

A History of the Research on the Early Marine Life of Pacific Salmon Off Canada's Pacific Coast

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Abstract: We review studies of the early ocean period of salmon life history conducted in the coastal areas off Canada's West Coast. The role of the ocean in the dynamics of salmon populations has received considerably less study than their life cycle in fresh water, even though Pacific salmon in general spend more time in the ocean than in fresh water and the survivals in the ocean are extremely low and variable. Feeding, growth and distribution studies from the late 1950s until the present have contributed to an improved appreciation of biology of salmon during the marine phase of their life history. However, conclusions about the processes that cause the high and variable mortality in the ocean remain speculative. How fishing impacts interact with natural processes also remain to be clarified. Recent studies have demonstrated that ocean and climate conditions are important contributors to the total marine mortality of a number of species, and to the stock and recruitment relationship. We suggest that it is time to conduct the definitive studies that will identify the processes that regulate the survival of Pacific salmon throughout their entire life cycle. We propose that an international effort to study the early marine period is the way to change the current beliefs and speculations into explanations.

INTRODUCTION

Pacific salmon have been an integral part of the culture on Canada's west coast for thousands of years. We now know that abundances have always fluctuated naturally (Finney et al. 2000), but that in the past 100 years fishing and degradation in freshwater habitat have intervened in these natural changes. Commercial harvests of Pacific salmon began on Canada's west coast about 1870. As stocks declined, it became necessary to manage salmon abundance, and to do this more information was required about their life histories. The Dominion of Canada Government was alarmed by the uncontrolled salmon fishery and gave the Reverend George Taylor \$7,000 Canadian to build the Pacific Biological Station through to its completion in 1908. However, it was not until 1955 that scientists started their investigations of the early marine phase of Pacific salmon.

This is a report on the history of these investigations and their key findings. The purpose is to provide a complete as possible summary of the information available on the early sea life of salmon in British Columbia waters

as a reference and information source for researchers attempting to work out the complex ecological relationships during this life phase. The approach for this review has been to consider published results of studies that were carried out in the ocean or were analyzed using the data from such investigations. Studies on smolts or fry in fresh water are not included even if they evaluated the impact of the ocean environment. Studies on the optimal size and time of release of juvenile hatchery salmon, for example, are referenced or not included. We constrained our report to the conclusions of the investigators and have not re-analyzed data or provided alternative interpretations. We have added commentary when it was necessary to put studies into historical perspective. We record the research results in chronological order and we provide a summary by topic. This leads to an apparent overlap of reports, but it also facilitates the review of material by readers who do not want to read through the entire report. We conclude with a list of questions that should be addressed and recommendations that relate to the expected impacts of ocean and freshwater habitat changes resulting from greenhouse gas accumulations.

CHRONOLOGICAL SUMMARY OF RESEARCH

Virtually all of the early work at the Pacific Biological Station on salmon focussed on propagation methods, migration, elucidation of life cycles, egg production, sex ratios, and freshwater mortality. Most research in the 1930s and 1940s was by R.E. Foerster on sockeye salmon (*Oncorhynchus nerka*), with some work on pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) by A.L. Pritchard and W.M. Cameron. The freshwater phase of the life history was given particular attention at a number of field stations along the Pacific coast, because it was believed that the factors most limiting to production were spawning and the development of the young alevin and fry in rivers, streams and lakes. This was consistent with the broadly accepted view in fisheries ecology that recruitment was determined in the egg and larval stages (Ricker 1954).

In 1953, Canada, Japan and the United States ratified a treaty, which established the International North Pacific Fisheries Commission (INPFC). Determining the distribution of Canadian salmon on the high seas became a priority. Scientists at the Pacific Biological Station initiated research in 1955 to determine where salmon originating in various rivers in Canada rear in the North Pacific Ocean. The active participation of Canada in the work of the INPFC brought about the funds and personnel to begin the study of the ocean phase of Pacific salmon.

The first research on juvenile salmon in the ocean (Table 1) occurred in 1955 by Ferris Neave who wrote, "In 1955 for the first time in the history of the Pacific salmon investigation, a sustained effort was made to find and catch young fish during the first few months of their life in the ocean." The objective of this pioneering program was to improve the prediction of adult returns. The main efforts were to find, catch, identify and tag salmon. Field operations were carried out from early June to early September in two study areas to facilitate comparisons: one in the north at Masset Inlet, Chatham Sound and adjacent waters (to catch fish from Skeena system) (Fig. 1) and one in the south in Queen Charlotte Strait, where concentrations of juvenile fish emerging from the northern exit of the Strait of Georgia were expected. A variety of gear types was used, including purse seines, beach seines, small-mesh gillnets, tow nets and mid-water trawls. The small juvenile salmon were examined for stomach contents, and lengths and weights were recorded. In addition, plankton samples were taken, and surface temperatures were determined. All five species were studied, but emphasis was on sockeye, pink and chum salmon. This fieldwork appears to have lasted for two years, although members of this research team carried out studies on a continuing

basis. It was apparently very easy to find and catch young salmon during the first two months of life in the ocean, a period when they frequented the shallow inshore waters in large concentrations. J. I. Manzer and G.T. Taylor reported on the results in an annual report, focussing on size, sex, food, distribution, abundance and movement of the young salmon. There was no indication that the studies could improve the prediction of returns, but the behaviour of young salmon when they first entered the ocean was documented. Juveniles were seen to move from near-shore areas to open water by late July to mid-August. An interesting observation was that sockeye were still moderately abundant in Queen Charlotte Strait in September. The diet studies indicated that the five species differed in feeding habits, with juvenile pink, chum and sockeye salmon feeding primarily on invertebrates, whereas juvenile coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon were more piscivorous. When chum and pink salmon occurred in the same locations, chum were found to be more catholic in their diet. Over 4,000 juveniles were tagged in Chatham Sound and Johnstone Strait using spaghetti tags, but very low numbers were recovered. A concurrent study of marine distributions of young salmon by LeBrasseur and Parker (1964) showed that seaward migrations of young salmon appeared to be related more to sea surface water temperature than to high concentrations of zooplankton or to any particular salinity levels.

