

The Ocean Ecology of Salmon in the Northeast Pacific Ocean—An Abridged History

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Abstract.—Research on the ecology of salmon in the northeast Pacific Ocean began in the early 20th century. Charles Gilbert and Willis Rich demonstrated the basis for the stock concept and were instrumental in changing common misconceptions of the times. Later in the 1900s, research endeavors, primarily under the auspices of the International North Pacific Fisheries Commission, led to important studies on the distribution and migration of maturing salmon on the high seas. Research on the early juvenile period was initiated later, especially after the 1982–1983 El Niño clearly showed the limits of the ocean's carrying capacity along the west coast of the United States. There is now good evidence for both intra- and interspecific competition among salmon in the open ocean and for correlations between variable physical environments, such as El Niños and regime shifts, and survival of salmon during early ocean life. How mortality rates are affected by physical forcing, food availability, predation, and food web structure and how these effects will be modified by climate change and global warming are all major challenges for the future.

Introduction

Scientific research has led to major advances in understanding the biology of Pacific salmon (Groot and Margolis 1991; Quinn 2005). But if we stop to consider how this progress was achieved, it becomes apparent that the steps to enlightenment have been far from linear. In this chapter, we explore some of the paradigms, the myths, and the science that have enhanced and sometimes misled our understanding of the biology of Pacific salmon *Oncorhynchus* spp. Although the quantity of research on the life of salmon in the sea has

increased exponentially over the years (e.g., Figure 1), we sought to examine more closely how the early pioneering research formed the basis of our current knowledge.

Although our focus is the history of research on the ocean ecology of salmon, we begin with the story of salmon in freshwater where they were first observed and harvested after leaving the ocean. Thereafter, the bulk of our discussion is organized around five paradigms that focused our thoughts:

- Homogeneous salmon versus home-stream theories,
- Migrations—local or distant,
- Critical periods,

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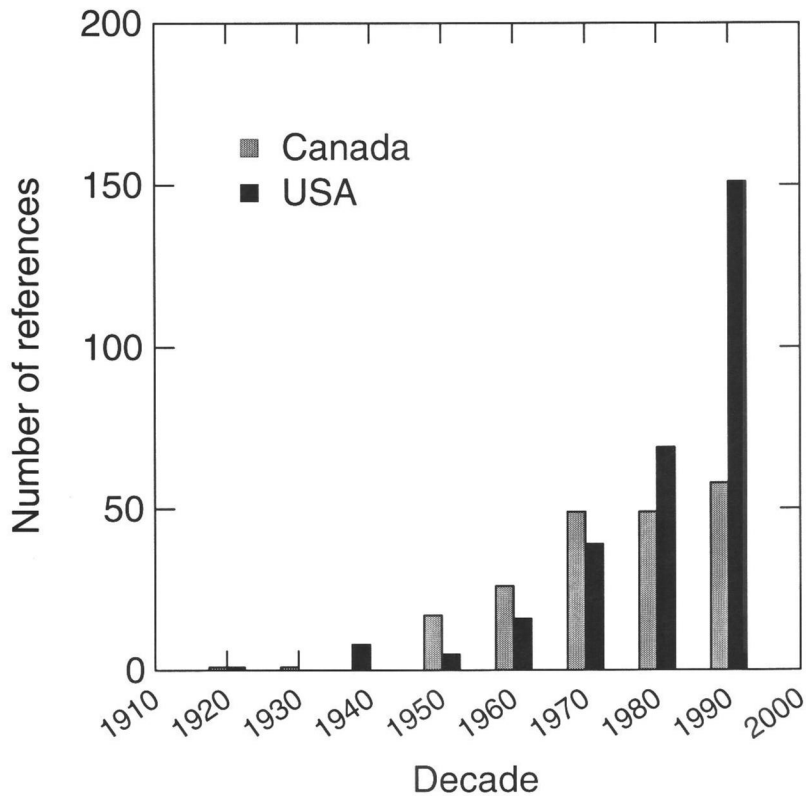


Figure 1. Summary of the research on juvenile salmon in the ocean, cited by decade, from Canadian and U.S. publications (Beamish et al. 2003; Brodeur et al. 2003).

- Ocean carrying capacity and density dependence, and
- Ocean variability.

We conclude with comments on future challenges to a better understanding of the importance of freshwater and ocean environments for the survival of Pacific salmon. In the interests of brevity, we are selective rather than inclusive in our choice of references, especially for the period of copious research in more recent times. We do not always follow a linear chronology of history and often hopscotch through time.

Homogenous Salmon

The anadromous life history of Pacific salmon, combined with their size and high local

densities bring about interactions with various terrestrial predators, including humans (*Homo sapiens*). Because the salmon were such an important food source for the indigenous peoples of western North America, the characteristics of their upstream migration were of great interest. The lack of a written history precludes an in-depth examination of the first ~8,000 years of the study of salmon biology, but some clues to the status of knowledge were captured by the first European-origin fur trappers and explorers. With the onset and growth of global commercial interests in salmon, the cannerymen added to our knowledge, and finally (after the stocks declined) the scientists began their study. During these early years, the ocean life of the salmon was unseen, unstudied, and unknown.

During the 19th and early 20th centuries, there were many misconceptions about the freshwater phase of the life history of these anadromous fishes. It was believed by many, including the renowned biologist from Indiana University, David Starr Jordan, that Pacific salmon did not have any special ability to find a home stream. Together with his former student at Indiana, Charles Henry Gilbert, they wrote, "It is the prevailing impression that the salmon have some special instinct which leads them to return to spawn in the same spawning-grounds where they were originally hatched. We fail to find any evidence of this in the case of the Pacific coast salmon, and we do not believe it to be true. It seems more probably that the young salmon, hatched in any river, mostly remain in the ocean within a radius of 20, 30, or 50 mi of its mouth" (Jordan and Gilbert 1887). Likewise, Hugh Smith, then director of the U.S. Bureau of Fisheries, believed that there were no significant differences between the races of salmon. The returning fish selected their spawning streams randomly and stocks of a particular species were genetically homogeneous, with any differences due to the effects of different environments (Jordan 1904; Ricker 1972).

