 8 percent compared with only 3.4 percent during "weak" upwelling years. Nickelson (1986) also noted a possible negative correlation between surface temperature and survival independent of upwelling. The specific mechanisms of these correlations are uncertain. Furthermore, in the years following the 1976 collapse, the correlation between survival and upwelling changed and, for the last ten years has been negative, suggesting that upwelling alone is not sufficient to explain variation in coho salmon production (Jamir et al. 1994).

The upwelling system of the California Current, which extends along the West Coast of the United States, has been the subject of extensive physical and biological research. Since 1949, large-scale systematic surveys have been conducted off California, primarily south of San Francisco, as part of the California Cooperative Fisheries Investigations (CALCOFI) (Huyer 1983). Detailed small-scale studies of the coastal upwelling system were completed off central Oregon in the 1960s and early 1970s (Peterson et al. 1979; Small and Menzies 1981; Smith 1983). The shorter time frames and local scales of most research off Washington and Oregon are

not directly comparable to the larger interannual scales of information collected off California. Several reviewers (Huyer 1983; Strub et al. 1987a; Landry et al. 1989) have synthesized a variety of data sets to better understand the broader-scale features of the Washington and Oregon coastal ocean. The results indicate considerable variability that may be important in the life history and production of salmon stocks. For example, depending on the specific time and location of their emigration, local populations may enter very different ocean environments. Selection of migratory patterns among stocks and species may have evolved in ways that optimize survival in relation to oceanographic as well as estuarine and riverine environments (Nicholas and Hankin 1988).

Four major characteristics of the local upwelling system appear to play an important role in the ocean survival of salmon.

1. Variations in the intensity, frequency, and relaxation of upwelling events influence biological production and the recruitment of pelagic marine fishes. Survival strategies associated with these patterns may vary by species.

Small and Menzies (1981) reported differences in the distribution of chlorophyll biomass and its productivity under different upwelling conditions off Oregon. During weak or intermittent periods of upwelling, the band of maximum chlorophyll was located against the coast and had very high concentrations. Productivity of chlorophyll bands during periods of relaxation between upwelling events could be twice that of the strong upwelling state and often 20 times that in the surrounding water. Peterson et al. (1979) found that very high concentrations of zooplankton off Oregon occurred shoreward of the upwelling front (the sharp interface between upwelled water and the warmer ocean water displaced offshore) and were carried below the pycnocline (density gradient) when upwelling relaxed. However, patterns of abundance of zooplankton populations varied by species.

The most favorable upwelling conditions for fish production also likely vary by species. Lasker (1978) found that physical factors associated with upwelling affected the survival of anchovy (*Engraulis mordax*) larvae and explained variations in year-class strength. Successful year classes were associated with calm periods between upwelling events that supported the production of favored prey species. Cury and Roy (1989) found evidence that successful recruitment of pelagic fishes depended on winds that were strong enough to promote upwelling but sufficiently calm to prevent turbulent mixing that disperses concentrations of food required for larval survival. They proposed upwelling speeds of 5-6 m/s as an optimal level. Cushing (1995) further notes that northern anchovy and sardine *Sardinops sagax* may have developed different survival strategies for upwelling systems: anchovy grow more slowly and can tolerate periods of low food availability and intermittent periods of stronger upwelling; sardine seem to

grow more rapidly and favor a weaker but more persistent upwelling state. But both species appear to avoid spawning locations of the strongest upwelling. Such nonlinear relationships raise questions about the apparent threshold level of upwelling associated with juvenile coho salmon survival in the 1960s and 1970s, (e.g., Nickelson, 1986) or the shift to a negative relationship over the last decade (Jamir et al., 1994).

2. Geographic variations in coastal currents and upwelling affect patterns of biological production off Washington and Oregon. Such variations may be important to the survival and adaptations of salmon populations originating from different river systems and following different migratory paths.

The gradient in atmospheric pressure that produces southward winds along the coast varies with location and with seasonal and daily changes, creating geographic and temporal variation in winds, currents, and the strength of coastal upwelling. South of about 40 degrees north latitude (approximately Cape Mendocino, California), winds are southward throughout the year, while north of this location, winds are northward, and therefore, unfavorable for upwelling during the winter months. Upwelling occurs year-round from San Francisco south (Figure 10.2). Yet upwelling in this region has little influence on temperature distributions much of the year and, therefore, may be ineffective in overcoming the strong California Undercurrent and the downward sloping density gradient associated with it (Huyer, 1983). The average intensity of upwelling is relatively weak northward from the central Oregon coast. Upwelling off the narrow Oregon continental shelf is generally stronger than off Washington and more evenly distributed throughout the summer (Landry et al., 1989). Maximum upwelling off Washington occurs in June, one or two months earlier than along the Oregon coast. South of Coos Bay, coastal currents show considerable short-term variability, while a smoother seasonal cycle is apparent in currents from the central Oregon coast northward (Strub et al. 1987b). Complex bathymetry and the orientation of the shoreline also result in considerable local variation in the intensity of upwelling (Huyer, 1983) with uncertain but potentially significant effects on local salmon stocks.
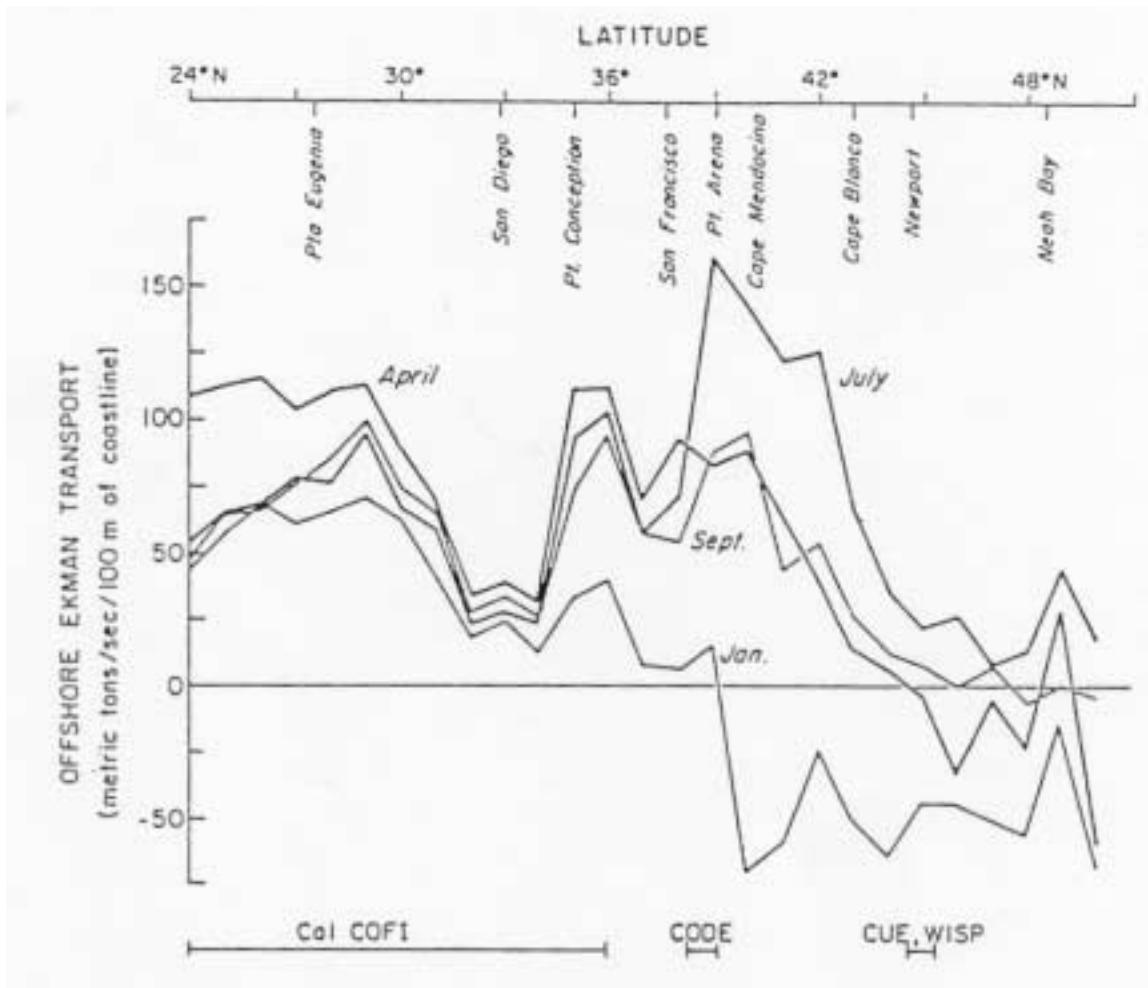
Figure 10.2. Geographic pattern in upwelling on the Pacific coast of North America from latitudes 24°N to 51°N including Neah Bay, Washington, United State to Pointa Eugenia, Mexico.
Upwelling is measured by offshore Ekman transport in metric tons/sec100m coastline.

From geographic differences in winds, currents, bathymetry, and upwelling, Bottom et al. (1989) classified three major physical regions of the continental margin north of Cape Mendocino, California: (1) A Washington coastal region south to the mouth of the Columbia River; (2) a northern Oregon coastal region (south of the Columbia River to Cape Blanco); and (3) a southern Oregon and Northern California region south to Cape Mendocino. The discontinuity in winds and currents at Cape Blanco is particularly noteworthy. The zone of upwelling and increased nutrients is wider south of Cape Blanco than along the central and northern Oregon

coast, and influence of the Columbia River plume is reduced. Summer winds and upwelling are stronger and more variable than in regions to the north. Furthermore, strong offshore flow much greater than is explained by typical upwelling processes may have an important influence on the transport of phytoplankton biomass and could explain large-scale patterns of zooplankton in areas of the California Current (Abbott and Zion 1987). It is interesting that the ocean migration patterns of coastal chinook *O. tshawytscha* stocks also show a discontinuity at Cape Blanco: Stocks from Elk River (located on the south side of Cape Blanco) and northward appear to rear in waters from Oregon to Alaska; stocks south of Elk River generally rear off southern Oregon and northern California (Nicholas and Hankin 1988).

3. The coastal ocean off Washington and Oregon exhibits distinct winter and summer regimes. The shift to the summer upwelling regime occurs suddenly and the specific timing varies between years. While areas of coastal upwelling involve local scale events, the transition to a coastal upwelling regime is regulated by large-scale atmospheric conditions.

The annual northward migration and strengthening of the North Pacific High pressure system causes a shift in wind direction that produces the transition from a winter to a spring/summer regime in the coastal ocean off Washington and Oregon (Huyer 1983). In the winter, coastal currents over the shelf are northward, sea levels are high, and downwelling occurs. Summer conditions are characterized by reduced sea levels, southward mean surface currents over a northward undercurrent, and a strong density gradient across the continental shelf (Strub et al. 1987b). Southward winds and the resulting offshore flow raises cold, nutrient-rich water at the surface along the West Coast of the United States. The zone of active upwelling is generally restricted to a narrow coastal band (about 10-25 km) but the affected region can be much broader. The response of the coastal system to southward winds is very rapid. A single upwelling event of a few days' duration, typically in March or April, may be sufficient to cause the shift to the spring/summer regime (Huyer, 1983). Thus, timing of the onset of the transition relative to the period of smolt migration may be important to the survival of juvenile coho salmon (Pearcy 1992).

Strub et al. (1987b) report that the spring transition in sea level, currents, and temperatures is driven by the large-scale wind system at scales of 500 to 2,000 km at latitudes north of approximately 37° N. Changes in wind patterns causing the transition are associated with the weakening and northward movement of the Aleutian Low Pressure system in March or April and the accompanying strengthening and movement of the North Pacific High. The progression of sea level, wind stress, and temperature from north to south suggests remote factors may be responsible for the large-scale spring transition.