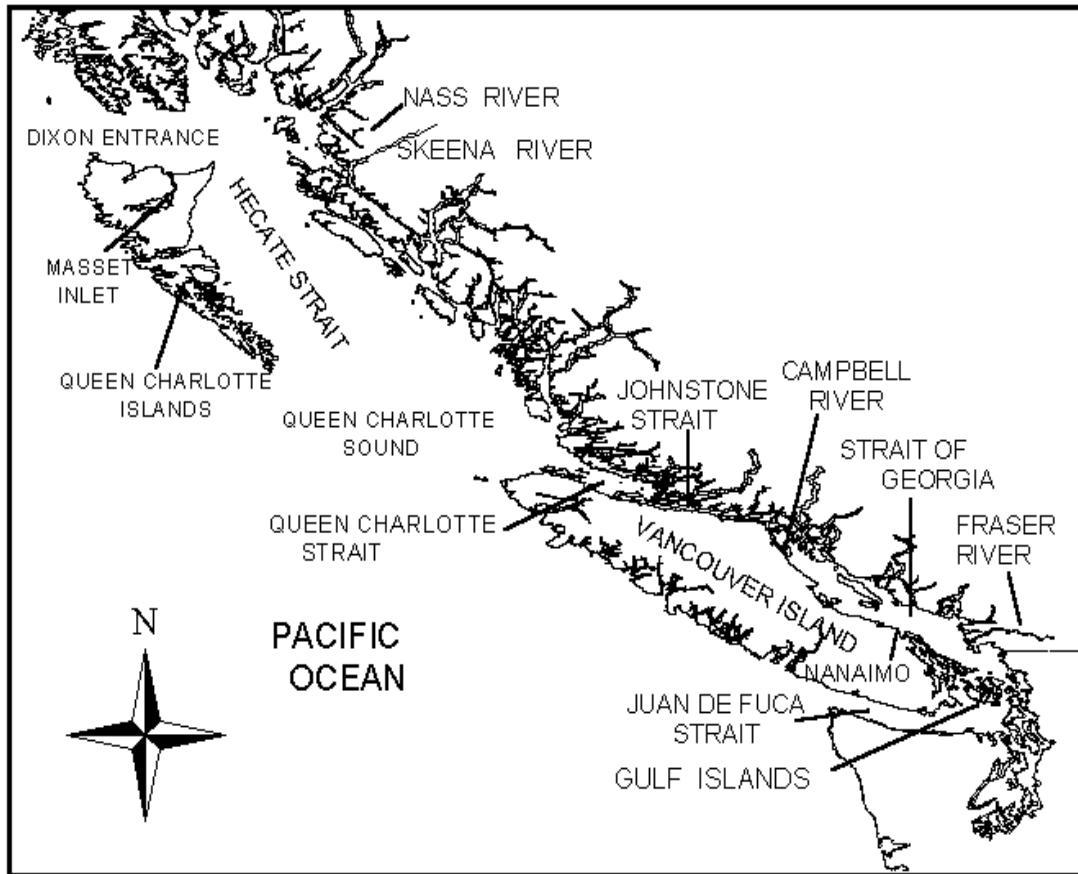
The period of the late 1950s appears to have been a time of broadening interest in the early oceanic phase of the life history of salmon. Steelhead trout (*Oncorhynchus mykiss*), however, which were later moved from the genus *Salmo* to *Oncorhynchus*, were not a priority. Early investigators were intrigued by the odd and even year life histories of pink salmon (Groot and Margolis 1991), and thus pink salmon received much more attention than in recent years. The general directive at the Pacific Biological Station was to examine the relationship between the many varying environmental factors and the survival of young salmon. A conclusion by Godfrey (1958) that the early marine environment encountered by Fraser River pink salmon was a determinant of adult abundance was one of the early indications that the ocean state played a role in the production of Pacific salmon. This may appear self-evident now, but the common view at the time was that density-related processes in fresh water determined the abundance of returning stocks. A prophetic, C.D. McAllister stated in 1960 that "it seems not impossible that winters with very sparse zooplankton, heavy cloud cover and unusual turbidity could be critical for the survival of young salmon" (McAllister 1961).

In the 1960s, the search for methods to forecast adult returns continued. There was a strong belief

Table 1. Major investigations of juvenile Pacific salmon

Investigator	Date of work	Type of Study
F. Neave J.I. Manzer G.T. Taylor R.J. LeBrasseur	1955–1957	Life history, migration, diet
R.R. Parker	1960–1971	Diet, early marine mortality, predation, early marine growth
J.I. Manzer M.P. Shepard	1953–1965	Diet, distribution and abundance
A.W. Argue R.W. Armstrong B. Hillaby D.E. Marshall	1963–1976	Migration, diet, distribution, abundance, growth
H. Goldfrey	1968–1974	Distribution and abundance
E.A.R. Ball	1974	Distribution and abundance
A.C. Phillips	1963–1978	Diet, distribution and abundance, early marine growth
W.E. Barraclough	1963–1978	Diet, distribution and abundance, early marine growth
J.D. Fulton	1967–1978	Diet
D.G. Robinson	1968–1976	Diet
J. Sibert	1972–1977	Diet
R.J. LeBrasseur	1964	Early marine growth
R.A.H. Sparrow	1967	Distribution and abundance
M.C. Healey J.F.T. Morris B.J. Waddell B. Hungar M. Abrahams	1974–1988	Distribution and abundance, diet, early marine growth, size selective mortality, (Nanaimo River estuary, Barkley Sound and Hecate Strait)
C.D. Levings C.D. McAllister M.S. Kotyk T.J. Brown	1970–2000	Hatchery vs. wild interactions, diet, distribution and abundance (Campbell River Estuary)
W.E. Dunford	1975	Distribution and abundance
W.E. Ricker	1976	Size selective mortality
D.A. Levy	1979–1985	Distribution and abundance, diet
T.J. Northcote	1979–1985	Distribution and abundance, diet
J-G.G. Godin	1980–1981	Diet
C. Groot	Barkley Sound (MASS, 1987–1991)	Migration
K. Cooke	Barkley Sound (MASS, 1987–1991)	Migration
B. Hargreaves B. Hungar B. Patten T. Carter	1982–1991	Predation, size selective mortality
K. Hyatt G.J. Steer P. Rankin I. Miki R. Traber D. Kolody	Barkley Sound (MASS, 1987–1991)	Early marine mortality, diet
R.J. Beamish C.M. Neville R. Sweeting J. King M. Folkes	1976–2000	Diet, early marine mortality, distribution and abundance, predation (Strait of Georgia and West Coast Vancouver Island)
C.W. Haegele	1990–1994	Diet
D.W. Welch	1980–2000	Migration, distribution and abundance, diet (High Seas)

Fig. 1. Major study areas.



that Pacific salmon abundance could be rebuilt to historic levels, but the factors limiting salmon were still “completely unknown”, according to R.R. Parker. In 1960–61, a field program was initiated at the Port John field station involving marking of half of the seaward migrating pink and chum fry from Hooknose Creek and observation of their movement, growth and survival after they entered salt water. This work was the start of a major study carried out over a 3 year period by R.R. Parker during which a wealth of data was produced as well as some classic publications. The main hypothesis being tested at this time was that annual survival in coastal waters determined, to a large degree, the numerical strength of the returning adult salmon populations because mortality rates in the high sea areas appeared to be low and relatively constant.

Separation of the natural mortality rates of Bella Coola pink salmon into two subsequent time periods was achieved by two-stage markings: tagging at age zero and at 40 days sea life. The two types of marking used were removal of the adipose and right ventral fins, and removal of the adipose and left ventral fins. Recovery was at the time of adult return. Samples were also retained for stomach analysis and the

usual measurement of size. It was observed that small schools of pink salmon from individual rivers formed larger aggregations close to shore. These aggregations remained inshore until June, then broke up into smaller schools in open areas of Queen Charlotte Sound. Pink and chum were captured together, but there were major differences in the diets of the two species. The composition of their food indicated that they were feeding selectively. Thus, although they shared a common habitat, the two species used it differently (a concept long ago reported for finches sharing arboreal habitats on the Galapagos Islands).