While Jordan was the first Pacific salmon biologist, Gilbert's eventual contribution to salmon science was considerably greater. Jordan came to the West Coast as president of the new Stanford University and shortly thereafter appointed Gilbert as its first professor of zoology. Both were involved in some of the historic cruises of the research steamer *Albatross*. This ship made many cruises into Alaskan waters to study salmon in the late 1800s and early 1900s (Roppel 2004).

Some of Gilbert's earliest successes concerned the interpretation of the age of a salmon from its scales. In a letter to John Pease Babcock, deputy commissioner of fisheries, Province of British Columbia, on January 20, 1913, Gilbert discussed how he collaborated with Willis Rich to demonstrate that fin-clipped

young coho salmon *O. kisutch* returned 3 years old, thus corroborating his age estimates from scales.

Ultimately, Charles Henry Gilbert (Figure 2) found that his observations were not consistent with Jordan's beliefs, and Gilbert evolved as a proponent of the stock concept in Pacific salmon. Gilbert's comparative research on Pacific salmon along the North American coast established his reputation (Dunn 1996). After 5 years of informal study of the salmon of British Columbia, Gilbert was retained in 1914 by John Pease Babcock to establish a program of ongoing scientific investigation of the biology of sockeye salmon *O. nerka* in British Columbia. Vestiges of that program continue today.

Gilbert's research on sockeye salmon in British Columbia was instrumental in the establishment of a full-time director and staff of biologists at the Pacific Biological Station at Nanaimo, British Columbia in 1924 (Foerster 1955). The first director of that station, Dr. W. A. Clemens, and his wife, Dr. Lucy S. Clemens, continued the work of measuring and aging sockeye salmon in the major fisheries into the late 1940s.

Gilbert studied the patterns of growth, recorded like tree rings, on salmon scales to learn about the basic life history of salmon in freshwater and the ocean. In his seminal 1914 paper on sockeye salmon from British Columbia, he showed that salmon from different rivers had different numbers of circuli in the freshwater phase of growth. He concluded that fish from different rivers had different life histories, returned to their natal streams as different age groups, and were essentially isolated from other populations (Gilbert 1914–1925). He describes the significance of this discovery on the occasion of his departure from the employ of the Province of British Columbia in 1924: "The practical significance of this determination is of great economic importance, since it demonstrates that, in order to maintain



Figure 2. Photograph of Charles Henry Gilbert, obtained with the assistance of the Gilbert Ichthyological Society and was provided for our use courtesy of Dorothy T. Gilbert.

the runs to a given district, it will not suffice to install a hatchery on any convenient stream into which the entire hatchery output may be liberated, or to make joint and uniform regulations apply to all streams alike. Each stream must be given separate consideration in order that each may receive its own quota of fry, as the run to each stream is self-dependent."

Willis Rich, one of Gilbert's first students, extended Gilbert's pioneering research on life history diversity to the Columbia

River and concluded that Chinook salmon *O. tshawytscha* also consisted of many distinct populations that migrated to sea at different sizes and at different times. Based on scale characteristics and distinct cycles of abundance, Rich (1939) reasoned that Pacific salmon returned to their natal streams to spawn and that each species was composed of many local, independent, and self-perpetuating populations. He wrote that "conservation of a species as a whole resolves into the

conservation of every one of the component groups." Much later, in a small coastal river, Reimers (1973) found that Chinook salmon had different life histories, residing in the river and estuary for different periods and experiencing different rates of return.

Homing to natal streams, fundamental to Gilbert and Rich's theories, was suspected many years before being clearly demonstrated (Chamberlain 1907). Once it was clear that salmon did home to a natal stream, the mechanism by which this was accomplished became the major scientific question. While tagging sockeye salmon off the west coast of British Columbia in 1924, Clemens (BCLA 1926) severed the olfactory nerves of 259 of 515 tagged individuals. Of the 256 that were not treated, 59 tags (23%) were recovered in or off the Fraser River while only 24 of 259 (9.3%) with severed olfactory nerves were taken in or off the Fraser River. No tags were recovered elsewhere, indicating the importance of olfaction in homing. Later, Hasler and Wisby (1951) performed several experiments that demonstrated the role of olfaction for homing of salmon in freshwater.

Less is known about homing and navigation of salmon from the open ocean to their spawning grounds. Larkin (1975) stated, "Certainly none of the present theories of migration is adequate to account for the apparent phenomenal ability of salmon to navigate where there are few apparent navigational cues" as each individual performs the migration once with no possibility of learning from a parent. Salmon often undertake remarkable long distance migrations at sea. Today, several hypotheses are postulated to explain the phenomenal orientation and navigation in the open ocean (see Healey 2000 and Quinn 2005 for reviews). On the basis of apparently directed and well-timed migrations, Healey and Groot (1987), Healey (2000), and others concluded that species use a combination of mechanisms, including compass and bicoordinate naviga-

tion in oceanic waters, switching to local cues such as olfaction in coastal waters.

The work of Gilbert and Rich dispelled the myth that salmon of the same species were one homogeneous population. This had enormous implications for the direction of salmon research, now based upon the stock concept, and the management of stocks as discrete units. The evolution of understanding that maturing salmon home to their natal streams is now key to their population biology and management. This is the basis for the stock concept, the principle that stocks are unique and should be managed as discrete units (Ricker 1972).

Later researchers, such as Russell Foerster, Ferris Neave, Andrew Pritchard, and William Ricker, made great contributions to our knowledge about the freshwater phases of salmon. Initially, they believed that factors in freshwater and fishing limited the abundance of returning spawners (see Foerster 1955; Beamish et al. 2003). These beliefs focused management on hatchery production, harvest, escapement targets, and production in freshwater.