4. The Columbia River plume influences the distribution of nutrients, salinity, and the upwelling front off Washington and Oregon. Changes in the river hydrograph associated with flow regulation may significantly impact coastal ecosystems.

Discharge from the Columbia River is the dominant source of freshwater runoff to the Washington and Oregon coast, particularly during the late spring and early summer. Both the Columbia and Fraser rivers are point sources of high nitrate, phosphate, and silicate near shore in winter and summer (Landry et al., 1989). The low salinity surface water of the plume represents an offshore extension of the estuary that varies seasonally in its location along the coast. During winter when surface currents are predominantly northward, the Columbia River plume forms a low-salinity tongue of cold water near the Washington coastline to the north (Landry et al. 1989). During the spring/summer regime, low salinity water from the Columbia River is located offshore and to the south off Oregon (Figure 10.3).
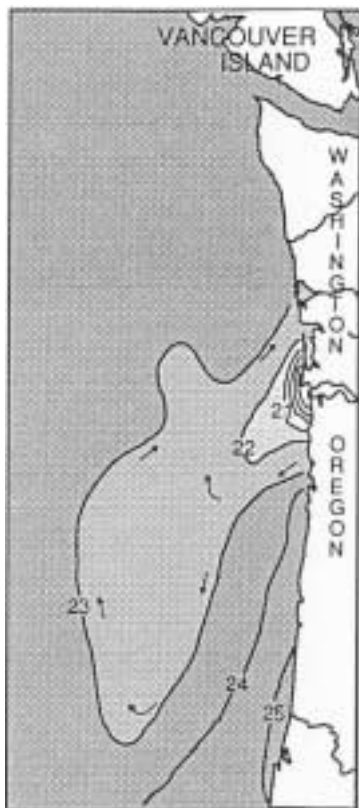

Figure 10.3. Isoclines in salinity as ppt during the spring/summer regime in the Pacific Ocean off the coast of Oregon. Figure shows the low salinity water from the Columbia River located offshore and to the south of Oregon.

The plume can extend beyond Cape Mendocino, California and its effects are even visible past San Francisco. Measurements in July 1961 reported the maximum depth of the plume as 2 meters off the Columbia River mouth and 0.5 meters off of Cape Blanco (Huyer, 1983). As a result of the influence of the Columbia River plume, variability in surface salinity is much greater in the Pacific Northwest than off California or in the subarctic region (Landry et al., 1989).

The Columbia River plume influences surface density gradients and the cross-shelf properties of coastal waters, which may affect patterns of biological production and biomass. Specifically, the plume can retard offshore transport during upwelling, particularly when river flow is maximum (e.g., June). The zone of upwelling influence can be most narrow off northern Oregon where the Columbia River plume forms a partial barrier to the offshore movement of surface water (Huyer, 1983). Interaction between upwelling intensity and the volume of flow from the Columbia River affect the location of the upwelling front and, therefore, the distribution of chlorophyll and zooplankton biomass (see #1 above). During strong upwelling the Columbia River plume is advected far offshore. Changes in the distribution of the upwelling front may not only influence environmental conditions for emigrating juveniles but may be important to the movements of adult salmon. Coho salmon, for example, prefer temperatures between 11 and 14 degrees C, which are intermediate between the offshore ocean water (15 degrees to 17 degrees C) and upwelled water at the coast (8 degrees to 10 degrees C) (Smith, 1983). Short-term changes in temperature and feeding conditions that concentrate or disperse fish, in turn, create significant variations in salmon catch rates and landings (Nickelson et al. 1992).

The region of the Columbia River plume is a summertime spawning area for an endemic subpopulation of northern anchovy (Bakun 1993). Local stability of the water column and circulation characteristics associated with the plume during the summer may provide the conditions needed to support larval production. A local minimum in wind velocity and upwelling intensity ($< 500 \text{ m}^3/\text{s}^3$) minimize offshore transport while the low salinity lens of the plume maintains vertical stability and reduces turbulence. Furthermore, the density gradient at the interface of the plume and higher salinity surface waters may provide a counterclockwise circulation (Figure 10.3) that would benefit retention of larvae and other organisms (Bakun, 1993). Because such convergence zones tend to concentrate larvae and food particles, they are often important areas of secondary production.

Ebbesmeyer and Tangborn (1993) conclude that impoundment of summer flows and releases during the winter by Columbia River dams have altered sea surface salinities from California to Alaska. In terms of the seasonal transition in coastal currents, this shift in the hydrograph results in a decrease in the volume of Columbia River water transported off the

Oregon coast during the summer and an increase off Washington in the winter. In the last 60 years, salinity has decreased approximately 1.0 ppt over a distance of 500 km to the north and increased 0.6 ppt over the same distance to the south (Ebbesmeyer and Tangborn, *review draft*). The influence of the plume on other physical and biological properties—e.g., temperature, nutrients, density gradients, and the upwelling front—suggests that regulation of Columbia River flows may significantly affect coastal ecosystems of the California Current and subarctic region.

Horizontal Advection

The "classical view" of the eastern boundary regions of the world's oceans has generally assumed that local upwelling is the major factor controlling pelagic production (Bernal and McGowan 1981). But over the last two decades, new evidence indicates that the productivity of the California Current is not entirely regulated by internal processes, but may be substantially influenced by input from outside the system. Both zoogeographic patterns and fluctuations of plankton biomass in the California Current point to large-scale processes that are not fully explained by upwelling.

The California Current is a transition zone between subarctic and subtropic water masses and the freshwater systems that enter the ocean along its landward boundary (Figure 10.4). Unlike the large semi-enclosed gyres that circulate in the Central and North Pacific, the California Current is a relatively open system affected by annual fluctuations in currents that contribute water of varying properties from adjacent water masses. After traversing eastward across the North Pacific, the Subarctic Current splits into the northward flowing and counterclockwise Alaskan Gyre and the southward flowing California Current. During the upwelling season, the California Current carries cold nutrient-rich water from the subarctic Pacific along the West Coast. When upwelling subsides in the fall and the downwelling season returns, the northward-flowing California Undercurrent (Davidson Current) appears at the surface and carries warm equatorial water inshore (Favorite et al. 1976).

In the 1960s, biogeographers discovered a close association between the major water masses of the Pacific Ocean as characterized by temperature and salinity profiles (Sverdrup et al. 1942) and the boundaries of large biotic provinces of the pelagic ocean as defined by the distributions of planktonic and nektonic species. North of the equator, Johnson and Brinton (1962) identified 3 major biotic provinces of the Pacific Ocean. A Subarctic assemblage associated with the nutrient-rich waters roughly north of 40 degrees north latitude, a Central Pacific faunal group corresponding to the oligotrophic waters of the central Pacific gyre, and a group of Transition Zone species occupying the boundary between these two groups along the east-west path of the Subarctic Current and West Wind Drift. Because these biological provinces

correspond generally with the boundaries of large semi-enclosed ocean gyres, McGowan (1971; 1974) suggested that they represent discrete, functional ecosystems.
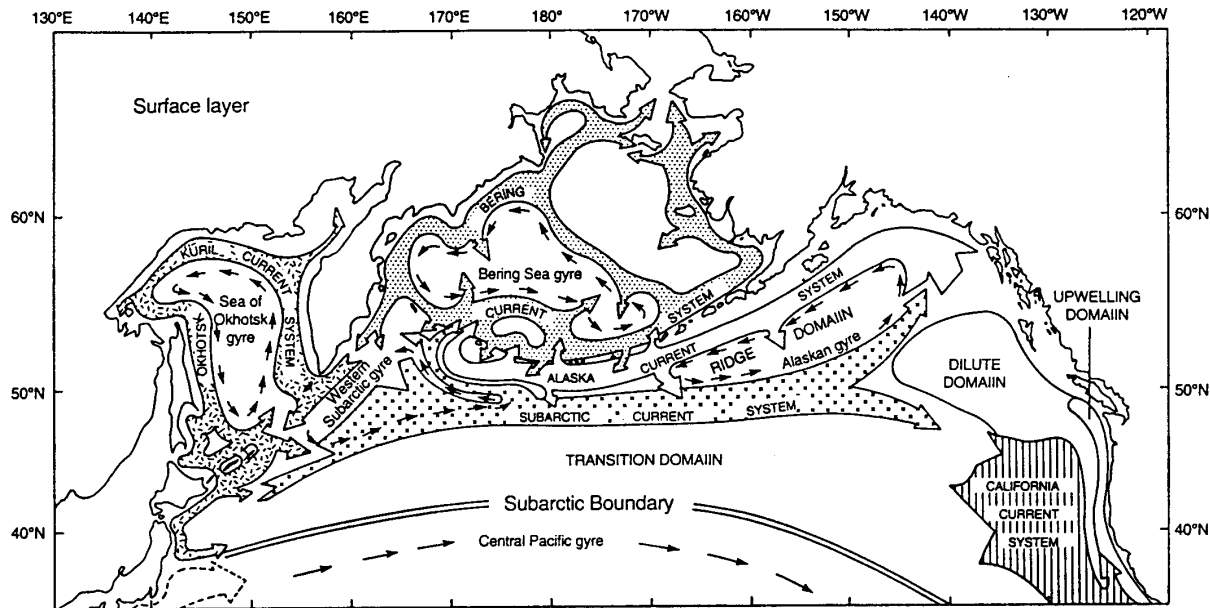

Figure 10.4. Oceanic currents and domains of the North Pacific Ocean north of the subarctic boundary (from Groot and Margolis 1991 as redrawn from Favorite et al. 1976).

A major exception to these patterns is the California Current system, where a small number of coastal species endemic to the region co-occur with a larger mixture of subarctic, subtropic, and equatorial species, many near the peripheries of their distributional range (Johnson and Brinton, 1962; McGowan, 1971; McGowan, 1974). Researchers inferred from these results that remote physical factors controlling the input of water and species from other regions may be more important determinants of species composition and abundance in the California Current than biological interactions such as competition and predation (Bernal 1981; Bernal and McGowan 1981).

Patterns of zooplankton biomass provide evidence that outside forces may regulate biological productivity within the California Current system. Wickett (1967) first reported that annual concentrations of zooplankton off southern California vary directly and concentrations in the western Bering Sea vary inversely with the southward transport of water at the divergence of the California Current and the Alaskan gyre (see Figure 10.4). The influence of advection in the

California Current was further supported by Bernal (1981) and Bernal and McGowan (1981) who correlated zooplankton abundance with the transport of low salinity water from the north. Chelton, et al. (1982) concluded that interannual variations in zooplankton biomass off California are not correlated with wind-induced upwelling but are explained by variations in the flow of the California Current itself. Zooplankton biomass may respond to changes in the amount of nutrients transported southward in the California Current and the depth of the thermocline, which influences the capacity of upwelling to enrich surface waters (Chelton 1981; McClain and Thomas 1983). Furthermore, fluctuations in the current are indicated by changes in coastal sea-level and are often but not always related to El Nino occurrences in the eastern tropical Pacific (Chelton et al., 1982). Thus, physical and biological properties are dominated by a large-scale, interannual signal generated outside the California Current system.