Parker (1965) found that during the first 40 days, the average daily loss to the pink salmon population was 2–4%. However, the average daily loss for the remaining period at sea (410 days) was 0.4–0.8%. Of the three brood years studied, 55–77% of pink salmon died over the first 40 days, and 78–94% of those remaining died over the remaining 410 days. However, he also found that the marine mortality was quite variable among the three years. He reported that the variability in coastal and ocean mortality was 36–38% of the average for the three brood years. The major predator was juvenile coho and it appeared that coho preferred to eat pink salmon compared to chum

salmon. Parker believed that squid could also be a predator, but he ruled out bird predation as a significant source of mortality.

This work became a standard reference for investigators proposing that brood year strength is determined very early after entry into the ocean. However, the significance of the large variability over only three years did not appear to influence subsequent thinking and management. In fact, R.R. Parker (1965) wrote that it was unwise to consider any portion of natural mortality in the ocean as a constant. He found that it was difficult to forecast returns using counts made in freshwater, and concluded that variation in marine survival "obscures the parental to filial generation relationships that are currently sought for in stock and recruitment curves".

In the late 1960s, there was a new emphasis on the trophodynamic relationships of salmon with other organisms. Research focussed on diets in relation to the changing distributions of juvenile salmon as they moved into the open water areas later in the summer. Studies were conducted by W.E. Barraclough, J.D. Fulton, D.G. Robinson, A.C. Phillips, and T.R. Parsons. Barraclough and Phillips (1978) reported on the early marine growth of juvenile salmon in the southern Strait of Georgia and Saanich Inlet as part of a larger study of production in the Fraser River plume (Parsons et al. 1969a, b). The project provided an opportunity to examine the extent to which the early marine life of various species of fish was dependent upon concentrations of zooplankton.

Understanding movements of immature coho and chinook salmon that were rearing at various locations in the Strait of Georgia and Johnstone Strait was the focus in the 1960s and early 1970s of a number of tagging studies (disc, Carlin and Floy spaghetti-anchor tags) conducted by A.W. Argue and D.E. Marshall (Argue and Heizer 1971; Heizer and Argue 1972; Argue and Heizer 1974). Of particular interest were movements of coho from winter rearing areas (Argue and Heizer 1974). Purse seining was the principal capture method and first ocean-year coho the main target species, although on occasion large numbers of juvenile pink salmon were caught and tagged during winter and early spring months (Heizer and Argue 1972).

The late 1960s and early 1970s was a somewhat unsettled period for fisheries research on Canada's west coast, and it appears to have influenced the kind of early marine research that was conducted. In the late 1960s, the management of fisheries research changed from an independent board to a government-run department. At the same time, a 'year class' of senior scientists was either retiring or leaving the Pacific Biological Station. There was an ominous and unexplained decline in Pacific salmon catch at this time, and this appeared to change the priority for

early marine studies from forecasting to understanding the productive capacity for young salmon in the coastal ecosystem. The preference for studying species also changed and coho and chinook salmon began to receive more attention. Chum salmon retained its priority, but pink and sockeye salmon were less studied. In particular, there was a strong emphasis on understanding the importance of estuaries as nursery areas for all species of salmon. There was interest in trying to use any improvement in understanding of the early marine period to increase salmon production. Areas for research included Alberni Inlet, Squamish River estuary, Nanaimo River estuary, Cowichan Bay, Saanich Inlet and the Strait of Georgia in general. In 1962, Ricker (1962) had calculated that it was possible to restore salmon abundance to levels of the late 1800s. These historic abundances were about double the numbers that existed at the time of his calculations.

The change in emphasis was characterized in the mid-1970s by the second Strait of Georgia program, which was never implemented as an integrated study. The objective was to provide fisheries information that was essential to management. Even though the full project was not supported, aspects of the plan were undertaken in the studies of M.C. Healey beginning in the 1970s. Healey tested the hypothesis that the movement of juvenile salmon out of the estuary or nearshore area was related to food availability. These studies were conducted in the Strait of Georgia and around the Nanaimo River estuary.

A growing recognition of ecological issues began in the 1970s arising from existing and proposed estuary developments (Hoos and Packman 1974). An Estuary Working Group under Environment Canada, led by Dr. Michael Waldichuk of the Pacific Environment Group, Fisheries and Marine Service, published a series of inventories of relevant bio-physical information, including information on juvenile salmon for British Columbia's major estuaries (e.g. Fraser River estuary, Hoos and Packman 1974; Cowichan-Chemainus River estuaries, Bell and Kallman 1976; Bella Coola River estuary, Leaney and Morris 1981). In 1975/1976 the Cowichan River estuary was the site of one of several focussed studies on distribution, abundance, residence times, growth and feeding of juvenile salmon (Argue et al. 1986) that arose from this enhanced concern for estuary habitat.

The dependence of juvenile salmon on estuaries was found to be species specific. An unexpected finding was that chinook fry used intermediate salinity estuarine waters as a nursery area (Healey 1980a, b). Prior to this finding it was believed that chinook fry that migrated seaward were unable to find nursery space in fresh water and were lost to the population. Young chinook salmon were unable to

make the transition to full sea water, however, and so were confined to estuarine waters of 20‰ or less until about 70 mm fork length. Chum salmon fry also made use of estuarine nursery habitats but, unlike chinook, chum were not restricted to the estuary and were able to use shallow marine nursery areas as well (Healey 1982c). Chum salmon remained well inshore when they first entered the ocean, and their diet in this early marine period was found to be associated with a detritus-based production. The residence of chum fry in the Nanaimo River estuary in particular was found to be associated with the abundance of their principal prey species, *Harpacticus uniremus*. Chum salmon left the estuary when this prey species declined sharply in abundance at the end of May. Thus young chum salmon were dependent on shallow marine habitats. The studies identified size selective mortality of chum, but it was only for a size range between 45 and 55 mm. This occurred at a time when 2–4 scale circuli were formed and at the time the juvenile chum salmon moved from the inshore area to an open water habitat. Like chum salmon, pink salmon made use of shallow marine nursery habitats for a few weeks following downstream migration. Unlike chum, however, pink salmon did not spend more than a day or two in estuarine habitats before moving to marine waters. Both pink and chum salmon left the near shore areas despite adequate feeding conditions, although as noted earlier, the departure of chum from the Nanaimo River estuary was associated with the decline in their main prey species. Thus, there was little evidence to relate the migration into open areas with decreasing food availability. Healey (1982c) suggested that the absence of a relationship may have been an indication that food resources were adequate in most habitats to allow for successful foraging, and that distribution may be controlled by another need such as avoiding predators or taking advantage of relatively warm nearshore temperatures to maximize growth efficiency. However, he did find that the emigration of pink and chum juveniles out of the Strait of Georgia and the regional distributions of chum, coho and chinook salmon juveniles in late summer were correlated with stomach contents. He assumed that food resources were low enough that the fish had to seek out the best feeding areas to satisfy their food requirements. For pink, chum and sockeye salmon, which are largely planktivorous, this meant that they had to leave the Strait of Georgia, whereas coho and chinook salmon, which are largely piscivorous, were able to satisfy their food requirements within the Strait. Healey (1980b) further suggested that the indication that food resources may be limiting in late summer should warn against the release of large numbers of hatchery juveniles, as this could overload the habitat.