Lichatowich (1999) pointed out that the belief in the homogeneous salmon often had self-serving implications for the commercial fisheries, for fish hatchery operators and their desire to transfer eggs among watersheds, and for a general lack of management of the salmon fisheries of the late 1800s and early 1900s. Individual stocks were simply not important. An example of the attitudes of the day was expressed by representatives of the commercial salmon industry: "The State of Washington Fish Commissioners are fully alive to the fact that only by a complete system of increasing the amount of fish by artificial propagation can it be hoped to save the industry from the experience of the Eastern States."¹

¹ Letter to Premier and Council of the Province of British Columbia by the Salmon Cannery Association. Pages 617-619 in *Sessional Papers, Second Session, Ninth Parliament of the Province of British Columbia, Session 1901*. Victoria, Canada.

The inclination to dabble in salmon biology has a long history. The belief that stocks could be transplanted among different river systems, an underlying assumption of the homogeneous concept, was advocated by the first explorer to cross North America to the Pacific Ocean by land. After leaving what is now Bella Coola, British Columbia on August 16, 1793, Alexander McKenzie recorded in his journal, "If I could have spared the time, and had been able to exert myself, [...] it was my intention to have taken some salmon alive, and colonized them in the Peace River; though it is very doubtful whether that fish would live in waters that have not a communication with the sea." (Sheppe 1962).

Although science made significant contributions to the early knowledge of Pacific salmon, it is important to remember that it was incremental. New science and ultimately better ideas were often ignored because they were inconvenient or contrary to local knowledge and prevailing paradigms of the times—viz, technology can improve nature. Exploitation or development of salmon resources usually preceded a good understanding of science. Accepted science arrived late. The first canneries were established in the 1860s so the industry had 40 years of experience with salmon, and the indigenous peoples had more than 8,000 years of experience, before any formally trained scientists appeared to assert their dominance in the knowledge of salmon biology. Some topics have not progressed far in more than 100 years. The rush to develop a salmon farming industry before their impacts could be evaluated, including those of escaped nonnative fish on native Pacific species, is a case in point.

Ocean Migrations: Local or Distant?

The first reports of the ocean life of Pacific salmon came from fishermen as they expanded their pursuits seaward from estuaries to the coastal regions. As we have noted,

some scientists thought that salmon entered the ocean and stayed relatively close to shore and, when mature, swam up the nearest available stream. By the early 1900s, there was a growing impression that sockeye salmon returning to the Fraser River arrived from the open sea to the northwest of the Strait of Juan de Fuca (BCLA 1903). The lack of food in their stomachs upon arrival led to speculation that these sockeye salmon had traveled a considerable distance from their feeding grounds. The indigenous peoples of British Columbia reported that the start of the run occurs in the outer islands a month or more before they make their appearance near the mouths of streams (Gilbert 1913).

Gilbert (1913) made some of the first observations on coastal migrations of juvenile salmon. He ascertained certain differences among the species, but the questions posed were rather simple: "After leaving the rivers, no young sockeyes are on record from salt water along the BC coast. The young of all other salmon species can be caught in traps in Juan de Fuca strait; the sockeye must pursue a different course. It is not improbable that they strike directly for the outer coasts, passing through the deep-water channels; but of this we have no direct evidence. During the years of their sojourn in the sea their habits are wholly a matter of inference." Gilbert and Rich (1927) published their investigations of sockeye salmon runs to the Karluk River, Alaska.

With the advent of motor-powered fish boats at the beginning of the 20th century, salmon fisheries expanded their range seaward of the estuaries, and interest grew in the ocean distribution and interception of Pacific salmon. Some of the first research on the ocean distribution of salmon was conducted by O'Malley and Rich (1919) who studied migrations of sockeye salmon approaching the Fraser River. In 1925, fisheries administrators and scientists from Alaska, British

Columbia, Washington, Oregon, and California met and established the International Pacific Salmon Investigating Federation to develop a cooperative plan for studying the problems associated with migrating Pacific salmon (BCLA 1926). One of the research priorities was to identify the origins and migrations of stocks under commercial exploitation by tagging and releasing salmon at sea. Tagging experiments in 1927 and 1928 revealed that Chinook salmon from California were feeding off the west coast of Vancouver Island and that Chinook salmon from the Columbia River, Skeena River, and Fraser River intermingled off the west coast of the Queen Charlotte Islands (Clemens 1932). Sockeye salmon from the Nass and Skeena rivers were captured in fish traps as far north as Sumner Strait, Alaska (BCLA 1926).

Collectively (reviewed by Foerster 1955), these studies showed limited migration of pink salmon *O. gorbuscha* and chum salmon *O. keta*, short travel distances for coho salmon, with all tagged fish recovered in the year they were tagged. Chinook salmon, on the other hand, traveled long distances along the coast. Those tagged west of Vancouver Island or in the Queen Charlotte area were recovered to the south in Puget Sound and off the Columbia River, supporting the theory of a northwest feeding migration of young fish and a southeast migration of maturing adults (Foerster 1955). Later, Davidson (1937) tagged fish off the west coast of British Columbia and recorded their recovery in rivers throughout the Pacific Northwest. He found that Chinook salmon made extensive migrations from the Columbia River to Vancouver Island. Such studies were a major impetus to treaties and agreements for the management of migratory stocks after it was recognized that ocean fisheries could affect the abundance of these migratory populations.