Local upwelling may play a somewhat greater role in interannual variability off the Washington and Oregon Coast than off California. Unlike California (Chelton et al. 1982), monthly anomalies of temperature and salinity off Washington and Oregon in the summer are negatively correlated (Landry et al. 1989), which is an indicator of the upward advection of cold, high-salinity water during upwelling (as opposed to lower salinity water transported from the north). Monthly nutrient (nitrate) anomalies along the midshelf of Washington are also positively correlated with temperature and with upwelling. Landry et al. (1989) conclude that interannual scales of variability off Washington and Oregon are probably influenced by both regional and global scale processes. A global influence is suggested by a consistent pattern of temperature anomalies throughout the California Current and subarctic regions and by the influence of El Nino events in the eastern tropical Pacific. It is likely that a gradient of factors affect biological production along the California Current as evidenced by the north-south pattern in the variability of winds, currents, and upwelling (Figure 10.2); the latitudinal cline in the relative proportions of subarctic, transitional, and equatorial species (Chelton et al. 1982); the north-south gradient in the amount of Columbia River water found along the Oregon coast during the summer (Figure 10.3); and the southward decline in the relative proportion of protected inland bay and estuarine habitat from British Columbia to California (Nickelson 1984; Bottom et al. 1986).

Interannual variations along this California Current ecotone create special challenges for southern salmonid stocks, which are generally less productive in Washington and Oregon compared with areas located nearer the center of their range (Fredin 1980). Fulton and LeBrasseur (1985) defined a subarctic boundary based on interannual variations in the distribution of mean zooplankton biomass (Figure 10.5).
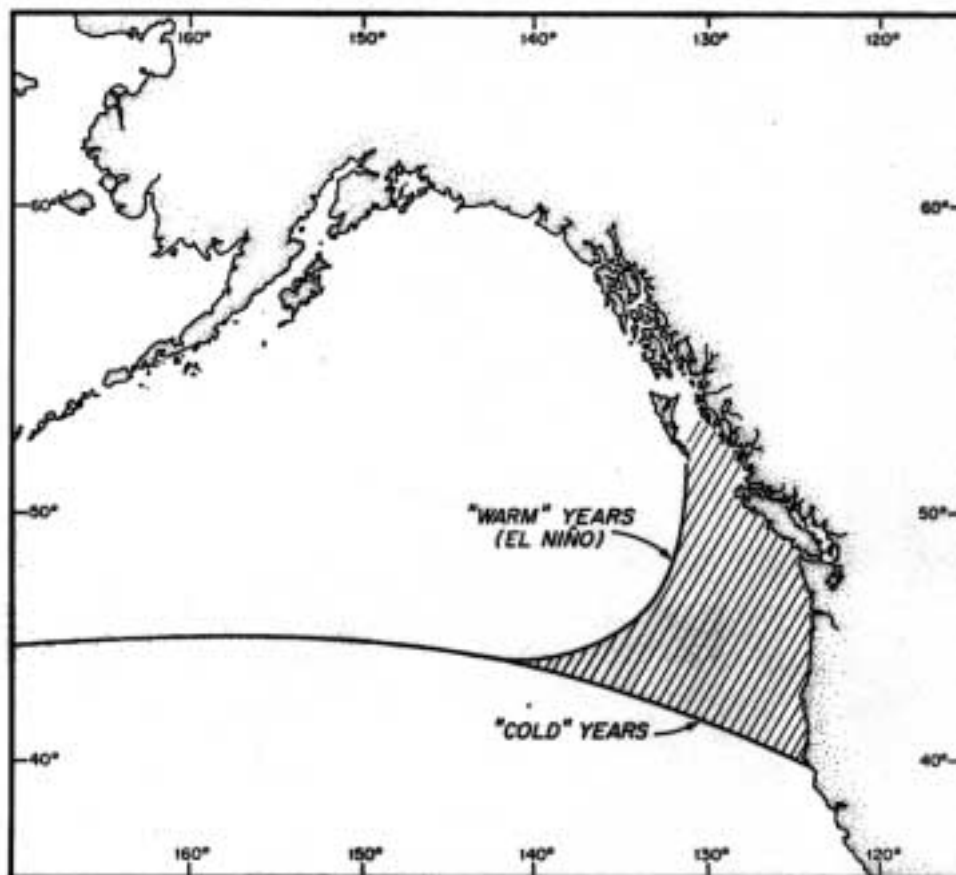
Figure 10.5. Changes in the subarctic boundary based on interannual variations in the distribution of mean zooplankton biomass.
The shaded area is between Cape Mendocino, California, and the Queen Charlotte Island, British Columbia, where the transition between high and low biomasses varies widely between extreme "cold" and "warm" years (from Fulton and LeBrasseur 1985).

They reported a large area between Cape Mendocino and the Queen Charlotte Islands where the transition between high and low biomass varied widely between extreme "cold" and "warm" years (e.g., during strong El Nino events). They hypothesized that in years of strong southward advection of cold water, the larger zooplankton characteristic of the subarctic water mass may provide a better source of food for juvenile pink salmon *O. gorbuscha* than the smaller species otherwise typical of the California Current. As noted above, the strength of southward advection changes not only during El Nino events. Interannual variations in the subarctic boundary; the location of the divergence of the California Current; and associated changes in temperature,

zooplankton, or other conditions may be particularly important to the survival of the southernmost stocks of subarctic salmon.

Attempts to explain variations in the year-class strength of marine fishes have often emphasized effects of food availability on larval survival (Lasker 1978; Cushing 1995). However, advective processes may also exert a direct physical influence on survival and interannual variability of some pelagic fishes. For example, survival rates to age 1 of Pacific mackerel *Scomber japonicus* increase during years of low southward transport (as indicated by high coastal sea level) and relatively low zooplankton biomass, which, in turn, are related to El Nino events in the eastern tropical Pacific (Sinclair et al. 1985). Conversely, poor survival is associated with strong southward flow of the California Current when zooplankton biomasses are generally higher. In this case, Sinclair et al. (1985) proposed that survival rates of Pacific mackerel during early life history may be influenced directly by interannual changes in hydrographic processes rather than by biological interactions. This hypothesis emphasizes that loss of larvae from the appropriate geographic location may be as critical to survival as the condition of the feeding environment.

The influence of advective processes on year-to-year salmon survival is unclear. Unlike larval fishes, salmon are free swimming when they enter the ocean, but at small sizes their distribution may be affected by the strength of surface currents. Pearcy (1992) found that juvenile salmon from Oregon and Washington generally swim northward against the current. However, during May and June soon after they entered the ocean, juvenile coho off Oregon were captured south of the area of ocean entrance, suggesting a southward advection of the smallest fish during their first few weeks in the ocean. Later in the summer, when currents were weaker and fish were larger, most young salmon were caught north of their point of ocean entry. The fact that year-class strength of coho salmon may be decided sometime within the first few weeks in the ocean (Fisher and Pearcy, 1988) suggests that early survival conditions perhaps not far from the point of ocean entry may be critical. Many of the juvenile coho salmon sampled by Pearcy and Fisher (1988) did not migrate long distances northward, although earlier tagging studies (1956-1970) of maturing salmon demonstrated that coho and chinook juveniles from California, Oregon, and Washington migrate into the Gulf of Alaska. In September, during the strong El Nino event of 1983, most juvenile salmon were distributed further north off Washington than in other years surveyed, suggesting either an increased northward migration of fish, or a proportionally greater mortality of those fish remaining in the southern portions of the study area (Pearcy and Fisher, 1988).

The surveys of salmon distribution off Washington and Oregon in the early 1980s (Pearcy and Fisher 1988; Pearcy and Fisher 1990) may or may not be representative of the movements of local salmon stocks under variable current conditions. These surveys were

completed after wild populations of salmon had been reduced to a small proportion of the total quantity in the region and during a period of relatively warm ocean conditions, poor upwelling, and reduced flow of the California Current. Wild stocks may or may not exhibit these same patterns, and movements could change under conditions of strong upwelling and increased southward transport. However, as proposed for larvae and fry of marine species (Sinclair, 1988), advective processes could have a direct physical influence on early migrant salmon by determining whether the geographic distributions of local stocks are appropriate to prevent losses from populations.

The El Nino-Southern Oscillation Cycle and Influences on Salmon Production

Until 30 years ago, El Nino was believed to be the result of local changes in the winds that produced upwelling along the coasts of Peru and Ecuador (Mann and Lazier 1991). Oceanographers later discovered that this upwelling system was part of a higher level of organization involving global winds and ocean dynamics across the entire Pacific Ocean basin. They concluded that the upwelling system is a component of the global heat budget such that the physical and biological characteristics of coastal systems change as the thermal budget of the ocean and atmosphere is disturbed (Barber 1988). While local upwelling may operate somewhat independently, it is also an integral part of the larger thermal structure of the ocean, which determines whether or not upwelling is able to enrich surface waters with nutrients (Barber and Chavez 1983). Barber (1988) describes this single interconnected system, which is structured by the El Nino/Southern Oscillation (ENSO) cycle in the tropical Pacific, as the "basinwide ocean ecosystem." Within this large ecosystem, habitats continually shift, producing opposing regions of abundance and scarcity with the displacement of entire water masses and changes in the thermal structure of particular locales (Sharp 1991). Although not all changes in the North Pacific can be traced to El Nino, the oscillations in the equatorial Pacific nonetheless provide important clues about the basinwide processes that shape the biotic structure and productivity of salmon ecosystems.

The ENSO cycle is reviewed by Mysak (1986), Barber (1988), and Enfield (1989) and is only briefly summarized here. El Nino originally referred to a warm southward current off the coast of Ecuador and Peru that generally begins around Christmas and persists for about three months. In more recent years, the term has been applied to periods of exceptionally strong warming that usually begin around January, last more than one season, and cause economic crisis associated with mortality of pelagic fish and guano birds (Mysak, 1986). El Nino is one part of a basinwide oscillation in the atmospheric pressure gradient of the equatorial Pacific known as the southern oscillation. The oscillation refers to shifts between the South Pacific high pressure system and the Indonesian low pressure system that cause changes in the westward trade winds

along the equator. The interaction of the trade winds and mid-latitude westerlies with the ocean creates a slope in the sea level and in temperature, density, and nutrient gradients across the ocean basin (Figure 10.6) (Barber, 1988).
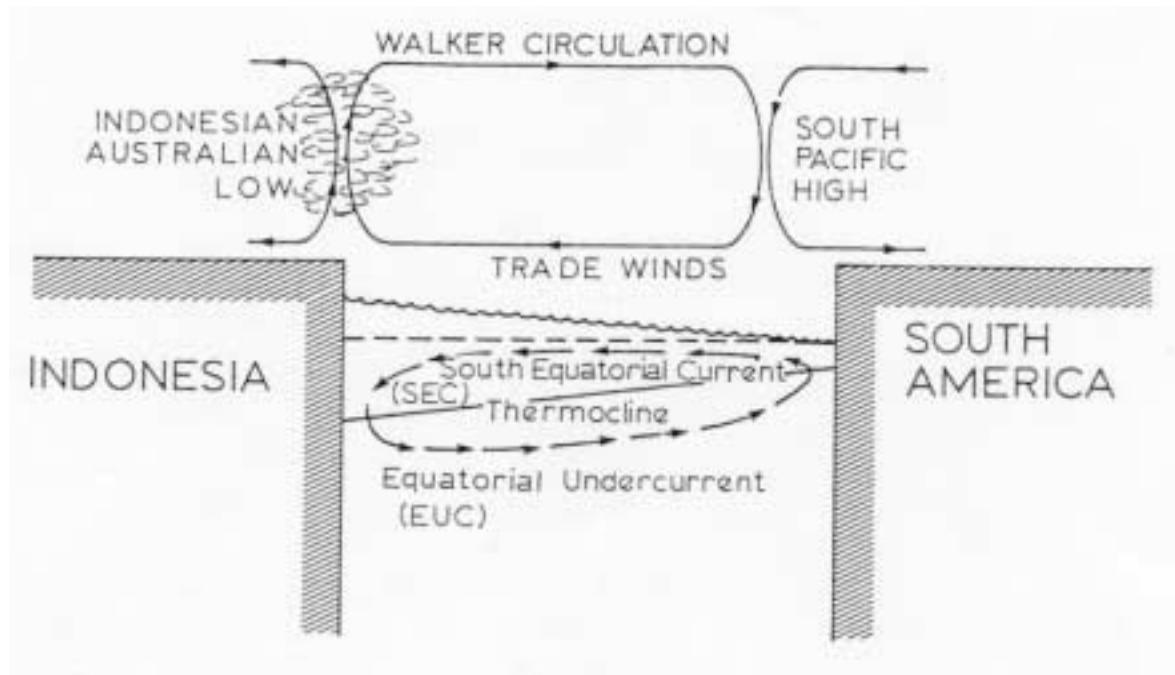

Figure 10.6. Patterns of oceanic and atmospheric circulation important to salmon production. Because the Pacific Ocean is warmest in the west, strong convection and evaporation cause air to rise, creating a low pressure system in the western basin, contributing to the upward portion of the east-west atmospheric circulation (from Mysak 1986).