Healey (1980b) and his co-workers also found

that the major concentrations of juvenile pink and sockeye and possibly chum salmon, occurred in the Gulf Islands across the Strait of Georgia from the Fraser River (Fig. 1). This small area, they concluded, had to support the bulk of the juvenile salmon that entered the Strait of Georgia. About 25 years later, it would be shown in the studies of Beamish and his colleagues that this area was no longer the main rearing area in the Strait of Georgia. In fact, the central area of the Strait of Georgia that Healey found to contain relatively low abundances of salmon would be shown to contain large numbers of juvenile chum, pink, coho and chinook salmon through to the fall of the first marine year (Beamish et al. 2000a). Healey and his colleagues, in the late 1970s and 1980s, provided much of the first information on the early marine period of juvenile salmon off the west coast of Canada. The results of their work have made a significant contribution to our understanding of the early marine life history.

The area of Masset Inlet was of concern during 1970–1980 since there appeared to be a significant decline in pink salmon returns. Masset Inlet was thought to be the primary rearing area for juvenile pink salmon from the Yakoun River. Thus, there were concerns that this decline may have been due to increased mortality during the early sea life period. A four year study of the early sea life of juvenile pink and chum salmon was started in Masset Inlet in 1982 by B. Hargreaves and R.J. LeBrasseur. Juvenile salmon and potential predators were collected with a variety of sampling gear including beach seines, two boat trawls, fish traps, and a purse seine. Hargreaves and LeBrasseur (1985) examined stomach contents of 15 potential predators, and found salmon remains in coho salmon, cutthroat trout (*S. clarki clarki*), silver-spotted sculpin (*Blepsias cirrhosus*), buffalo sculpin (*Enophrys bison*), whitespotted greenling (*Hexagrammos stelleri*), Dolly Varden (*Salvelinus malma*), tidepool sculpin (*Oligocottus maculosus*), great sculpin (*Myoxocephalus polyacanthocephalus*) and possibly in Pacific staghorn sculpin (*Leptocottus armatus*). Although these potential predators were examined, they were not able to determine the cause of the decline in pink salmon numbers and the data were not analysed. Using a number of marine enclosure experiments, Hargreaves and LeBrasseur (1985) showed that coho salmon preferred pink salmon as prey even when small chum were available, but these net pen studies provided conflicting evidence of size dependent predation and even preference for chum rather than pink salmon in some situations. A consistent conclusion was that coho are an important potential predator of pink salmon juveniles and in some cases of chum salmon.

A difficulty with the early marine studies of salmon was that the gear available to catch salmon

could not be fished in all kinds of weather and in all areas. The reliance on purse seines with small mesh bunts, restricted sampling to areas where currents, including tides, were not excessive and to seas that were unusually calm. A technical improvement in gear could greatly affect the sampling ability. Purse seining and beach seining were effective methods of catching juvenile salmon close to shore, but sampling in the areas deeper than about 30 m would benefit from the development of new gear. A fisherman (Norm Sigmund) and two scientists (F. Bernard and B. Hargreaves) designed twin beam trawls that could fish the surface waters down to 10 m. The trawls were towed on either side of the *W.E. Ricker* at about 3 knots. This was a much-improved method of sampling compared to purse seining or the use of small trawls. The specifications for the gear, however, were not published.

The first major scientific survey using the new Bernard-Sigmund beam trawls on the *W.E. Ricker* was successfully completed between 23 July and 10 August 1990 by Hargreaves. These trawls were used to survey the distribution and abundance of juvenile salmon along the entire west coast of Vancouver Island from Juan de Fuca Strait to Cape Scott. A total of 329 trawl sets was completed over a 16 day period, providing much greater detail regarding the distribution and biology of juvenile salmon and other pelagic species than had previously been possible. The catches included a total of over 6,000 juvenile salmon, 1,100 juvenile sablefish (*Anoplopoma fimbria*) and 61,000 juvenile herring (*Clupea harengus pallasii*). The observations of distribution and abundance of the juvenile salmon showed a very different pattern than previously reported. Juvenile salmon were distributed evenly across the continental shelf and farther seaward to distances of at least 70 km offshore. This observation differed from the conventional wisdom, based on purse seine data collected during the 1950s to 1970s, that most juvenile salmon along the coast of Washington and British Columbia migrated within 15–20 km of the shore. Studies by scientists from the United States, and by Healey, also showed that large numbers of juvenile salmon were caught 50–70 km offshore. There was no indication that the nearshore Vancouver Island Coastal Current acted as either a conduit or as a cross-shelf barrier. A variety of potential predators of juvenile salmon was collected including various rockfish, Pacific hake (*Merluccius productus*), spiny dogfish (*Squalus acanthias*), blue shark (*Prionace glauca*) and chub mackerel (*Scomber japonicus*). Several specimens of black rockfish (*Sebastes melanops*) had juvenile salmon in their stomachs. A survey of the abundance and distribution of juvenile salmon and other pelagic species was also carried out between 15 June and 4 July 1992, off the west coast of Vancouver Island, in

which 480 trawl tows were completed and 5,418 juvenile salmon were caught. In 1992, all juvenile salmon were concentrated close to shore and very few were caught between 30–55 km offshore. The El Niño conditions that occurred along the North American coast in 1991–1992 may have strongly affected the distribution and abundance of juvenile salmon and many other fish species. There were large changes in ocean conditions including a 1.5–2.0°C increase in average sea surface temperature along the southwest coast of Vancouver Island. The abundance, distribution, migration routes and migration timing of all salmon species and other pelagic fish species differed significantly from 1991 to 1992. The high influx of mackerel seen in 1992 was, no doubt, the result of the warm water conditions in 1992. The results of three beam trawl surveys in 1990, 1991 and 1992 clearly indicated that there were large interannual variations in the abundance, distribution, migration routes and migration timing of the various species of salmon.

The beam trawl was eventually replaced by a rope trawl, because it was found that sampling only the surface 10 m did not effectively sample the populations of chinook and coho, as juveniles of these species occupied a greater depth range than chum, sockeye or pink salmon. Comparative fishing of the beam trawl and rope trawls in the Strait of Georgia in 1996 by R.J. Beamish (Beamish unpublished data) showed that the rope trawls were a more reliable method of sampling a population because they could be towed faster, at 5 knots, and could catch all sizes of salmon. The beam trawl was restricted to the surface and could not be towed fast enough to catch the larger salmon. Also, the rope trawl could be towed at all depths and thus could be used to study predators (and other species interacting with salmon in the ecosystem).

In the 1980s, there was a series of studies on juvenile salmon in the early marine period. These included studies by R.J. Beamish and co-workers to examine the predators of young salmon (Beamish et al. 1992; Beamish and Neville 1995). It had recently been discovered that there were large abundances of Pacific hake in the Strait of Georgia. Hake was a known predator of herring, and it was proposed that it was also an important predator of juvenile salmon. The belief that the productivity of salmon could be improved by reducing the abundance of predators had persisted since the 1960s. Extensive studies of hake diets continued for over 20 years with only a few hake being found with salmon in their stomachs. An important predator of juvenile Pacific salmon was identified by Beamish and staff. They identified river lamprey (*Lampetra ayresi*) as a major predator of juvenile salmon (Beamish and Youson 1987). An important component of these predation studies was

what was not found. Extensive studies of the diets of various species resident in the Strait of Georgia including Pacific hake, did not identify predators of juvenile salmon as important as spiny dogfish, river lamprey, and Pacific lamprey (*L. tridentata*) (Beamish and Williams 1976; Beamish et al. 1992; Beamish and Neville 1995). This was important, because it was clear that the sources of predation mortality from other fish were not mysterious. Discussions relating to predation-based mortality could be specific.