The International North Pacific Fisheries Commission

The most significant period of ocean research on the distribution and migrations of salmon followed formation of the International North Pacific Fisheries Commission (INPFC). By the 1930s, the Japanese salmon fleet was fishing throughout the northwest Pacific and into the Bering Sea to gain access to an abundance of salmon and other species that are relatively rare along the coast of Japan. Following the war in the Pacific in the early 1940s, the victors insisted on a clause in the 1951 San Francisco Peace Treaty that obligated Japan to be part of an international fisheries regulatory body in the North Pacific. This led to the International Convention for the High Seas Fisheries of the North Pacific Ocean with three signatories: Canada, Japan, and the United States. The terms of the convention established the International North Pacific Fisheries Commission in 1953. As little was known of the biology of Pacific salmon or their prey and predators on the high seas (Hartt 1962), a key role of the new commission was to conduct research on the distribution and biology of salmon and other marine fishes that swam in the open North Pacific Ocean (Foerster 1955). After 1992, the INPFC metamorphosed into the North Pacific Anadromous Fish Commission, which continues research on salmonids in the open ocean today.

Within a year of ratification of the convention by the governments, scientific studies of the biology of Pacific salmon on the high seas were underway and tagging salmon on the high seas was an integral part of these investigations. Bulletins of the INPFC provided information on the distribution patterns of each species of Pacific salmon in the ocean—coho (Godfrey et al. 1975), sockeye (French et al. 1976), chum (Neave et al. 1976), Chinook (Major et al. 1978 and Takagi et al. 1981), and steelhead *O. mykiss* (Burgner et al. 1992). These studies revealed the broad

ranges and overlapping oceanic distributions of many species. Individuals were often tagged thousands of kilometers from their natal streams. Because Canada and the United States were primarily interested in potential interceptions of various stocks, these studies tended to focus on oceanic migrations in relation to continent or country of origin.

Few studies considered distributions of Pacific salmon on the high seas at the stock/population level because suitable techniques for identifying discrete salmon populations had not yet been developed. Gilbert (1914) was aware of the possibility of stock-specific patterns of freshwater scale growth from his studies of scales of maturing sockeye salmon as they returned to the Fraser River. The patterns of freshwater growth on the scales of returning adults varied by date and fishing location. Gilbert surmised that these differences reflected the different origins of these sockeye salmon from among the many sockeye nursery lakes within the Fraser basin. Exploiting the knowledge of regional variations in scale growth patterns was one of the techniques used to estimate the continent of origin of salmon caught on the high seas, but it was many years before studies of the distributions of individual populations could be considered. Most early studies of migrations were based on tagging (Foerster 1955). A notable study by Straty (1975) based on exploratory fishing and marking fish described the adult migration of Bristol Bay sockeye salmon and how stocks segregated by river of origin (as much as 200 km from the mouths of home rivers).

The first extensive research on juvenile salmonids in the sea was the pioneering research by Hartt (1980) and Hartt and Dell (1986). They provided information on diets, growth, travel directions and rates, and migration patterns based on purse seining and tagging of fish during the summers of 1956–1970 in the eastern North Pacific from

Vancouver Island into the Bering Sea. From catches, they concluded that most juvenile salmon (but not juvenile steelhead) migrated north and west along a narrow coastal belt or corridor. Later studies confirmed that juvenile sockeye, pink, chum, coho, and Chinook salmon were rarely found beyond the continental shelf (Jaenicke and Celewycz 1994; Welch et al. 2003).

Research on juvenile salmonids in the oceans off California, Oregon, Washington, Canada, and Alaska are reviewed by Brodeur et al. (2003), Beamish et al. (2000, 2003), and Heard et al. (2001), respectively. Straty (1974) was one of the first to sample juvenile salmon with purse seines to show the distribution and migratory routes of separate stocks of sockeye salmon from Bristol Bay. Healey (1980) related differences in estuarine residence times and life histories of juvenile salmon to their feeding habits, offshore movements, and foraging success in the Strait of Georgia. Groot et al. (1985) followed juvenile sockeye from the mouth of the Fraser River to Queen Charlotte Strait in a study that spanned four seasons.

With the advent of tiny coded-wire tags in the 1970s that could be injected into large numbers of juvenile salmonids, more detailed information became available on migrations during and after the first year in the ocean, especially for coho and Chinook salmon (e.g., see Myers et al. 1996 based on catches in the open ocean and Weitkamp and Neely 2002 for correlations between hatchery latitudes and the location of ocean catches). Walker and Myers (1992) reviewed stock identification techniques for salmon on the high seas.

Genetic markers are now used to distinguish different stocks at sea (Seeb et al. 2004; Beacham et al. 2005). Recently, it has been possible to test hypotheses about stock-specific aggregations of salmon using coded-wire tags recovered from salmon caught on the high seas (McKinnell et al. 1997). How-

ever, even with these new genetic and adult tagging techniques, there is still much to learn about ocean migrations and where stocks are at specific times of the year when critical events influence their survival.

Besides the prolific research on ocean migrations, the INPFC fostered important research by Canadian, Japanese, and U.S. scientists on the physical oceanography of the environment occupied by salmon in the North Pacific (e.g., Fleming 1955; Dodimead et al. 1963; Favorite et al. 1976), including ocean circulation, temperature and salinity structure, and fronts and domains that related to the distribution of salmon. Relationships among salmon distributions and ocean conditions revealed that various species and age groups had affinities for certain environmental conditions and water masses in the North Pacific, such as the subarctic boundary, the Alaskan Stream and subarctic gyre. Favorite and Hanavan (1960) reported that the salinity front at about 42°N coincided approximately with the southern distribution of salmon in the spring. Temperatures also influence distributions and migrations. Manzer et al. (1965) listed preferred temperature ranges for each species, how they changed seasonally, and the importance of upward doming of isotherms.