Because the Pacific Ocean is warmest in the west, strong convection and evaporation cause air to rise, creating a low pressure system in the western basin, and contributing to the upward portion of the east-west atmospheric circulation shown in Figure 10.6. Equatorward trade winds in the eastern boundary of the basin cause upwelling of cool subsurface water, which extracts heat from the atmosphere and forms the South Pacific high pressure system. The trade winds associated with this high pressure transport water westward across the basin, where it is warmed by the sun, and maintain the westward tilt in the thermocline. This ocean-air interaction involves a positive feedback system that amplifies initial conditions: the basinwide temperature gradient produces the pressure gradient that forces the trade winds, while the trade winds cause

the ocean circulation that sustains the temperature differential between east and west (Barber 1988).

El Nino occurs when a critical break-point is reached in this feedback process causing a sudden "flip" in the system, which otherwise maintains higher productivity in the eastern portion of the tropical Pacific due to the shallow thermal structure and upwelling of nutrients. Increasing instability in the east-west thermal gradient results as the trade winds continue to increase the volume of warm surface water in the west, causing the warm pool to expand eastward together with the region of atmospheric heating. As the associated low pressure system also migrates eastward, weakening and reversals in the trade winds produce internal waves that cause warm surface water to rush into the eastern basin. These waves and the migration of warm water deepen the thermocline, so that upwelling is less effective in raising cool water to the surface. Further warming and migration of the zone of atmospheric heating eastward finally produces the sustained low productivity state of El Nino (Barber 1988). Thus the eastern upwelling region takes on the physical and biological characteristics of the less productive western basin.

Through its connections to the equatorial Pacific, the upwelling system, thermal structure, and biotic assemblage of the California Current may be directly affected by El Nino. At the height of El Nino, warm water drains toward both poles, reducing the warm pool in the eastern basin and influencing conditions in the northeast Pacific and the Southern Ocean. The California Undercurrent, which carries warm water northward along the West Coast of the United States, thus may serve as a "release valve" for the build-up of heat in the tropical Pacific, and may be involved in the resetting of the ENSO cycle to the cold (La Nina) phase (Barber 1988). Following the mature phase of El Nino in the winter and spring, southward flow of the California Current is reduced (Chelton et al. 1982) and the strength of northward flow in the California Undercurrent is increased (McClain and Thomas 1983; Mysak 1986). Responses to El Nino along the West Coast of the United States may include elevated sea levels and sea surface temperatures, increased thermocline depths, and the northward expansion of the ranges of southern species (McClain and Thomas 1983).

Two mechanisms have been suggested to explain El Nino responses along the North American coast (Mysak 1986). The first involves the northward propagation of coastal Kelvin waves, a class of shallow-water waves, which are generated along the coast by changes in the tilt of the thermocline toward the western Pacific. Evidence of this connection is shown by interannual variations in sea level in the Gulf of California that are correlated with El Nino occurrences and the slowing or reversal of the California Current during strong El Nino events (Mysak 1986; Mann and Lazier 1991). Mysak (1986) argues, however, that the strong influence of the 1982-83 El Nino as far north as Alaska may be more indicative of an atmospheric link (teleconnection) with the tropics rather than a direct oceanic influence. The waves generated at

the equator may not propagate to the far north because their movement will halt at a point where the thermocline rises to the surface. However, anomalously high temperatures in the eastern tropical Pacific transfers energy to the atmosphere that can influence winds and weather patterns thousands of miles to the north (Norton et al. 1985). Mysak (1986) proposes that atmospheric changes associated with the strengthening of the Aleutian Low Pressure system during the winter may explain warm conditions in the Northeast Pacific. The pattern of anomalous pressure that often forms during the warm phase of El Nino involves an atmospheric chain of low and high pressure systems (Figure 10.7). This pattern brings westerlies further north than usual and causes a southward shift in the paths of storm tracks along the west coast of the United States. During periods of an intensified Aleutian Low pressure system, surface winds along the west coast are generally strong from the southwest, causing a longer than normal period of downwelling and an anomalous onshore transport of warm water from the south.

Although many researchers now emphasize the role of atmospheric teleconnections as the primary link between El Nino and conditions in the North Pacific region, e.g., (Mysak 1986), recent evidence suggests that direct oceanic linkages might also involve greater distances, higher latitudes, and a longer "memory" of tropical disturbances than previously thought. Jacobs et al. (1994) offer indirect evidence that planetary-scale (Rossby) waves, which are a class of waves that depend on the curvature and rotation of the earth, were reflected westward from the American coasts following the strong 1982-83 El Nino. They hypothesize that these may have crossed the North Pacific and a decade later caused a northward displacement (to approximately 40° N) of the Kuroshio Extension off Japan, a current that advects heat eastward along the path of the Subarctic Current (Figure 10.4). Results of both satellite data and numerical modeling suggest these changes may have caused transport of anomalously warm water into the North Pacific. If these interpretations are correct, then effects of El Nino conditions on North Pacific circulation and weather patterns may persist long after an event has dissipated in the tropics. Chelton and Schlax (1996) note that Rossby waves are important in adjusting ocean circulation to large-scale changes in the atmosphere, but that recent satellite observations suggest a more rapid response than is generally predicted by accepted theory.
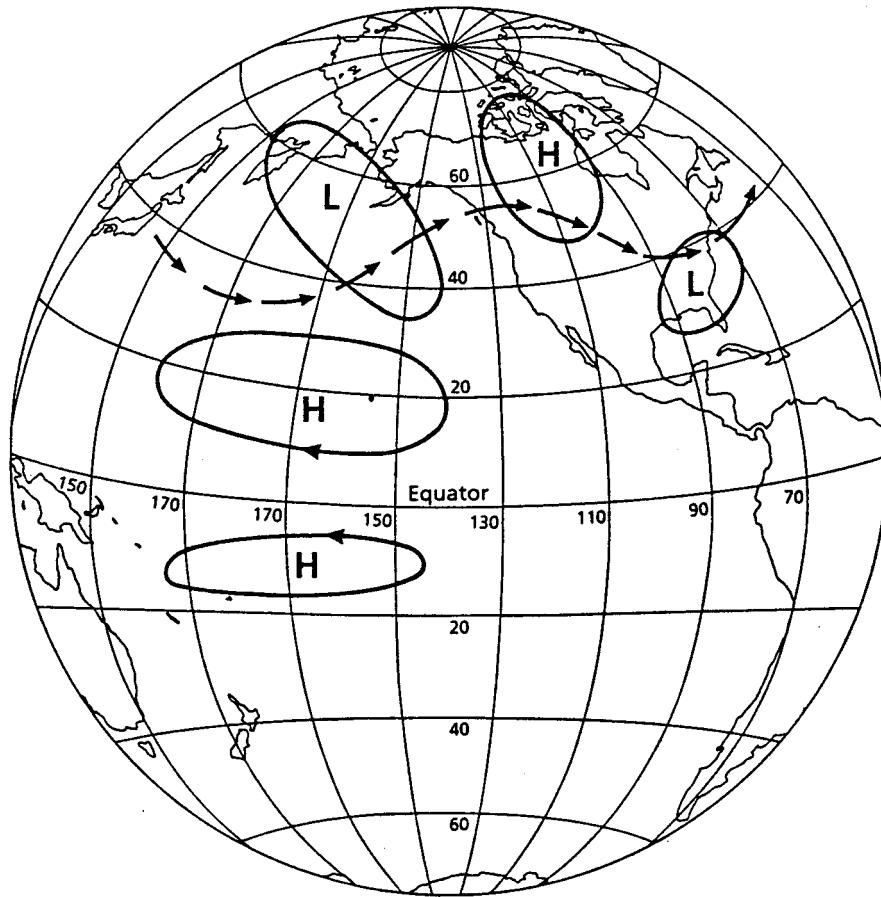
Figure 10.7. Atmospheric changes associated with the strengthening of the Aleutian Low
Pressure system during the winter may explain warm conditions in the Northeast Pacific.
The pattern of anomalous pressure that often forms during the warm phase of El Nino
involves an atmospheric chain of low and high pressure systems.

While El Nino events usually occur with a frequency of 3 to 7 years, climatologists and
oceanographers have also described abrupt shifts in the predominant patterns of atmospheric
circulation, oceanic currents, and thermal regimes that may persist for several decades. These
interdecadal shifts, which may be linked by teleconnections to conditions in the tropical Pacific
and often follow strong El Nino events, involve extended periods of eastward migration and
intensification of the Aleutian Low pressure system during the winter half of the year (Trenberth
1990). The most recent shift occurred in 1976-77, when a strengthened Aleutian Low caused a
southward migration of storm tracks, anomalous southerly winds and warming along the west

coast of North America and Alaska, and anomalous northerly winds and cold temperatures in the Central North Pacific region (between Japan and 160° N) (Trenberth 1990; Ebbesmeyer et al. 1991). In the Northeast Pacific, the pattern of strong Aleutian Low is associated with a rise in sea level and ocean surface temperature; reduced flow of the California Current (Mann and Lazier, 1991); and reduced precipitation, increased river temperatures, and low stream flow conditions in Oregon (Greenland 1994a).

The relationship between El Nino and atmospheric and oceanic conditions in the North Pacific is not a simple one-to-one correspondence. For example, ENSO events can occur without causing a change in the Aleutian Low pressure system, and warm water conditions in the North Pacific may be present in the absence of El Nino (Mysak 1986). A 1972-73 warming off California occurred without a change in the atmospheric circulation, suggesting a direct oceanic connection to a strong El Nino event (Norton et al. 1985), while the moderate El Nino of 1976 produced the strongest Aleutian Low in a 36-year period of record (Mysak 1986). The climatic effects of large pressure anomalies that often form in response to strong El Ninos also may vary. The degree of warming and the effects on precipitation depend on the particular latitude of storm tracks and the position of the low pressure system relative to the coast (Roden 1989). The climatic response to El Nino in the Pacific Northwest, for example, may vary with the strength of the teleconnections. Thus the Northwest may fall inside or on the southern edge of a region of lower rainfall following a particular ENSO event (Melack et al. *In press*).

The frequency and intensity of El Nino events also exhibit patterns of variation. Through a reconstruction of El Nino occurrences over the last 450 years, Quinn et al. (1987) note that intervals between strong and very strong events have averaged close to 10 years, but may range from 4 or 5-year intervals to as high as 14 to 20 years. El Ninos classified as "very strong" events are relatively rare, and have occurred with a frequency of 14 to 63 years. Thus the 15 years between the most recent very-strong El Niño events (1982 to 1997) is near the high end of the frequency spectrum for the last 450 years.