During the spring through winter months of 1988 to 1991, surveys were conducted by R. Beamish to examine the incidence of juvenile salmon in the diets of dogfish (Beamish et al. 1992). The study area was immediately offshore of the river into which hatchery fish were released from Big Qualicum Hatchery. At the time, this hatchery produced the largest number of salmon of all those releasing salmon into the Strait of Georgia. The study included the identification of dogfish stomach contents and the estimation of dogfish abundance in the study area. Spiny dogfish accounted for 94% to 98% of the total catch in all years of the bottom gillnet study and the percentage of dogfish feeding on salmon was different in all years: 11.9% in 1988, 0.8% in 1989, 1.1% in 1990 and 1.5% in 1991. The estimates of juvenile salmon predation indicated that a minimum of 1.4% in 1990 to a maximum of 10% in 1988 of the Big Qualicum Hatchery chinook and coho salmon releases were killed by spiny dogfish within four weeks of entering saltwater.

Surveys to study lamprey predation were conducted in the Fraser River plume and adjacent waters using a surface trawl (Beamish and Neville 1995). Using estimates of numbers of prey killed per lamprey from laboratory studies, it was determined that lamprey predation could account for 13% of all coho hatchery production from Strait of Georgia hatcheries in 1990 and 65% of all coho production in 1991.

Other studies carried out during this period included C. D. Levings's work on juvenile salmon in estuaries (particularly the Campbell River estuary), C. Groot and K.D. Cooke on sockeye migrations, and M. Healey's work with the Hecate Strait project. In the early 1980s, C. Levings began extensive studies of how juvenile salmon use the Campbell River estuary (Levings et al. 1986). His work, together with that of Healey, established that the use of estuaries and shallow water habitats (< 10 m) by juvenile salmon varies among species. Based on estimates of residency time, juvenile chinook and chum salmon are the species that reside the longest in estuaries. Most of the information from these two investigators is for these two species. There is significant stock variation in the use of estuaries by the other species of salmon, but in general the data supporting observations for other species are weak. There are also some popula-

tions of Fraser River sockeye salmon whose juveniles rear in the lower river or estuary or both (Levings et al. 1995).

The research of Levings and associates (Levings et al. 1986) found that the chinook fry population in the Campbell River estuary took about two and a half months to move from the inner estuary to fully marine habitats farther offshore. In estuaries on larger river systems with numerous tributaries, chinook fry and smolts were found to trickle through the estuary from March to August. It was believed that hatchery smolts and wild fry at the Campbell River estuary competed for resources such as habitat space and food. There was evidence of density-dependent growth of the latter in years when this small estuary was dominated by the larger hatchery fish.

The Hecate Strait (between the northern mainland of British Columbia and the Queen Charlotte Islands) project started in 1984 with the overall objective of conducting research into the ecological basis for multi-species stock assessment and management among groundfish, herring and salmon. This region serves as a temporary residence for all five species of juvenile Pacific salmon, particularly those originating from stocks in southern and central British Columbia. The objective of the juvenile salmon component, which was carried out by M. Healey was to determine the residency, growth, and food requirements of juvenile salmon and provide information on their growth and migratory paths. Weights of stomach contents and estimated daily rations of juvenile pink and chum salmon were small enough to limit growth rates, and the hypothesis that the limitation of growth during early ocean life affected survival and recruitment was not rejected (Healey 1980b). Haegele (1997) carried out a five-year study, from 1990 to 1994, in which he examined the diets of juvenile Pacific herring and juvenile salmon in the Strait of Georgia. The study by Haegele was designed to survey for Pacific herring in their first ocean year and most effort was in the open areas of the Strait of Georgia.

The work of the MASS program (Marine Survival of Salmon) was carried out between 1987 and 1991 in Barkley Sound, off the west coast of Vancouver Island. This study attempted to integrate biological and physical sciences that affected the dispersal and survival of salmon during their first few months at sea. There were three objectives: (1) to examine the direct effects of coastal circulation and water mass structure on the dispersion and migratory behaviour of juvenile salmon; (2) to determine the relationship between food chain productivity, food distribution and survival; and (3) to examine the predation mortality of young salmon. The stocks studied included sockeye salmon from the Alberni Inlet system, chinook and coho salmon from Robertson Creek

hatchery, and juvenile chinook and coho salmon of various origins on fishing banks off southwestern Vancouver Island. Work on the first objective was mainly to examine residence (distribution and abundance) of all five species in the inlet, and migrations of sockeye in particular, within Barkley Sound (Groot and Cooke 1988), on offshore banks (Morris et al. 1990; Morris and Welch 1992a, b; Morris et al. 1992, 1993, 1997) and along the west coast of Vancouver Island (Hargreaves et al. 1990). Hyatt et al. (1988, 1990) conducted work on sockeye salmon recruitment variations. The second objective was also addressed by the latter group (Hyatt et al. 1988, 1990) who (1) examined diets of juvenile sockeye migrating through Barkley Sound to identify prey sizes and taxa of greatest importance for early marine growth; (2) examined prey abundance in Barkley Sound to characterise the food available relative to the cropping potential of juvenile salmon; and (3) analysed scale samples from adult sockeye to provide an index of early marine growth rates (first year) associated with sockeye year classes exhibiting high versus low marine survivals. In general, this was the most ambitious study of factors affecting the early marine survival of Pacific salmon undertaken by Canada. To date, there have been few reviewed publications from this study.

Results from diet analyses suggested that there could be interspecific competition for food supplies as various species of juvenile salmon (sockeye, chinook and chum) migrating through Barkley Sound relied on similar prey taxa (early stage euphausiids, medium sizes of copepods and brackish water cladocerans) during the spring and early summer period. However, scale pattern analysis indicated that first year marine growth rates of juvenile sockeye salmon that experienced the lowest survival rate (1983 smolt year) were not significantly lower than growth rates achieved by juvenile sockeye showing one of the highest survival rates (1978 smolt year). Later, Beamish and Mahnken (1998) proposed that similar results from another sockeye salmon stock could be explained by hypothesising that only the individuals that grew to a critical size could survive the first marine winter. Thus, the slower growing ocean age 0 fish were expected to be rare in any sample of returning adults.

The work on the second objective of the MASS program (carried out by Morris et al. 1990) provided information on diet and feeding success, but was not able to confirm the original hypothesis that aggregations of salmon would be associated with local circulation.