Studies of the migration routes of returning Fraser sockeye salmon have also been related to ocean conditions. Babcock was the first to report (BCLA 1903) that maturing sockeye salmon appeared to migrate around Vancouver Island either from the north through Johnstone Strait or from the south through Juan de Fuca Strait (e.g., Hamilton 1985; Groot and Quinn 1987). The percentage of fish migrating to the north or south has varied greatly, with most arriving via the southern route during 1953–1977, and thereafter, more to the north (Groot and Quinn 1987; McKinnell et al. 1999). These variations have been correlated with Fraser

River discharge and sea surface temperatures that may affect the distribution of sockeye in the ocean prior to migration (Wickett 1977; Groot and Quinn 1987). Blackburn (1987) proposed a temperature model to explain how run timing was related to ocean temperatures in the Gulf of Alaska, and Thomson et al. (1992) modeled how ocean currents affect the latitude of landfall and migration speeds of Fraser River sockeye.

The Critical Period Concept

A critical period is an interval of time of high and variable mortality that is believed to determine the survival of a year-class. The hypothesis for critical periods in the early ocean life of Pacific salmon is based on the mortality schedules observed in the life tables of fishes and other animals where mortality rates usually decrease rapidly and abruptly with the age of a cohort. Godfrey (1958) concluded that it was the early marine life of salmon that determined subsequent adult abundances. Parker's (1962) postulate of additional mortality during the first year associated with estuarine and early ocean life was later verified by his research (Parker 1968) where he showed the highest mortality rates for pink salmon (2–4%/d) occurred during the first 40 d at sea. Later, Hartt (1980) called this period the first critical summer in the ocean. Bax (1983) also found highest mortality rates very early in ocean life for chum salmon.

By the late 1900s, it was apparent that we understood less about salmon during the first few months at sea than all the other phases of their life history (Healey 1980). This was due, in part, to the fact that the overwhelming majority of salmon biologists were studying either freshwater or maturing ocean phases. During the late 1970s and early 1980s, many studies were initiated on the ecology of juvenile salmonids at sea (Figure 1). Major reasons for a spate of new ocean research were the drastic declines of many stocks in

the U.S. Pacific Northwest following the big 1982–1983 El Niño, low-population abundances in the Pacific Northwest and the ensuing listings of many species/stocks under the U.S. Endangered Species Act. The 1982–1983 El Niño was the nail in the coffin of the idea that the ocean had an unlimited capacity to support whatever salmon juveniles could be produced in freshwater.

Studies that found correlations between environmental factors during early ocean life and subsequent adult returns supported the critical period hypothesis. Vernon (1958) found that high April–August temperatures and low salinities in Georgia Strait were inversely related to abundance of pink salmon the following year (see also Holtby et al. 1990). Wickett (1958) found that low sea surface temperature in June was associated with low pink salmon survival along the central coast of British Columbia, and Blackburn (1985) showed a significant relationship between marine survival and salinity during summer and fall of ocean entry. A positive relationship between early ocean growth of Fraser River sockeye and marine survival suggested to Henry (1961) that conditions favoring good growth also favor good survival. Van Hynning (1973) found an inverse trend between the fall Chinook abundances in the Columbia River and sea surface temperatures during the first few months of life at sea.

Research on coho salmon from Oregon also provided evidence for the importance of ocean conditions to survival. The number of early-maturing male coho salmon (jacks) was usually a good predictor of the number of adult coho returning the following year, indicating that the adult run size was determined largely during the first few months in the ocean. Moreover, a strong relationship was found between the intensity of coastal upwelling during the first summer in the ocean and subsequent survival (Gunsolus 1978; Scarnecchia 1981; Nickelson 1986),

but this relationship broke down after 1981 (see Pearcy 1992, 1996). Recent studies are consistent with a critical period in early ocean life and indicate survival rates of several species of salmon are related to marine conditions experienced by juvenile salmon just prior to or during out-migration (e.g., Mueter et al. 2005). A suite of environmental factors have been correlated with the ocean survival of Oregon coho salmon. These include conditions during the winter before ocean entry, the period of ocean entry, and the winter after ocean entry (e.g., Koslow et al. 2002; Logerwell et al. 2003). Beamish and Mahnken (2001) posited that early marine growth and attainment of a critical size by the end of the first summer determines mortality during the first fall and winter in the ocean.

We conclude that mortality of salmon in the ocean generally decreases with age and that high rates of mortality often occur soon after ocean entrance but may also occur later in life before, during, or after their first winter in the ocean. During unusually poor ocean conditions, high rates of mortality may occur after the first summer in the ocean life as evidenced by several salmon populations during the 1982–1983 El Niño (Wooster and Fluharty 1985). Although mortality rates are known to be correlated with ocean conditions, the exact mechanisms are still basically unknown.

Carrying Capacity of the Ocean

“Carrying capacity is a measure of the biomass of a given population that can be supported by the ecosystem. It changes over time with the abundance of predators and resources. Resources are a function of productivity of prey populations and competition” (U.S. GLOBEC 1996). By this definition, processes that affect abundances, either through lower trophic levels and availability of food (bottom-up) or predation (top-down), as well as density-dependent factors, and both intra-

and interspecific competition, all affect the ocean carrying capacity for salmonids and their survival rates.

Unlimited carrying capacity of the ocean for salmon was an early paradigm and a stimulus for increased hatchery production. Several studies based on the standing stocks of zooplankton supported this theory. LeBrasseur (1972) estimated that salmon ate only about 10% of the annual net production, directly or indirectly, of large copepods. Sanger (1972) estimated that salmon consume only about 3.4% of the zooplankton production in the North Pacific. Similarly, Favorite and Laevastu (1979) postulated that salmon consumed only a small fraction of the available zooplankton and that the ocean could support more salmon at that time. Walters et al. (1978) also concluded that ocean food limitation was unlikely for juvenile salmon unless only a small fraction of the total zooplankton is available. These estimates assumed that salmon were relatively unselective feeders on zooplankton and did not consider seasonality of the food supply. We now know that chum salmon often specialize on gelatinous zooplankton (Welch and Parsons 1993; Welch 1997), and maturing salmon in the open ocean often select micronekton as prey, including gonatid squids (LeBrasseur 1966; Percy et al. 1988; Kaeriyama et al. 2004). In coastal waters off Oregon, juvenile salmonids consume only a small portion of the total available prey and do not appear to be food limited during most years (Peterson et al. 1982; Brodeur et al. 1992). Fisher and Percy (1988) also found little evidence that chronic food shortages affected the growth of surviving juvenile coho salmon, except during El Niño years of very low productivity.