Decadal or longer climatic changes are indicated by extended periods of unusually strong El Nino activity. Examples include the periods 1701-1728, 1812-1832, 1864-1891, and 1925-1932 (Quinn et al. 1987). Several studies note that El Nino events have become more frequent and intense during the extended period of climatic change that followed the most recent shift in the Aleutian Low pressure system in 1976-77 (Guilderson and Schrag 1998). For example, four major El Ninos have been recorded since 1981 with only two major intervening cold (La Nina) events, including the recent return to cold conditions following the very strong 1997-98 El Nino (Kumar et al. 1994; McPhaden 1999).

Recent changes in the tropical Pacific are raising questions about whether the general warming trend after 1976 might have influenced the frequency of ENSO cycles, and whether the

increased heat itself could be an early sign of global warming from greenhouse gases (Kerr 1994; Kumar et al. 1994). Such concerns are heightened by observations off southern California where, since 1950, the upper 100 meters of the ocean has shown a uniform 0.8° C increase and associated mean sea level has increased by 0.9 mm/year (Roemmich 1992). This warming has occurred despite an apparent increase in the intensity of upwelling favorable winds off southern California over the same period (Bakun 1990). Roemmich and McGowan (1995) speculate that increased stratification from ocean warming has made upwelling less effective in raising nutrients to the surface and may account for an approximately 70 percent decline in zooplankton volume documented since 1951. While the causes of this general warming are not clear, the results illustrate how even moderate increases in temperature and adjustments in the ocean thermal structure might override the benefits of local upwelling to pelagic food chains.

Johnson (1988) summarized the direct effects of the very strong 1982-83 El Nino on Oregon coastal and Columbia River stocks of salmon. Both adult and juvenile salmon experienced increased mortality. Higher mortality was indicated by returns of adult coho salmon to the Oregon Production Area and tule fall chinook to the lower Columbia-Bonneville pool area – that were much lower than the preseason predictions. Mean sizes of chinook and coho salmon that survived El Nino were much smaller than average, and fecundity of female coho salmon also was reduced. Unlike chinook stocks off southern Oregon and locally distributed stocks from the Columbia River, northward migrating populations from the Columbia River showed little or no decline in abundance during the El Nino (Johnson 1988).

Similar effects on coho salmon production may have occurred during a strong 1957-58 El Nino (McGie 1984; Pearcy 1992). The mean weight of returning adults was low in 1959 (Johnson, 1988), and total ocean landings in 1960 from smolts that entered the ocean the previous year declined to its lowest level since 1917. Anomalously high water temperatures from 1957 to 1960 probably indicate that the relatively strong upwelling during this period was not effective in raising cold, nutrient-rich water above a deepened thermocline (Pearcy 1992). Decreases in zooplankton biomass and abundance of larval fish in the California Current coincided with a depressed thermocline during the 1958 to 1960 warming (McGowan et al. 1998).

From scale analyses of survivors returning to Tenmile Lakes, Oregon, Bottom (1985) reported little interannual variability in the relative growth of juvenile coho salmon over a wide range of upwelling conditions and salmon survival rates (among 13 brood years of salmon sampled between 1954 and 1981). A major exception to these results was the larger than average growth rates among those juveniles that entered the ocean during the 1983 El Nino and survived to return as adults in 1984. These results are consistent with the hypothesis of a brood failure during 1983, which might have caused better than average growth rates among the survivors if

ocean habitats were not seeded to their capacity (Isles 1980; Lichatowich 1993). Survival of smolts entering the ocean during El Nino was very poor and stock density was likely quite low as indicated by the return of two-year-old coho jacks in the fall of 1983 (Johnson 1988). The direct mortality of adults during this strong El Nino (Johnson, 1988) suggests a different scale, habitat, and mechanism of population regulation than the control of juvenile survival, which occurs soon after smolts enter the coastal ocean (Nickelson, 1986; Pearcy, 1992).

In summary, local responses to remote atmospheric and oceanic disturbances support the concept of an interconnected basinwide ecosystem in which the background conditions for different regions of the Pacific Ocean continually shift in response to the global heat budget (Barber, 1988). It is within this shifting background of oceanic and atmospheric conditions that local and regional scales of processes are embedded. Basinwide forcing produces different responses among regions based on the distribution of atmospheric pressure gradients and their influence on local winds, currents, upwelling, ocean thermal structure, and precipitation patterns. Thus, for example, an increase in the intensity and extent of the wintertime Aleutian Low tends to cause cooling in the western subarctic Pacific at the same time it is warming the eastern subarctic Pacific.

Within the California Current, remote forces regulate the thermal structure and, through advective processes, determine the along-shore distribution of nutrients and the location of the subarctic boundary (Figure 10.5). Three types of forcing mechanisms may be involved in periods of warming in the California Current: (1) depression of the thermocline, strengthening of the California Undercurrent, and decreased effectiveness of upwelling during El Nino events; (2) decreased southward advection from the subarctic divergence into the California Current and increased northward advection into the Alaskan gyre related to the strengthening of the wintertime Aleutian Low pressure system; and (3) increased periods of downwelling, decreased intensity of upwelling, and changes in the onset of the spring transition caused by shifts in the regional wind field also associated with patterns of the Aleutian Low (Norton et al. 1985). The specific responses along the Washington or Oregon coast involve the interaction of many scales of variability. Different scales of processes may invoke different mechanisms of population regulation as illustrated, for example, by the interannual influence of upwelling on the survival of juvenile coho salmon (Nickelson 1986) and the less frequent effects of strong El Nino conditions on the growth and survival of adults and juveniles (Johnson 1988).

Interdecadal Cycles in Salmon Production

In recent years interdecadal variations in fish populations have been traced to large-scale climatic changes influencing oceanic regimes. Perhaps most dramatic are the analyses indicating synchronous trends in sardine *Sardinops* sp. abundance (as indicated by harvest) from three

widely separated regions of the Pacific Ocean basin: California, Japan, and Chile (Figure 10.8) (Kawasaki 1983).
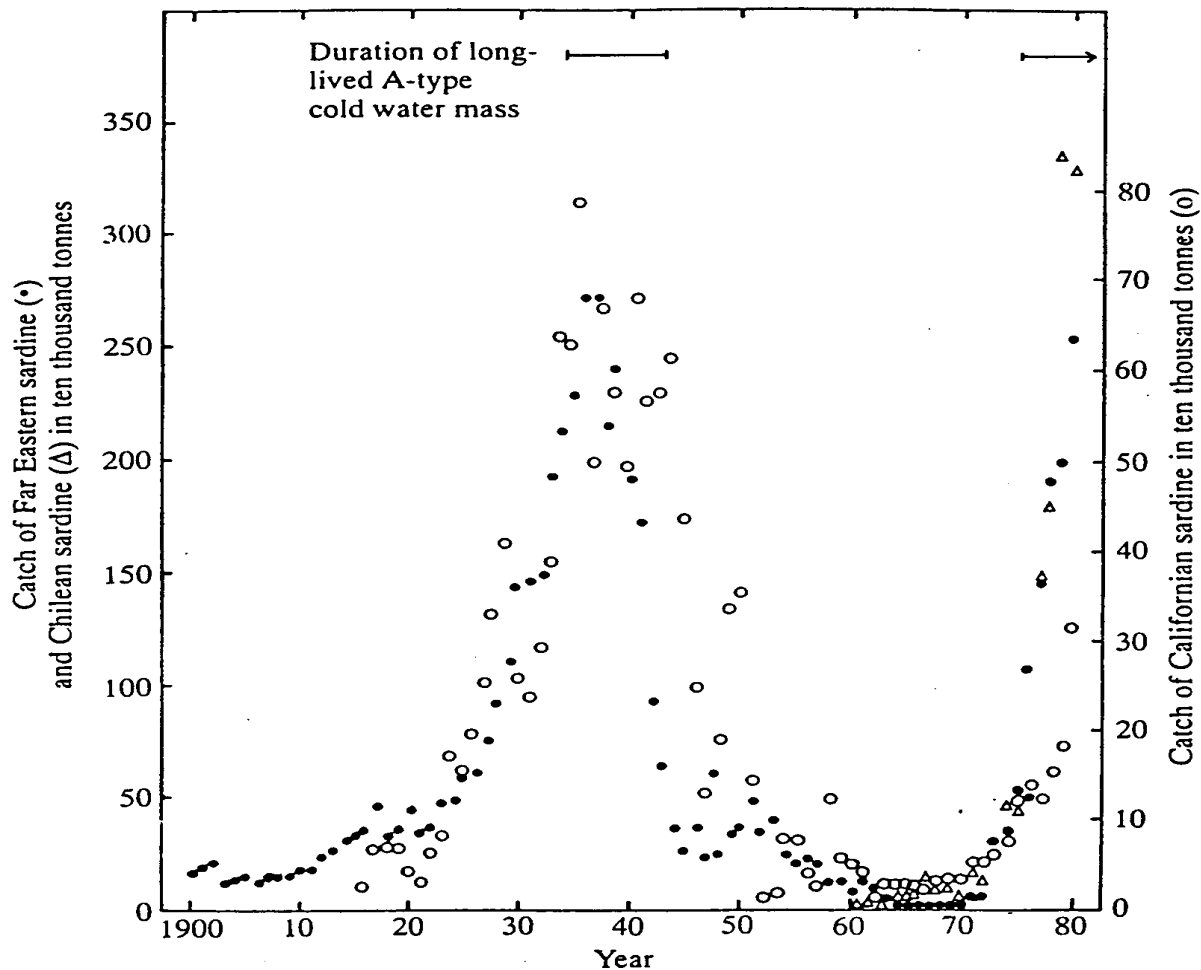

Figure 10.8. Trends in sardine *Sardinops* sp. abundance, as indicated by harvest in ten thousand tonnes, from three widely separated regions of the Pacific Ocean basin: California, Japan, and Chile (from Kawasaki 1983).

The specific relationships explaining the 40-year cycle in abundance is not clear, but all three stocks appear to track variations in mean surface air temperatures in the northern hemisphere. These relationships may be a proxy for changes associated with basinwide winds and conditions in upwelling systems that somehow influence sardine recruitment. In the eastern Pacific, sardine appear to favor shifts from a cool, upwelling-dominated regime to periods of reduced wind strength (Sharp 1992; Cushing 1995). Although the region of sardines off Japan is not generally

considered an upwelling system, the same large-scale changes in wind stress may influence the frontal system shoreward of the Kuroshio Current to the benefit of sardine (Cushing 1995). A rapid increase in Japan sardine from a very strong 1970 year class was related to a shift in the Kuroshio Current, which created an expanded sardine spawning area, increased egg abundance, a broad area favoring copepod production, and increased survival of sardine post-larvae (Lluch-Belda et al. 1992). Basinwide regime shifts are not only reflected in patterns of sardine abundance, but involve coherent changes in the organization of entire pelagic assemblages. Anchovies *Engraulis* spp. and their associated predators—hake (Merlucidae), mackerel *Scomber scomber*, bonito *Sarda* spp*)*, and seabirds—are abundant during the opposing cooler upwelling periods. On the other hand, Jack mackerels *Trachurus* spp., chub mackerels (other *Scomber* spp.), and other Transition Zone predators are associated with the warmer periods favored by sardine (Sharp 1992).