Work on the third objective, was done by Hargreaves et al. (1988, 1990) and Hargreaves and Hungar (1990), who examined juvenile salmon abundance, distribution and predation mortality in Alberni

Inlet and Barkley Sound. Their objectives included (1) determining the abundance and distribution of juvenile chinook, coho, chum and sockeye salmon; (2) identifying and assessing the relative abundance of potential predators of juvenile salmonids; and (3) determining the intensity of predation by examination of the stomach contents of major predators. One hypothesis to explain the variability in marine survival of salmon was that variation in ocean conditions changed the abundance, distribution or species composition of predators. Variation in ocean conditions could be interannual, decadal or both. The Barkley Sound predation study was an intensive effort carried out by B. Hargreaves and co-workers between early-April and mid-July for each of the four years. Sockeye salmon juveniles were the most abundant in this region, although chinook salmon used the areas as a juvenile rearing area more than chum, coho and pink salmon. Resident Pacific hake, walleye pollock (*Theragra chalcogramma*) and spiny dogfish were the most important predators of the juvenile salmon. The results do not appear to have been published as a final analysis, but preliminary conclusions were that in 1989, about 12 million juvenile sockeye (> 50% of total production) and 7 million juvenile chinook (equivalent to about 75% of the hatchery production) may have been consumed by predators during the early sea life period in this region. These estimates were based on very small numbers of salmon observed in Pacific hake stomachs, so there is high uncertainty. The mortalities were much lower in 1990.

Shortly after the MASS program ended in 1991, there were some major changes in the ocean that resulted in declines in survival of a number of salmon species. The declining survival was followed by management decisions to reduce fishing impacts and this resulted in catches of all species declining to historic low levels. Coho salmon marine survival in particular declined to less than 2%. At this time, there were other major changes in the ocean ecosystems. Pacific sardines (*Sardinops sagax*) returned to Canadian waters after an absence of over 40 years. Chub mackerel first appeared as a new and important predator in 1991, and there was considerable evidence that they became the major predator of juvenile salmon in Barkley Sound.

In the 1990s there were dramatic declines in the production of coho and chinook salmon in the Strait of Georgia. The declines of adult chinook salmon occurred despite a more than doubling of production of smolts (Beamish et al. 1995). The decline in the abundance of adult chinook was proposed to result from a natural decline in the carrying capacity for chinook salmon in the Strait of Georgia (Beamish et al. 1995). A similar explanation was proposed for the decline in adult coho abundance in the late 1990s (Beamish et al. 2000b). The decline in marine

survival in the Strait of Georgia was shown to be synchronous with declines in average marine survival in Puget Sound and off the coast of Oregon (Beamish et al. 2000b). The synchrony in the declines in marine survival was similar to large scale shifts in climate indices which indicated that climate and climate change affected the ocean carrying capacity for juvenile Pacific salmon over a large area. It is interesting that another major climate shift occurred in 1998 which affected the productivity of the Strait of Georgia in 2000. This recent change resulted in better marine survival, and better growth (Beamish et al. 2000c, 2001a). As a result of this change, juvenile salmon had more volume in their stomachs and fewer empty stomachs (Beamish et al. 2000c, 2001a). Similar food items were consumed; juveniles simply ate more and grew to larger sizes.

During the 1990s, the use of the rope trawl provided a tool that could be used to estimate abundances using swept volumes. A fixed survey design with a randomised depth component and a large rope trawl that fished surface waters at a speed of approximately 5 knots was used to estimate the abundance of juvenile coho salmon in the Strait of Georgia (Beamish et al. 2000a). The estimates were 4.2 million in September 1996, 3 million in September 1997, and 3 million in September 1998; these were assumed to be minimal estimates as catchability by the net was probably lower than used in the analyses. Using hatchery marked percentages, it was estimated that 3.4 million wild juvenile coho salmon entered the Strait of Georgia from Canadian rivers in 1997. In the Strait of Georgia, abundance estimates of juvenile Pacific salmon were shown to be large for some species relative to the numbers that returned. Because abundances were larger late in the first marine year and mortalities over the fall and winter exceeded 90%, Beamish and Mahnken (2001) proposed that the natural regulation of adult returns of salmon occurred in two stages, an early predation-based mortality, and a fall/winter mortality that was related to growth.

Survival and behaviour of juvenile salmon in the Strait of Georgia were linked by Beamish and co-workers to changes in climate that produced persistent and distinct climate-ocean states called regimes (Beamish et al. 1997, 2000d). Regime shifts occurred in 1977, 1989 and in 1998 (Beamish et al. , 2000a, d, 2001b). These regimes are characterized by changes in ocean temperature, sea level heights and Fraser River flows. The pattern of marine survival of chinook and coho salmon was related to the particular regimes. The decline in survival of coho after the 1989 regime shift was also associated with a behavioural change that resulted in virtually all juvenile coho salmon leaving the Strait of Georgia in the late fall and not returning until the spawning migration in the following late summer (Beamish et al. 2000d).

This resulted in an absence of ocean age 1+ coho and a collapse of the sport fishery in the Strait of Georgia. The abundance estimates and the release of marked hatchery fish were combined to study the changes in the percentages of hatchery and wild coho salmon. The percentages of hatchery coho salmon in the late 1990s exceeded 70%, indicating that, under the current management approach, hatchery coho were replacing wild coho salmon (Beamish et al. 1998b; Sweeting et al. 2003).

Offshore salmon research in Canada began again in 1990 by D. Welch and staff, after a pause of a quarter century when research surveys stopped in 1967. The initial impetus for the new work was provided through a co-operative research cruise on the USSR research vessel *Tinro* in the Gulf of Alaska. This co-operative effort provided an opportunity to assess the performance of the rope trawl being used to sample salmon in the open ocean by the Soviet Union (Morris et al. 1991, 1992). After a number of small-scale trials, a rope trawl capable of being successfully fished offshore was developed in 1995 (Welch and Carlson 1995). During offshore trials in March of 1995, it proved possible to tow the net at 5 to 5.5 knots, very near the surface (headrope depth 2–3 m under calm conditions) using a chartered trawler. Substantial catches of young salmon (> 100 salmon per 1 hour tow) were reported at some offshore stations, establishing the usefulness of the net.

Following the autumn 1995 trials, the High Seas program began to focus on autumn and early winter surveys to study the migration pathways of juvenile salmon. This work showed that no juveniles were found beyond the region of the shelf break (i.e. waters of 200–1,000 m depth). During multiple cross-shelf transects consisting of a linear sequence of closely spaced tows, catches of juvenile salmon abruptly dropped to zero as the shelf break was reached. In over 550 tows, roughly divided between those on and off the shelf, virtually no juveniles were found beyond the shelf break. The only exceptions to this general rule were a few catches of juvenile coho found just seaward of the 1,000 m isobath, each catch consisting of just one or two fish.

The results from these surveys indicated, by the end of 1996, that all of the juvenile salmon appeared to be staying on the shelf at least as far as Kodiak until October. The sharpness of the distribution of juvenile salmon in the eastern Pacific was described as remarkable (Welch et al. 1995a, b, 1997). Earlier work had postulated that juvenile salmon from SE Alaska and British Columbia probably turned west and moved out into the open North Pacific in the autumn (Hart and Dell 1986). Stocks of coho and chinook salmon were known to contribute to winter fisheries. They must migrate to specific feeding grounds along the coast where they take up residence and

make up the majority of the salmon left in the fall, such as the locations in the Strait of Georgia (e.g. Saanich Inlet, Stuart Channel) and Johnstone Strait (e.g. Bauza Cove, Frederick Arm) where over several years thousands of coho were seined for tagging (Argue and Heizer 1971, Heizer and Argue 1972). These fall-caught salmon were proposed to have a much lower rate of migration than the summer-caught fish, since the latter do not move as far, and presumably stay on fairly well-defined coastal feeding grounds once they reach these regions.