Perry et al. (1998) reviewed bottom-up and top-down processes regulating epipelagic fish production in the subarctic Pacific. They noted evidence for top-down control of zooplankton by salmon but concluded that

production of fishes is “likely controlled by bottom-up (food web) processes rather than self-regulated by effects of fish abundance on their zooplankton prey...at least when considered over the entire life history and entire North Pacific.” This conclusion finds some support in the large-scale and concurrent increases in both zooplankton and fish biomass in the North Pacific (e.g., Beamish and Bouillon 1993; Brodeur and Ware 1992) and recently developed estimates of the relationship between primary production and fish catches (Ware and Thomson 2005). Sugimoto and Tadokoro (1997) also thought that bottom-up processes were most important on decadal and longer time scales, but that top-down control may affect zooplankton dynamics on shorter time scales.

Some studies clearly document top-down control of salmon survival in the ocean (Fresh 1996; Beamish et al. 2003; Brodeur et al. 2003). Predation by coho salmon on pink and chum fry and size-selective mortality has been reported by Parker (1971) and Hargreaves and LeBrasseur (1985). Common murre *Uria aalge* prey on coho juveniles (Bayer 1986) as do spiny dogfish *Squalus acanthias* (Beamish et al. 1992). Top-down effects have been documented in other ecosystems—in California kelp forests (Halpern et al. 2006) and by the removal of a top predator, the Atlantic cod *Gadus morhua* that produced cascading effects through lower trophic levels (Worm and Myers 2003; Frank et al. 2005).

Although coastal upwelling enhances primary and secondary production, it also affects the distribution and abundance of other animals and salmon predators. Fisher and Percy (1988) and Percy (1992) hypothesized that during periods of weak coastal upwelling and low productivity, coho smolts off Oregon and Washington are confined to a narrow zone of upwelled waters close to shore where both competitors and predators

are concentrated and where growth may be slow and predation intense. Moreover, during warm years, there is an influx of predators from the south that probably increases predation mortality. On the other hand, during years of strong upwelling, a broad region of cool, turbid water exists where forage animals such as northern anchovy *Engraulis mordax*, smelts (Osmeridae), and herring *Clupea pallasii* are more common and provide a buffer to predation on juvenile salmon, which are dispersed over a large area and less susceptible to predation. This interaction is supported by Holtby et al.'s (1990) research that showed that marine survival and early ocean growth of juvenile coho salmon was positively related to the intensity of coastal upwelling and that the survival of juvenile coho salmon was positively related to the abundances of juvenile herring of about the same size, suggesting that herring provide a buffer to predation. The interaction between bottom-up and top-down processes is again clearly illustrated for juvenile pink salmon in Prince William Sound where predation rates are linked to food availability and prey switching (Willette et al. 2001). In sum, both top-down and bottom-up processes are undoubtedly important. They are not mutually exclusive and likely interact in complex ways in the ocean. How the ecosystems react to the changes in the relative strengths of these processes in response to changes in external forcing and how these processes affect salmon productivity are all relevant issues that will affect management and conservation of salmon resources in the future.

Density Dependence

Gilbert appears to have been the first to consider the possibility of density effects. As early as 1914, he observed that the length and weight of sockeye salmon returning in the dominant cycle year of 1913 were smaller than those returning in 1912 or 1914 and that

the cause of the variable growth might be due to "more rigorous competition among the school" (Gilbert 1914). He also looked at the number of cases of salmon packed per year versus the average weight of sockeye salmon from the Fraser River but found no positive trend, no doubt in part because of the 4-year cycle of abundance in the Fraser River.

Larkin (1975) questioned whether there were density-dependent interactions among different stocks of salmon at sea. He concluded that good evidence was lacking since fluctuations in both American and Asian regions were usually in phase, indicating large-scale environmental influences rather than out-of-phase competitive interactions. Later, Beamish and Bouillon (1993) summarized the total landings of pink, chum, and sockeye salmon from America and Asia and found similar long-term trends that suggested that climate and ocean conditions are important in basin-wide salmon production, possibly overriding any obvious density-related signal.

Contrary to the earlier paradigm of unlimited ocean carrying capacity, many researchers have found evidence for competition among maturing fish in the high seas. Rogers (1980) related the annual mean weight of returning sockeye salmon to run size for Bristol Bay sockeye salmon and found an inverse relationship (Figure 3). Peterman (1984) found inverse relationships between reconstructed total abundances of sockeye salmon in the Gulf of Alaska and the mean length of British Columbia sockeye salmon, also suggesting density-dependence. McKinnell (1995) showed that the negative relationship between mean length of British Columbia sockeye salmon and Bristol Bay sockeye salmon abundance held only for age-classes that had spent 3 years at sea, presumably sharing a common feeding area. Peterman (1987) also noted that the mean adult size of returning Fraser River pink salmon was inversely related to the ratio of abundance of pink salmon to