Climate changes across the Pacific Basin also may explain interdecadal cycles in salmon production. Beamish and Bouillon (1993) document synchronous trends in pink, chum, and sockeye salmon abundance estimated from the combined annual harvests in U.S., Canadian, Japanese, and Russian fisheries. These trends as well as abundance of copepods sampled at Ocean Station P (50°N, 145°W) were associated with an Aleutian Low Pressure Index. Combined all-nation harvest for all salmon species averaged 673,100 t from the mid-1920s to the early 1940s and reached a peak of 837,400 t in 1939. After a period of low catch from the mid-1940s to a minimum in 1974, production again climbed to nearly 720,000 t in 1985. These patterns generally follow trends in the Aleutian Low Pressure Index (Figure 10.9). A profound shift in climatic regime of the North Pacific in 1976-77 (Ebbesmeyer et al. 1991) was associated with the strongest Aleutian Low since 1940-41. In addition to corresponding increases in salmon abundance, this shift is implicated in the almost doubling of chlorophyll *a* in the central north Pacific north of Hawaii (Venrick et al. 1987), a doubling of summer zooplankton abundance in the Alaskan gyral between 1956 to 1962 and 1980 to 1989 (Brodeur and Ware 1992), simultaneous increases in the abundance of a variety of nonsalmonid fishes in various regions of the North Pacific (Beamish 1993), and increases in prey availability for marine birds and mammals (Francis et al. 1996).
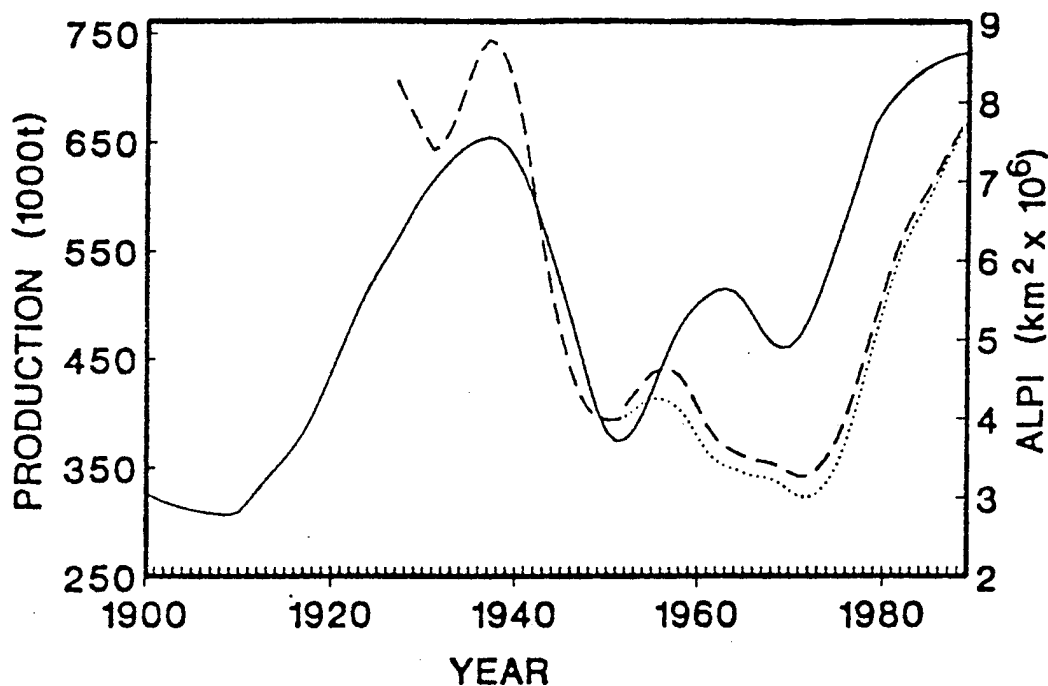
Figure 10.9. Annual changes in the combined annual harvests (landings) of all salmon species in the U.S., Canadian, Japanese, and Russian fisheries, 1900 to 1990 in thousand metric tons (solid line) compared to annual changes in climate using the Aleutian Low Pressure Index (broken line) (from Beamish and Bouillon 1993).

Through time series analysis, Francis and Hare (1994) and Francis et al. (1996) described multidecadal variations in salmon production associated with sudden changes in atmospheric conditions of the North Pacific. These findings were further supported by Mantua et al. (1997) who described a recurrent interdecadal pattern of climate across the Pacific Basin—the Pacific (inter) Decadal Oscillation (PDO)—that shifts between alternative climatic regimes every 20 to 30 years. These results show a close correlation between physical and biological conditions of the North Pacific spanning four major oceanic/atmospheric regimes this century: 1900 to 1924, 1925 to 1946, 1947 to 1976, and 1977 to the present. The regimes beginning in 1925 and in 1977 were associated with periods of high salmon abundance in the Gulf of Alaska. Variations in the harvest of coho and chinook salmon from Washington and Oregon also show interdecadal patterns, but these fluctuate out of phase with the more northerly stocks of pink, chum, and sockeye salmon in the Gulf of Alaska (Figure 10.10) (Francis 1993; Hare et al. 1999).
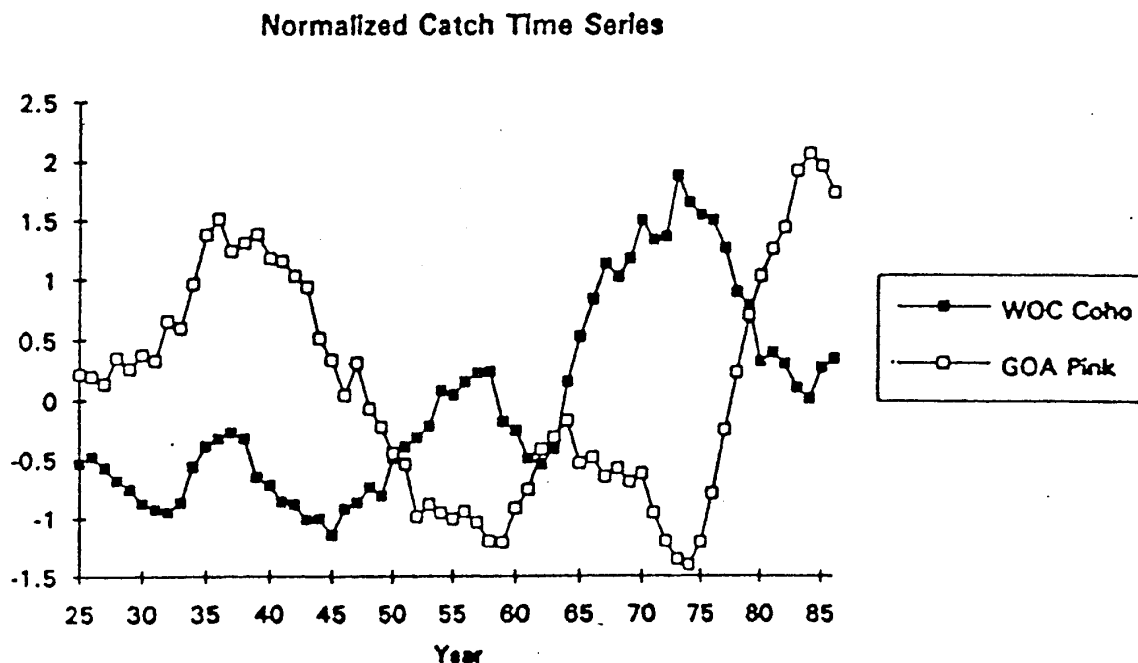
Normalized Catch Time Series

Figure 10.10. Variations in the harvest of coho salmon from Washington and Oregon (solid
squares) also show interdecadal patterns, but these fluctuate out of phase with the more
northerly stocks of pink salmon in the Gulf of Alaska (open squares) (from Francis and Sibley
1991).

The influence of large-scale atmospheric changes on the ocean environment and, in turn,
Oregon salmon, are further indicated by an inverse relationship between salmon harvest and
annual mean temperatures in western Oregon (Figure 10.11) (Greenland 1994b). This contrasts
with a positive relationship between pink salmon harvest, winter air temperatures, and winter sea
surface temperatures in the Gulf of Alaska (Francis and Sibley 1991). These opposing patterns
have been explained by atmospheric forcing that may influence the position of the subarctic
divergence and relative flows into the Alaska and California Currents: periods of a strong
Aleutian Low and increased northward flows into the Alaska Current may reduce southward
flows into the California Current and vice versa with inverse effects on the productivities of each
region (Wickett 1967). To explain these regional differences, Francis and Sibley (1991) and
Francis (1993) use a model by Hollowed and Wooster (1992) which proposes two average
conditions in the North Pacific designated as Type A and Type B. Type B conditions are
represented by a strong Aleutian Low centered in the east, increased southwesterly winds and
increased downwelling, greater northward advection into the Alaska Current, decreased

southward flow of the California Current, and above average temperatures in the northeast Pacific. Type A conditions are characterized by the opposite trends. Francis (1993) proposes that salmon production tracks abrupt shifts in these sets of conditions with periods of high productivity in the Gulf of Alaska generally associated with the type B state. Interestingly, the shift from Type A to Type B conditions over the last 60 years has always coincided with significant El Nino events in the tropical Pacific (Francis 1993).
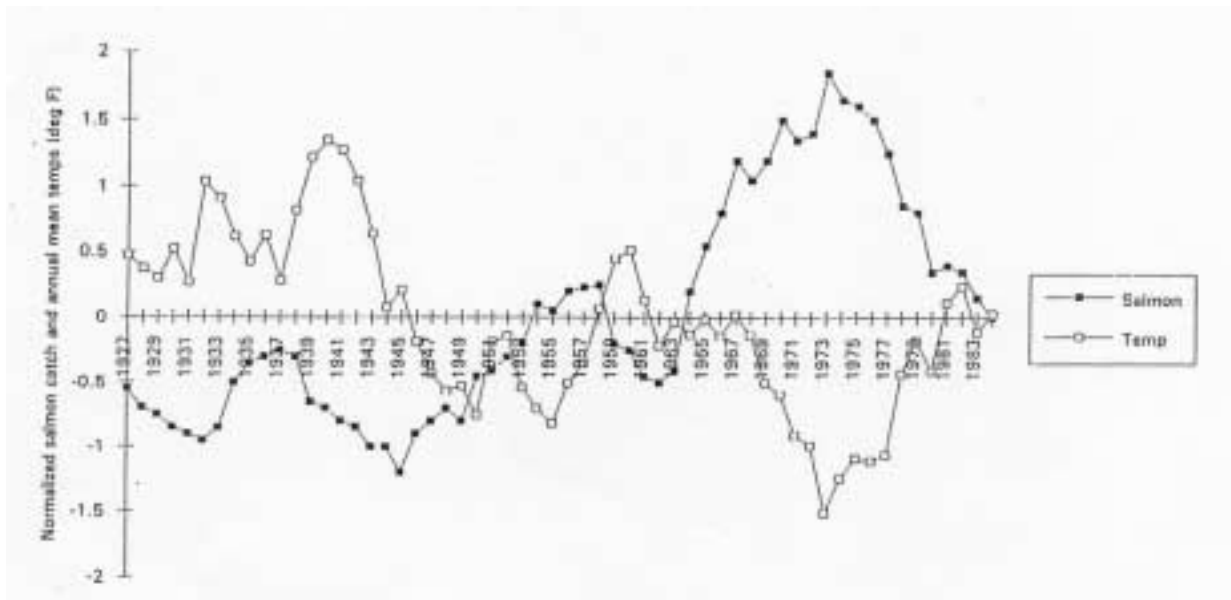

Figure 10.11. Comparison of annual mean temperatures at the H. J. Andrews Experimental Forest (5-year filter) and catch of coho salmon off Washington and Oregon (7-year filter) between 1927 and 1983 (Greenland 1994b).