SPECIFIC RESEARCH TOPICS

Estuaries and Nearshore Habitats

Juvenile Pacific salmon in their migration from inland rearing areas to oceanic feeding areas often pass through littoral estuarine habitats. Studies of juvenile salmon in estuaries have been carried out primarily by M. Healey, C.D. Levings, B.A. Bravender, (formerly B.A. Kask), K.S. Kotyk, and T.J. Brown. Healey (1980a, b, 1989, unpublished data) studied juvenile salmon in the Nanaimo and Nitinat estuaries in southern British Columbia and put together the results of a number of studies of juvenile salmon in other BC estuaries, such as the Fraser, Squamish, Courtney, and Somass in southern British Columbia (Kask and Parker 1971, 1972a, b, 1974; Barraclough and Phillips 1978; Birtwell 1978; Levy and Levings 1978; Levy et al. 1979; Morris and Leaney 1980; Levy and Northcote 1981; Healey 1982a). Some species remain in these habitats for several days and in some cases for several months (Reimers 1973; Dunford 1975; Healey 1979, 1980a, b; Levy and Northcote 1982). There have been many studies to assess timing of migration into estuaries, length of residence, distribution and abundance of juvenile fish, possible interactions among the different species of salmon and among hatchery and wild fish in estuarine areas.

Most young salmon enter estuaries in the spring, and move into the coastal oceans in the spring and early summer. Juvenile pink salmon were only found in any abundance in the Fraser River, and pink fry were found in the tidal marshes of the Fraser River delta only during their downstream migration. Pink fry were found to move into the tidal marshes at high tide and to leave on the first of the ebb, thus their residence time in the marsh (area) was found to be no more than one or two days (Levy et al. 1979). Most of the fry migrating seaward each day were found to move directly through the delta (area) and into the river plume (Barraclough and Phillips 1978). Healey (1980b, 1982b) found that pink fry were swept across the southern Strait of Georgia by the Fraser River plume, and congregated in dense schools close to

shore along the east coast of Vancouver Island. Healey (1982b) also found some pink fry, probably of Fraser River origin, rearing in the outer Nanaimo River estuary in May and June. Phillips and Barraclough (1978) and Healey (1980b, 1982b) found that juvenile pink salmon left the Nanaimo River estuary and other habitats in the southern Strait of Georgia in late June or July when they reached 80 mm fork length.

Chum salmon have shown similar behaviour in estuaries (Healey 1979; Levy et al. 1979; Levy and Northcote 1981; Healey 1982a, b, c). Chum fry were shown to disperse several kilometres within a few hours once they had reached the river mouth, although some remained in the estuary to rear. The first habitats occupied by the fry were found to be tidal creeks and sloughs high in the delta area, and also marsh habitats and intertidal areas. During high tide, the chum fry apparently congregated in the upper intertidal at the fringe of marshes, moving deep into the marsh along tidal creeks. At low tide, the fry were seen to retreat into tidal creeks that have flowing water at high tide, and into delta channels. Healey (1982a) noted that the preferred habitats appeared to be the junction of major and minor tributaries in the delta. Levy et al. (1979) found that abundances of pink and chum fry peaked in the tidal channels of the Fraser River during late April, that juvenile chinook were most abundant during late April and May, and that nearly all juvenile salmon moved into coastal waters by mid-June. Healey (1982a) examined the seasonal changes in catch of chum, coho, chinook and pink salmon in the Nanaimo river estuary. He found maximum catches in the inner estuary during April and May for chum salmon, and in the outer estuary during May and June for chum, coho and pink salmon. Most juvenile chinook salmon were caught later during June and July. Most salmon except for chinook had left the estuary by July.

Healey (1978) detailed the timing of arrival of Pacific salmon juveniles into the Strait of Georgia. Young salmon that enter the Strait of Georgia in spring and early summer spend between a few weeks and a few months exploiting the food resources there, and then move out to the open ocean. During even years, large numbers of juvenile pink salmon are present in the Strait of Georgia, most are from the Fraser River but some are from rivers that flow into the northern end of the strait. Pink fry migrate down the Fraser River in March and April and disperse quickly across the Strait of Georgia to occupy shallower near-shore nursery areas in the Gulf Islands region, although some are carried north into the central strait region or south into the San Juan Islands area. Juvenile pink salmon from central British Columbia also show the same behaviour (LeBrasseur and Parker 1964; Healey 1987). For the first few weeks the fry

stay close to shore often in large schools in just a few centimetres of water. They disperse along the shore but tend to accumulate in various places. In the Nanaimo area, the juvenile pink salmon move offshore in late May and also become abundant along the east side of the outer chain of the Gulf Islands (Fig. 1) (Barraclough and Phillips 1978). By June offshore purse seine catches peaked in the Gulf Islands and the Nanaimo region, but by July they dropped dramatically, illustrating that most pink salmon had left the Strait of Georgia by that time. Apparently a few persist and leave in September and as late as March or April of their second ocean-year based on the purse seine catches by Argue in Johnstone Strait (Heizer and Argue 1972; Argue and Heizer 1974).

Chum salmon rear in the lower Fraser River and many other rivers flowing into the Strait of Georgia. Most chum salmon migrate downstream in April and May. Those from the Fraser River disperse similarly to pink salmon and occur with them in the nearshore areas. Juvenile chum salmon from smaller rivers disperse along shore after leaving the river mouths. Unlike pink salmon fry, many chum salmon rear in sloughs and side channels of the Fraser River delta and in other river estuaries for many weeks after migrating downstream (Dunford 1975; Healey et al. 1977a; Healey 1979 and unpublished data). Chum salmon and pink salmon fry are a similar size, both about 30–40 mm in length (0.25–0.4 g), when they migrate seaward.

Chum salmon fry from the early part of the run from the Nanaimo River remain in estuary nursery areas, whereas fry from the latter part of the run move directly into deeper water (Healey et al. 1977a; Healey 1979). Juveniles in the estuary nursery areas appeared to occupy waters of 1 m or less until late May when they moved from the shallow nearshore into deep water. They appeared to leave the Strait of Georgia more slowly than pink salmon, but catches declined after June no doubt due to their emigration. Some chum salmon, however, stay as late as October.

There was a decline in catches of chum, pink and yearling sockeye salmon in June and July in the Strait of Georgia which is coincident with an increase in the abundance of these species off the outer coast (Hartt 1980; Healey 1982b;). Healey (1982b) suggests that July is the time of outmigration for each of these species. However, in the 1990s, large numbers of chum and pink salmon were observed in September by Beamish (Beamish and Folkes 1998; Beamish et al. 2000a, 2001b), and in the 1970s Argue encountered significant numbers of immature pink and chum salmon, and a few sockeye, in Johnstone Strait as late as April (Heizer and Argue 1972; Argue and Heizer 1974). However, Beamish and Folkes (1998) showed that relatively large numbers of juvenile chum salmon

remained in the Strait of Georgia until late in the year, and that this behaviour was quite different from that observed during the studies of Healey and others during the 1960s and 1970s. It was possible that more chum salmon remained in the Strait of Georgia because of increased releases of hatchery reared chum salmon. However, except for 1992 and 1994, the total releases from Canada had not changed since the late 1980s. It appeared that pink and sockeye salmon were also found later in the year. Thus the behaviour change was believed to be real. The reason for the change in behaviour was unknown, although it was seen to coincide with a change in the pattern of the Aleutian Low Pressure Index (ALPI) about 1989–1990 (Beamish et al. 2000d). Another change which occurred at the same time was the earlier beginning of the increased Fraser River flows and a general increase in sea surface temperatures. Beamish and Folkes (1998) hypothesised that these changes led to improved feeding conditions for the juvenile chum salmon. The change in behaviour from the Healey studies may be related to physical changes resulting from the 1989 regime shift or from increased hatchery production of chum salmon. However, it may also represent a growth-related response.