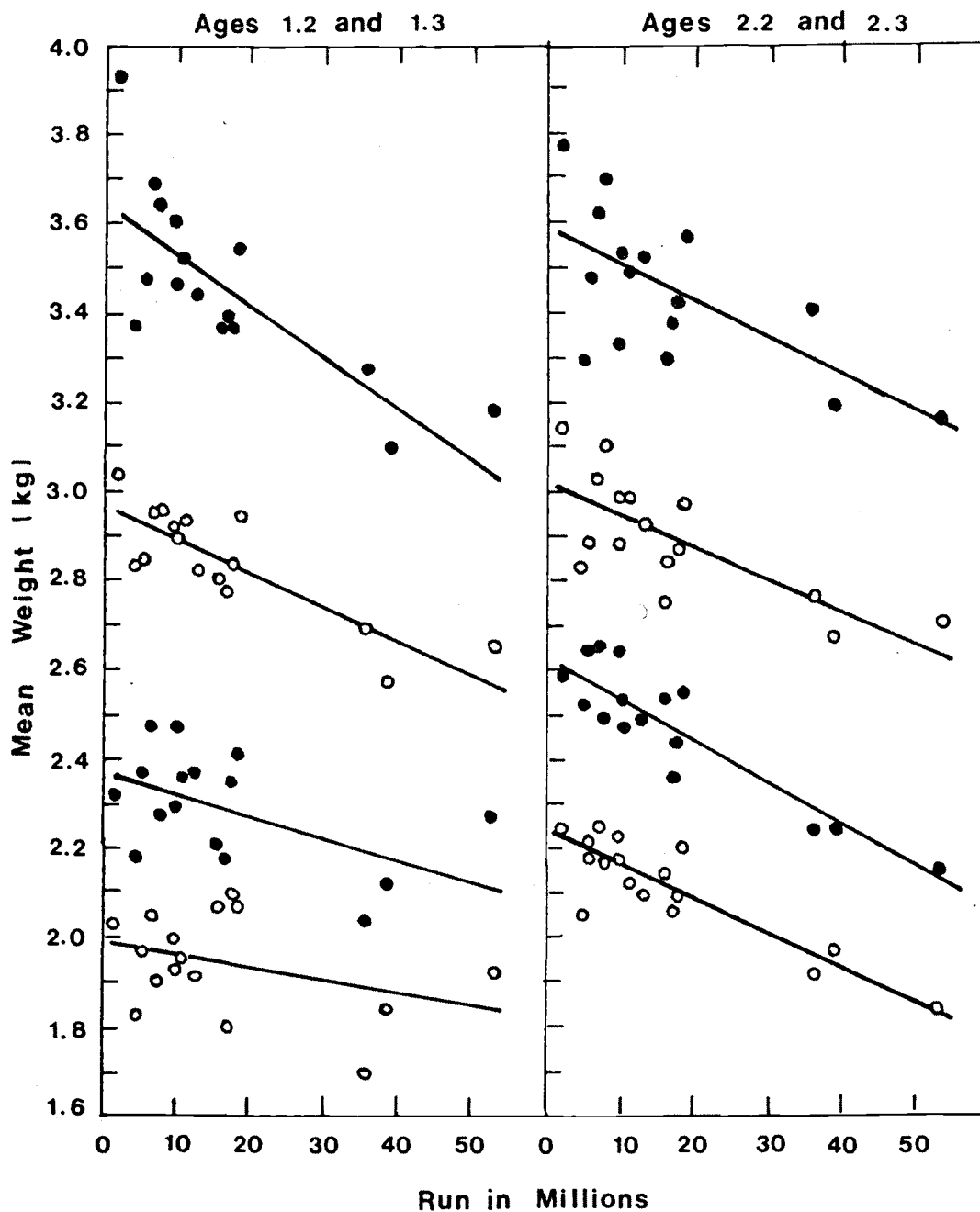


Figure 3. Mean weights of sockeye salmon in the Bristol Bay runs as a function of the number of fish in the run (from Rogers 1980). Females are indicated by open circles, males by solid dots.

zooplankton at Ocean Station "P," again suggesting competition. Pink salmon are usually smaller during years of high abundance than in years of low abundance (Davidson and Vaughan 1941; Blackburn and Tasaka 1984;

Peterman 1984, 1987), a likely result of intraspecific competition for food.

Others have reported evidence for interspecific interactions among salmon in the ocean. Tadokoro et al. (1996) observed that

the diet of chum salmon depended on the abundance of pink salmon. When pink salmon abundance was high, macrozooplankton biomass can be reduced by intense feeding by pink salmon (Shiomoto et al. 1997). Both sockeye salmon growth at sea and abundance declined significantly following years of high Asian pink salmon abundance (Ruggerone et al. 2003), with pink salmon influencing the abundance, species, and energetic content of the prey of the other salmon species (Aydin et al. 2000; Ruggerone and Nielsen 2004). These studies clearly indicate how interspecific competition among species of salmonids for food can influence the population dynamics among species and suggest that pink salmon can exert top-down control on their prey.

Declines in the average size or size-at-age of maturing salmon at sea is more recent evidence for density-dependence (Ishida et al. 1993; Bigler et al. 1996; Helle and Hoffman 1998; Pyper and Peterman 1999). These declines were associated with increased total abundance of salmon during the 1980s and 1990s in the subarctic Pacific, including large increases in hatchery production on both sides of the Pacific (Beamish et al. 1997). This again suggests that density-dependence in the open ocean could be an important consideration in the enhancement and management of salmon stocks. Abundance during the 1990s may have approached the carrying capacity of the ocean to produce salmon. Several alternative hypotheses have been proposed to explain these changes, however, including changes in ocean productivity and selection of larger fish by fishermen resulting in genetic changes (Ricker 1981; Quinn 2005).