McGowan et al. (1998) argue that the physical evidence for interdecadal changes in A and B types of circulation affecting the strength of the California Current is lacking. Although interannual variations in zooplankton biomass and temperatures are well correlated with transport of the California Current, physical changes accompanying interdecadal regimes suggest a different physical mechanism related to the vertical density structure of the upper water column: long-term increases in surface temperatures reduce density of the upper layer and decrease the depth of mixing. These changes, in turn, decrease the supply of plant nutrients and rates of biological production throughout the California Current. Although it is uncertain whether this physical forcing is related to El Nino activity, regime shifts produce sudden increases in

surface temperatures and vertical stratification across the eastern North Pacific (McGowan et al. 1998).

Observed patterns of salmon production in Oregon reflect coherent ecological changes throughout the region of the California Current. Trends in average harvest of coho salmon, for example, appear to follow a similar pattern to the combined biomass of dominant pelagic species (hake, anchovy, and California sardine) estimated from fish scales deposited in anaerobic marine sediments off California (Figure 10.12; Smith 1978; Lichatowich 1993). Ware and Thomson (1991) identified a 40 to 60-year cycle in wind and upwelling conditions that may influence long period fluctuations in pelagic fish biomass off southern California. They report an extended period of relaxation in upwelling and primary production between 1916 and 1942, which also coincides with the decline in total fish biomass. However, abundances of California sardine this century are out-of-phase with the trends in combined biomasses of pelagic species (including sardine) shown in Figure 10.12 (Lluch-Belda et al. 1992). Sardine populations off California were abundant before the 1950s, very low in abundance between 1950 and the late 1970s, and increased from the late 1970s to the mid-1980s. Both the period of peak sardine production this century and the recent recovery beginning in the late 1970s coincide with periods of relaxation of upwelling, which, as noted above, tend to favor strong recruitment of sardine (Bakun 1990; Lluch-Belda et al. 1992).

The same climatic conditions that influence the ocean environment of salmon also affect the quality of their freshwater habitats. For example, in a review of the climate on the H.J. Andrews (HJA) Experimental Forest in western Oregon, Greenland (1994a) found correlations between various indices of atmospheric circulation with temperature and precipitation. The results indicate that during periods of a strong Aleutian low (as suggested by correlations with the Pacific North America and Central North Pacific teleconnective indices), storms are pushed north of Oregon, causing relatively dry weather during the winter and raising January air temperatures due to the southwesterly flow of warm air into the region. These patterns are also associated with El Nino events.
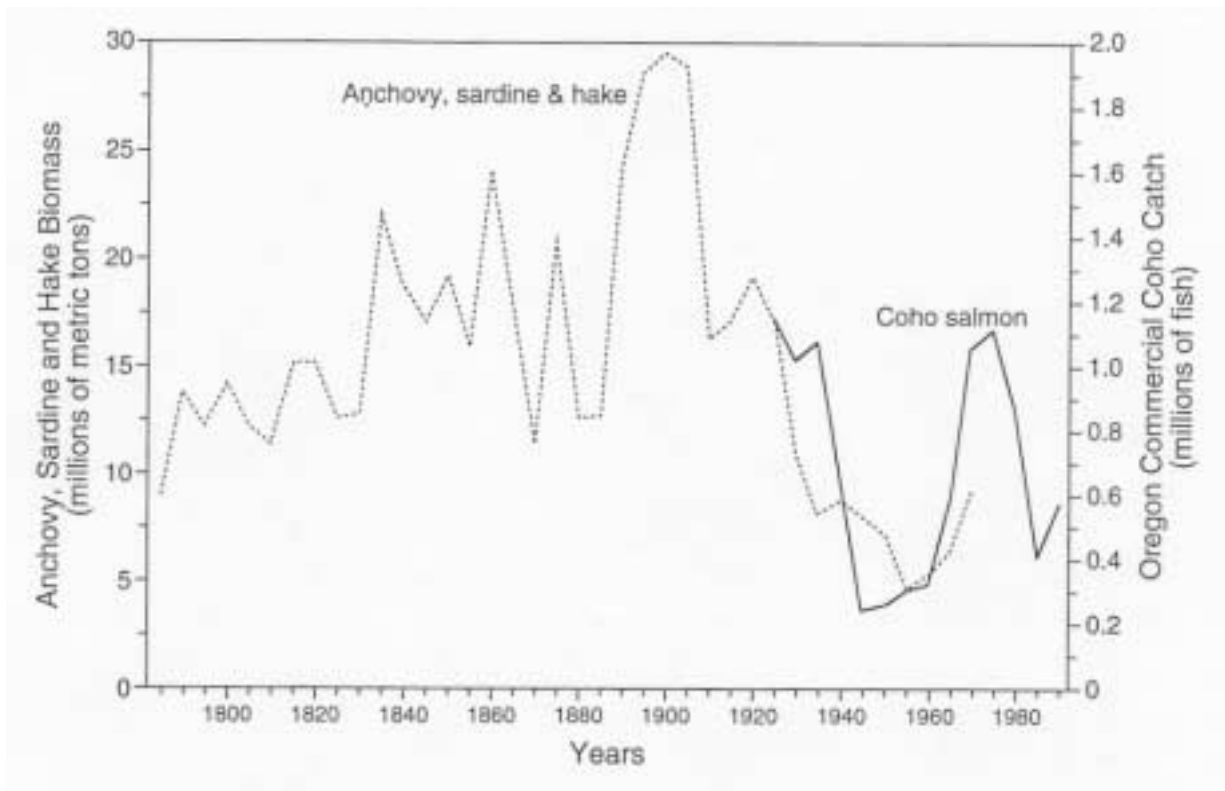
Figure 10.12. Total biomass of anchovy, sardine, and hake in the California Current compared with five-year averages of the annual commercial harvest of coho salmon in Oregon. Adapted from Lichatowich (1993). Standing stock of California Current species is inferred from contemporary stock sizes and scale deposition rates in the eighteenth and nineteenth centuries (reported by Smith 1978).

During many El Nino years, winter water year precipitation on the HJA Forest is low, and annual mean temperatures are high, while in La Nina years, winter precipitation increases, particularly a year later, and annual temperatures are below average. The influence of both low precipitation and high stream temperatures in much of the Pacific Northwest may cause a reduced snowpack during El Nino years (Greenland 1994a).

These results underscore the importance of geographic heterogeneity to salmon production in a shifting climate. While interdecadal regimes affect vast areas, the degree of independence between freshwater and ocean conditions may be important to salmon resilience. In western Oregon, stream and ocean conditions affecting salmon survival tend to oscillate in

phase. That is, during periods of warm ocean conditions and reduced biological productivity, freshwater habitat conditions may also decline due to reduced stream flows and increasing river temperatures in western Oregon (Greenland 1994a). These effects suggest a kind of "double jeopardy" for salmon stocks caused by a synchrony of mortality factors that involve more than one stage of life history. It is also possible that in other regions or among diverse watersheds within large basins like the Columbia River, ocean and river conditions for salmon survival are not in phase so that the effects of large-scale climatic change may be dampened. For example, since 1980, during a favorable regime for salmon survival in the Gulf of Alaska, annual precipitation on the coast of British Columbia has been above average. On the other hand, discharge of the large Fraser River declined during the same period due to reduced snowpack in the interior of British Columbia (Beamish 1993). These varying degrees of "connectedness" between the environments supporting different salmon life stages illustrate the importance of stock diversity and habitat heterogeneity to dampen the otherwise synchronous effects of large-scale climatic change.

Salmon Management in a Sea of Change

The Pacific Ocean and atmosphere do not move toward a steady state condition but continually shift in response to changes in the global heat budget. In fact, it is the lack of stability in the basinwide ecosystem that stimulates periods of enhanced biological production (Sharp, 1992). For example, the spring/summer transition to an upwelling regime disrupts a stable water column, raising cold nutrient-rich water trapped below the thermocline and increasing primary and secondary productivity along the Washington and Oregon coast. Interannual shifts in basinwide winds similarly change the flow of the California Current and the southward advection of nutrients from the subarctic region. Shifts in ocean currents and water masses are nonlinear and occur suddenly as environmental variations are amplified by positive feedbacks between the ocean and atmosphere. Thus, the gradual build-up of warm water in the western Pacific, for example, suddenly triggers the shift to El Nino. Strong teleconnections during some ENSO events, in turn, may influence the shift to a strengthened wintertime Aleutian Low and benefit salmon production in the subarctic Pacific to the detriment of production off Washington and Oregon. It is only at a basinwide scale that the shifting of locations of biological increase and decline become apparent.

Regime shifts reset ecological conditions within different oceanic regions by changing the composition of marine assemblages and altering the physical environment. Thus, local salmon populations may encounter different combinations of conditions each year they enter the coastal ocean as determined by the basinwide climatic regime and its interactions with regional and local scales of variation. Such changes alter the carrying capacity "rules" by changing the

interrelationships that govern how much of the ocean's productive capacity may be realized by salmon or other species. New interactions might explain, for example, why coho salmon survival was positively correlated with upwelling under one oceanic regime in the 1960s and early 1970s, and negatively correlated under a different regime during the last decade (Jamir et al. 1994). A similar shift in environmental relationships is described by Skud (1982), who concluded that correlations between a species and environmental factors may shift from positive to negative with changes in the dominance hierarchy. In this case, Atlantic herring *Clupea harengus* abundance was positively correlated with temperature when herring was the dominant species and negatively correlated when Atlantic mackerel *Scomber scombrus* assumed the dominant position (and visa versa). Skud (1982) proposed that abiotic factors determine the overall composition of assemblages but that absolute population density of the subordinate species is regulated by density-dependent interactions. This does not argue that the failure of correlations with physical parameters always involve a shift in dominance. Regardless of the specific mechanisms of control, oceanic regime shifts may introduce new sets of conditions that qualitatively change the relationships between a species and selected environmental indicators. Thus, forecasts based on short-term statistical analyses are likely to fail because the biological response patterns may vary under different environmental regimes (Sharp 1992).

Nonlinear changes in the basinwide ecosystem that dramatically alter both freshwater and marine conditions for salmon call into question management programs that emphasize constancy of the natural environment. Conservation programs that were designed under one climatic regime may not be appropriately applied under another. For example, the same levels of artificial propagation established during optimum ocean conditions may not be appropriate following a shift to a low productivity state (Beamish and Bouillon 1993). Genetic or ecological risks of hatchery programs on wild salmonids might increase disproportionately during poor survival conditions due to intensified harvest pressures or interactions with hatchery fish. The costs of hatchery production alone raise questions about continuing high levels of smolt release following a shift to a low survival regime.

Variations in the ocean environment also undermine the assumptions of traditional population models that are often used to establish escapement goals and set harvest levels in fisheries. The maximum sustained yield (MSY) concept is based on a logistic growth curve developed from animal populations held under a constant food supply and environmental conditions (Botkin 1990). According to this theory, natural populations reach a stable equilibrium level (carrying capacity) which is set by available resources. Stock recruitment models thus assume that abundance of a salmon population is regulated primarily by density-dependent factors during early life stages in fresh water. In practice, spawner-recruit relationships used to manage fisheries rely on multiple years of observation to show an "average"

relationship between population size and the resulting recruitment. Thus, rather than trying to understand the effects of environmental change on populations, traditional harvest models assume that change is insignificant by averaging conditions over the period of observation (Cushing 1995). In a system that oscillates unpredictably between different climatic states, and where physical changes continually reset ecological conditions and regulate ocean survival of salmon smolts, theoretical population models may offer little practical guidance for long-term conservation.

Within the Columbia River basin, salmon management has been designed around efforts to create a stable river system for the benefit of various economic uses. The idea that hatcheries could increase salmon production by eliminating variability ("limiting factors") in the freshwater environment was consistent with efforts to regulate the river (discussed in detail in Chapter 5 of this report). One important result of regulating the river with dams and controlling salmon production in hatcheries has been the narrowing of salmon life histories to conform to the rigid conditions imposed by the management system itself. Hatchery programs replace diverse riverine habitats with a constant rearing environment and replace diverse native stocks with a genetically uniform hatchery "product." By dampening seasonal fluctuations in the hydrograph, dam operations also reduce the diversity of freshwater habitats and the variety of flow conditions represented in the river. Furthermore, release strategies for hatchery salmon are programmed to fit the scheduled releases of water through the dams. Selective advantage is given to those fish that migrate downstream according to the operations of bypass, spill, and transportation systems. Unlike historical patterns of migration, which maximized use of freshwater habitats throughout the year and varied the time of ocean entry through a wide array of migratory behaviors, river operations concentrate the migrations of salmon through narrow "windows of opportunity" prescribed by the management system.

The problem with this approach is that it has failed to account for the effects of environmental control on other ecosystems or life stages of salmon "downstream." Regulation of river flows also directly controls the density and dynamics of offshore waters of the coastal ocean (Ebbesmeyer and Tangborn 1993) and the inland waters of the Juan de Fuca Strait (Ebbesmeyer and Tangborn 1992) with unknown consequences for natural production processes in these areas. Similarly, control of salmon life histories in the river may directly regulate the subsequent survival of salmon in the estuary and ocean. A variable ocean requires flexibility for anadromous species to successfully respond to a wide array of potential conditions. This flexibility may be particularly important in the highly variable environment of the California Current ecotone, which encompasses the southern edge of a shifting subarctic boundary (Figure 10.5) and the distributional limit of subarctic salmonids. A narrowing of the time of migration and physiological condition of salmon leaving the Columbia River limits the array of possible

responses that may otherwise enable species to cope with fluctuations in the ocean. Different times of migration, for example, may be advantageous in different years depending on the onset of the spring/summer transition, the distribution of the Columbia River plume, the timing and location of upwelling episodes, or the northward extent of warming caused by occasional strong ENSO events in the tropics.

Loss of freshwater habitats within the Columbia River basin and the shift to production of a few hatchery stocks may also limit the variety of migratory pathways in the ocean to the detriment of salmon production. For example, since oceanic regimes in the California Current oscillate out of phase with those of the central North Pacific, we might expect north and south migrating stocks to be favored under opposing climatic states. This could explain the recent increasing trend in abundance of upriver bright fall chinook, which spawn in the Hanford area and tend to migrate off Southeast Alaska, and the coincidental decline of tule fall chinook from the lower river, which have a more southerly ocean migration. This pattern was reinforced during the 1982-83 El Nino when abundance of tule fall chinook decreased below preseason predictions while northward migrating populations in the Columbia River showed little or no decline (Johnson 1988). As in this example, maintenance of a variety of migratory patterns in the ocean may depend on the protection of different freshwater habitats that support different populations and life histories.

The critical point is that the performance of salmon in the estuary or ocean is not independent of the selection processes in fresh water. Management manipulations that alter population structure, life histories, or habitat diversity during the fresh-water phase of life history may directly influence the capacity of salmon to withstand natural fluctuations in the estuary and ocean. Efforts to control variability in fresh water may unwittingly eliminate behaviors that buffer salmon production in an unstable marine environment. By the 1970s, about 2/3 of the coho salmon smolts produced in the Oregon Production Area consisted of only 2 stocks of fish released from numerous hatcheries in the Columbia River basin. Across Oregon, the replacement of a diversity of wild populations and life history patterns with relatively few hatchery-produced stocks may have depressed survival rates of smolts during poor ocean conditions and increased interannual variability of returning adult salmon (Bottom et al. 1986).

The location of Columbia River populations toward the southern range of salmon species and their sensitivity to changes in the coastal ocean raise concerns about the effects of global climate change on salmon production. Neitzel et al. (1991) discuss effects of global warming on fresh-water habitats of the Columbia River Basin. Significant ecological changes in the ocean environment could also be critical to local salmon production. For example, Peterson et al. (1993) suggests that El Nino events in the eastern Pacific provide an indication of the kind of biogeographic shifts in the California Current that may accompany global warming. Although it is

expected that upwelling favorable winds will increase in the northern hemisphere due to differential heating of the land and ocean (Bakun 1990), depression of the nutricline will likely cause a decrease in the capacity of upwelling to raise nutrients to the surface (Peterson et al. 1993). This same mechanism has already been suggested as one possible explanation for a significant decline in zooplankton abundance off southern California since 1951 (Roemmich and McGowan 1995). Increased upwelling will also increase offshore transport and thereby decrease the number of areas and time periods suitable for the spawning of many pelagic fishes such as anchovy and sardine. Peterson et al. (1993) hypothesize a shift in the California Current from short food chains leading to anchovy and sardine production to longer food chains favoring large migratory species such as albacore tuna *Thunnus alalunga* and jack mackerel *Trachurus symmetricus*. Alternative energy pathways may also increase the production of demersal species. While the specific effects may vary in the northern reaches of the California Current off Washington and Oregon, the results may be detrimental to local salmon stocks if El Nino is an appropriate model of the qualities of future change. These results underscore the importance of maintaining habitat complexity and stock diversity in fresh water to help buffer potential effects of global warming on salmon survival in coastal environments.

Conclusions and Recommendations

Conclusions

1. Global and regional scale processes in the ocean and atmosphere can regulate the productivity of local marine, estuarine, and freshwater habitats for salmon. Although managers cannot control these processes, natural variability must be understood to correctly interpret the response of salmon to management actions in the Columbia Basin.

2. The North Pacific Ocean oscillates on an interdecadal time scale between alternate climatic states associated with changes in the Aleutian Low Pressure system. Years when the winter Aleutian Low is strong and centered in the eastern North Pacific are associated with high mean sea levels, increased ocean surface temperatures, and increased stratification of the upper water column in the northeast Pacific; increased southwesterly winds and downwelling off Oregon and Washington; and reduced precipitation levels, low stream flows, and increased water temperatures in Oregon streams. Conversely, periods characterized by a weak winter Aleutian Low centered in the western North Pacific are associated with reduced surface temperatures and stratification in the California Current, enhanced westerly winds and upwelling in the Northeast Pacific, and increased rainfall and stream flows in Oregon. The timing of interdecadal shifts from a weak to a strong Aleutian Low regime may be linked to the Southern Oscillation in the tropics.

3. Because salmon migrations are tied to major ocean circulation systems and, because the life cycles of salmon are shorter than the interdecadal periods of large-scale climatic change, abundance of salmon "tracks" large-scale shifts in climatic regime. The specific mechanisms of this tracking are poorly understood.

4. Salmon abundances in the California Current region (off Washington, Oregon, and California) and in the Central North Pacific Ocean domain (off British Columbia and Alaska) respond in opposite ways to shifts in climatic regime. During periods of a strong Aleutian Low, zooplankton and salmon production generally increase in the Central North Pacific and decrease in the California Current, suggesting geographically distinct mechanisms of aquatic production. Climatic shifts characteristic of the strong Aleutian Low regime occurred twice this century: one beginning about 1925 (to 1946) and another in 1976/77 (to the present). Both periods were marked by precipitous declines in the coho salmon fishery off Oregon.

5. Opposing cycles of salmon abundance between the Central North Pacific and the California Current regions underscore the importance of stock-specific regulation of ocean fisheries. Even during periods of high marine survival off Oregon, harvest limits must ensure that Columbia Basin stocks are not overexploited by northern fisheries trying to compensate for coincidental decreases in the production of stocks from Alaska and British Columbia.

6. Stocks with different life history traits and ocean migration patterns may be favored under (or differentially tolerant of) different combinations of climatic regime and local habitat characteristics. Such differences afford stability to salmon species over multiple scales of environmental variability.

7. Together landscape modifications, construction of dams, overharvest in sport and commercial fisheries, and hatchery programs have simplified the geographic mosaic of habitat conditions in the Columbia River Basin and reduced the variety of salmon life histories formerly associated with this mosaic. Such changes limit the capacity of salmon to adapt to periodic shifts in large-scale atmospheric and oceanic conditions.

8. The cumulative effects of human disturbance may not become apparent until severe climatic stresses trigger a dramatic response. Such interactions may be particularly severe in the Pacific Northwest where periods of reduced ocean survival of salmon and periods of stressful freshwater conditions (due to reduced precipitation, low stream flow, and increased stream temperatures) tend to co-occur. Although climatic fluctuations may be a proximate factor in regional salmon decline, the ultimate causes may involve a longer history of change affecting species and population resilience into the future. Conservative standards of salmon protection may be necessary even during a high productivity state in order to maintain the genetic "slack" needed to withstand subsequent productivity troughs.

9. The dynamics of salmon metapopulations will change under different climatic regimes if, for example, the dispersal of core populations or the rate of extinction of satellite populations is a function of fish density. Habitat fragmentation and loss of local stocks will likely magnify the effects of productivity "troughs" by also increasing freshwater mortality, inhibiting recolonization of disturbed habitats, and slowing rates of population recovery. Thus, in concert with large-scale changes in climate, increases in the rates of local extinction and loss of stock diversity may lead to greater "synchrony" in the dynamics of salmon populations. Regional patterns of salmon decline in the Columbia Basin and throughout much of the Pacific Northwest are generally consistent with this synchronization hypothesis.

10. Shifts in oceanic regime involve substantial changes in the distribution of species, the structure of marine food chains, and the physical processes of biological production. Anticipating such change and understanding its effects on salmon production in the Columbia Basin will require ecological indicators other than just the abundance of salmon.

Critical uncertainties

1. Lack of long-term monitoring of ocean conditions and the factors influencing survival of salmon during their first weeks or months at sea severely limit understanding of the specific causes of interdecadal fluctuations in salmon production. Such understanding is needed if management programs are to adapt to natural variations to insure rebuilding of salmon populations in the Columbia River.

2. Stock-specific distributions of Columbia Basin salmon in the ocean and the migratory patterns of hatchery versus wild salmon are poorly understood. It is important to know whether hatchery practices affect the migratory patterns and potential marine survival of salmon.

3. There is increasing evidence worldwide that ocean fisheries can have a destabilizing influence on marine food chains. Harvest management programs based on stock recruitment relationships and monitoring of individual species do not provide adequate indicators of the effects of harvest activities on ocean food webs.

4. The risks of global warming are potentially great for Columbia Basin salmon due to the sensitivity of southern salmon stocks to climate-related shifts in the position of the subarctic boundary, the strength of the California Current, the intensity of coastal upwelling, and the frequency and intensity of El Nino events. Some modelers believe that persistent warmth in the ocean and increased frequency of El Ninos after 1976 (without intervening "cold" La Nina episodes) may be among the early signs of global warming from greenhouse gases. Others speculate that an observed 70% decrease in the biomass of macrozooplankton off southern

California since 1951 could be related to ocean warming associated with the 1976/77 regime shift or a climate-induced change in ocean circulation. While the potential effects of global warming on ocean circulation patterns are poorly understood, the implications for salmon restoration efforts throughout the Pacific Northwest are tremendous.

Recommendations

1. Research on the uncertainties listed above should be encouraged because salmon management in freshwater must be linked to ocean properties and patterns if our alternative conceptual foundation that builds around the salmon life history ecosystem is adopted.

2. Research on effects of ocean conditions on productivity of salmon must to be integrated with estuarine and riverine research.