Issues concerning competition between wild and hatchery salmon arose during the late 20th century. Gunsolus (1978) noted that during periods of weak upwelling along the Oregon coast, releasing more hatchery fish did not result in greater production. However,

neither Emlen et al. (1990) nor Nickelson (1986) found evidence for interactions between wild and hatchery coho from Oregon that affected survival. Cooney and Brodeur (1998) and Beamish et al. (1997) questioned whether massive production of hatchery salmon could increase returns, especially during periods of low ocean productivity. Peterman (1991) felt that because of density-dependent growth and survival, in addition to potential responses by predators, increased production of more smolts by hatcheries may have limited benefits. In the Columbia River, Levin et al. (2001) showed that during years of poor upwelling, greater releases of hatchery Chinook corresponded with years of higher mortality of wild Chinook salmon. The billions of hatchery-reared salmon released into the North Pacific Ocean along with the depressed runs of endangered or threatened stocks raise concerns about hatchery-wild stock interactions in the ocean (Beamish et al. 1997; Heard 1998). Replacement of wild salmon with hatchery-reared salmon has been observed in some regions of the Pacific Ocean in recent years (e.g., Sweeting et al. 2003). This practice is a major management issue that needs broad ecological assessment, especially in view of climate shifts in ocean productivity.

Ocean Variability

As in most other environments, ocean ecosystems fluctuate on various temporal and spatial scales that ultimately lead to variations in the productivity of Pacific salmon. El Niños have affected coastal fisheries off South America for centuries (Quinn et al. 1987), but only recently have their full effects in the Pacific Northwest been described in detail (Sette and Isaacs 1960; Wooster and Fluharty 1985; Chavez et al. 2002). The warming in the California Current system during the 1958 El Niño was associated with a significantly higher proportion of Fraser River sockeye

migrating north around Vancouver Island and later arrival at the Fraser River (Royal and Tully 1961) and the record delay of the run of Columbia River fall Chinook (Van Hyning 1973). The 1982–1983 El Niño and the climate regime shift of 1976–1977 were historic events that woke up many salmon biologists about the critical importance of the ocean conditions to survival and run size of Pacific salmon (Pearcy et al. 1985; Wooster and Fluharty 1985; Johnson 1988).

One of the first scientists to recognize what we might now call production regimes was Tanaka (1962). He fit a series of Ricker curves to different sequences of years to illustrate how the years of variable productivity appeared to occur in stanzas. Canadian scientists argued against this interpretation (Anonymous 1962). Given the absence of evidence to the contrary, Ricker (1958) assumed that the variability of points around his stock-recruit curves was the result of stochastic interannual variability rather than persistent production regimes, an idea that persisted at least into the 1990s.

Low-frequency fluctuations in average levels of salmon abundance are known from long-term records (e.g., Chatters et al. 1995; Finney et al. 2000). Variations in abundance during the past century have been linked to large-scale atmosphere–ocean interactions over the North Pacific. The Pacific Decadal Oscillation is an index of the dominant pattern of sea surface temperature variability in the North Pacific Ocean (Mantua et al. 1997). It shows that regime shifts (i.e., periods of abrupt change) occurred in 1925, 1947, 1977, 1989, and 1998 (Hare and Mantua 2000). These climate regimes tend to be correlated with periods of change in salmon catches in the North Pacific and often show inverse production trends in Alaska and the Pacific Northwest (Pearcy 1992, 1996; Beamish and Bouillon 1993; Francis and Hare 1994; Mantua et al. 1997; Hare et al. 1999; Helle et

al. 2000). Similar patterns of low-frequency variability are also apparent in the standing stocks of zooplankton in the California Current (Roemmich and McGowan 1995) and in the subarctic Pacific (Brodeur and Ware 1992). They also appear in variations in freshwater conditions that affect salmonid production (Lawson et al. 2004) and in the dramatic changes in the species abundances of pelagic nekton off Oregon and Washington (Emmett and Brodeur 2000). Regime changes in ocean and freshwater productivity are important considerations in management of salmonid resources. These changes also need to be considered when evaluating our efforts to improve habitat conditions for rearing and spawning fish.

Challenges for the Future

Although we now know that the carrying capacity of the ocean for salmon varies over a range of time and space scales, from interannual variability in seasonal upwelling to El Niño–Southern Oscillation frequencies to interdecadal and millennial events, we are still uncertain about how these external forcings affect food web structure, community dynamics, and salmon ecology. How do varying conditions affect the relative importance of interactions among trophic levels, bottom-up and top-down processes, and the rates of predation, growth, and survival of salmon? What stages in the life history of salmon have rapid and variable changes in survival that affect year-class success? Where do these interactions occur in the ocean? Are all species or stocks of salmon affected by similar processes? After more than 100 years of study, there is no life table for any species of Pacific salmon and rarely are we able to distinguish freshwater and marine mortality. Interactions between freshwater, estuarine, and marine phases need to be evaluated and measured. Furthermore, what are the effects and roles of hatchery salmon in this variable ocean?

Technology will be important in answering some of these questions. Tagging with coded-wire tags, external macrotags, and archival tags has already provided important information, but the information typically relies on a fishery to provide recaptures. New types of tags, smart tags, are providing exciting new information, and their contributions to our knowledge will increase in the future. Archival or data storage tags that record temperature, depth, swim speed, and geolocation are available (Boehlert 1997). Some of these have revealed surprising information on diel changes in the thermal environment and vertical distribution of salmon (Walker et al. 2000). Acoustic tagging studies hope to provide new data on early ocean survival and migrations (Welch et al. 2004). And genetic data will be important to identify the stock compositions, distributions, and migrations (e.g., Seeb et al. 2004; Beacham et al. 2005). Satellites and remote sensors will continue to provide valuable information on the structure and dynamics of the ocean that can be related via geographical information systems to distributions and migrations of salmon. New and improved modeling and statistical approaches will also become important with our increasing ability to collect these new and more extensive data on salmonid behavior and their dynamic environments. All of these will enhance our knowledge of the environments and ecology of salmon at sea and improve our ability to manage and conserve stocks in the future.

Climate change and its effects on Pacific salmon is a big challenge for the future (e.g., Beauprand and Reid 2003; Mote et al. 2003; Payne et al. 2004). Understanding the impacts of climate change on the physical and biological environments, in both freshwater and the ocean, how they interact, and how we can ameliorate these effects, will be vital to the productivity of many populations in the future.

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