Coho salmon smolts entered the Strait of Georgia during May and June from just about all the streams and rivers around the strait. They are rare in the open water before May, although a few were captured in the Fraser River plume in April (Barraclough and Phillips 1978). Smolts became common in purse seine and trawl samples at the end of May and remained common throughout the summer. Tag returns suggested that whereas many coho rear in the open Pacific, some also rear to maturity in the open Strait of Georgia. Some also rear through the fall and winter months amongst islands of the southern Strait of Georgia and Johnstone Strait (Argue and Heizer 1971; Heizer and Argue 1972; Argue and Heizer 1974). Purse seine catches taken monthly in the Gulf Island region of the Strait of Georgia from May to October 1976, and weekly in the Nanaimo area (Fig. 1) from April to August 1975 and 1976, did not reveal any decline in the coho salmon catch that would signal the timing of an outmigration (Healey et al. 1977a; Healey 1978 and unpublished data; Schmidt et al. 1979; Healey 1980b). The extensive studies by Beamish and colleagues in the 1990s and early 2000s documented the migration of virtually all coho salmon out of the Strait of Georgia in 1991 and from 1995 to 2000 (Beamish et al. 2000a, d). Coded-wire tags in coho salmon caught outside of the Strait of Georgia indicated that few left the Strait of Georgia until late September (Beamish and Sweeting 1999). In Puget Sound, coho salmon left in August while chum and chinook salmon remained (Beamish et al. 1998a; Beamish and Sweeting 1999). The reason for

the change in behaviour from the mid- to late-1990s remains to be discovered but the change in behaviour was clear. It is important to note that the movement out of the Strait of Georgia without returning until the spawning migration of the following late summer was associated with a dramatic decline in marine survival.

Chinook salmon are produced in most medium to large rivers with the Fraser River producing the greatest numbers. Chinook have the most complex life history among Pacific salmon. Upon hatching and emerging from the gravel, some go directly to estuaries and rear in intermediate salinity waters, whereas some stay in fresh water. Thus, they migrate to sea as recently emerged fry from March to May, as underyearling smolts in June, and as yearling smolts from March to May of their second year (Rich 1920; Reimers 1971; Healey 1980b and unpublished data). Juveniles that rear in the estuary tend to leave it about the time that those reared in fresh water move downstream. Catches of underyearling smolts in open waters of the Strait of Georgia remained constant through July to November and declined during the winter (Healey 1980a, b). Yearling smolts were common in seine catches in the Strait of Georgia only during May to July after which they disappear from the Strait (Healey 1980a, b). Chinook salmon fry enter the estuary at a length of 40 mm (0.5 g), fingerling smolts are 60–80 mm in length (2–5 g), and yearling smolts are 80–110 mm, (5–18 g).

Barraclough and Phillips (1978) produced a series of distribution maps which suggested that most salmon found off the Fraser River estuary in April migrated across the Strait of Georgia, through Active and Porlier passes during May and June, and were virtually absent from the central Strait of Georgia by July. Distribution appeared to be influenced by tide and wind-generated surface currents and by the volume of fresh water discharge from the Fraser River. They found that during their migration across the Strait of Georgia, pink, chinook and coho salmon tended to be more confined to low salinity plume water than chum or sockeye salmon. During April to mid-June, the bulk of the juvenile salmon populations of pink, chum and chinook were close inshore rather than in the open waters of the Strait. The authors suggested that fry of these three species may remain for a time in the Fraser River estuary or in the proximate nearshore areas before resuming oceanward migration. They believed that entry of young salmon into the open Strait of Georgia may be a response to local environmental conditions resulting in the intermittent discharge of groups of fish into the Strait.

Holtby et al. (1989) found that downstream movements of chum and coho salmon were different, even though stream temperatures affected both. They found that the outmigration of chum was more predictable and more synchronous within a year than was

that of coho salmon. Coho salmon do not remain in estuaries, enter the ocean when larger, and have a more extended migratory period from fresh water than do chum salmon (Holtby et al. 1989). It was suggested that this difference might exist because peaks in productivity of large zooplankton may be less predictable in coastal waters, where juvenile coho salmon forage, than peaks of small epibenthos in estuaries, on which chum fry initially depend.

Healey (1979) and Levy et al. (1979), using release of marked fry in the Nanaimo and Fraser River estuaries, showed that chum salmon may spend up to three weeks rearing in the inner estuary, and appeared to be localized in their movement patterns. In addition to the twice-daily migration of fry from low tide regions to marshes and back again, Healey (unpublished data) demonstrated that there is also a seasonal migration seaward in the estuary. Thus, in the Nanaimo, Courtney and Cowichan River estuaries, chum salmon fry are found in the inner estuary in April and May and move into the outer estuary during May and June. Most chum salmon have moved out of estuarine habitats in southern British Columbia by mid July (Healey 1982a, b).

Almost all sockeye salmon migrate to sea in April and May as yearling smolts, but some migrate seaward as fry and rear in the Fraser River delta until July or August. In late April the yearling smolts are concentrated just off the river mouth, by late May they have dispersed rapidly south and east and are concentrated along the east and west sides of the outer Gulf Islands chain (Groot and Cooke 1987). By June most are concentrated in the Gulf Islands region, especially along the Vancouver Island shore (Barraclough and Phillips 1978; Healey 1978). Most sockeye leave the Strait of Georgia in late June and July through the northern passage (Groot and Cooke 1987). Timing of peak catches in the Fraser River plume and Gulf Islands region suggests that the smolts take 20 to 30 days to move through the Strait of Georgia. The sockeye fry that accompany the smolts downstream in the Fraser River in the spring rear in the estuary over the early summer and leave with the plume once they have reached 60–70 mm fork length.

DNA of ocean age 0 sockeye salmon sampled in the Strait of Georgia in one of the surveys conducted by R. Beamish was analyzed for 24 of the sample of 67 fish. Maximum likelihood analysis of microsatellite genotypes indicated that all fish were of Fraser River origin. Bayesian classification of these fish indicated that they originated from 12 different stocks: Pitt River, Weaver Creek, Birkenhead River, Portage Creek, Chilko River, Horsefly River, Mitchell River, Stuart River (early stock), North Thompson River, Lower Shuswap River, Little Shuswap River, and Lower Adams River (St-Hilaire

et al. 2002). A second DNA analysis was made from a sample of 63 ocean age 0 sockeye smolts collected in July 2001. The results from this analysis were compared to those from sockeye salmon in a baseline data set that contained information for the same 15 loci from 130 stocks from Washington to Russia (R. Withler, Pacific Biological Station, Nanaimo, BC, Canada, personal communications). All of the 63 ocean age 0 sockeye, except two, originated in the Fraser River drainage. The remaining two were from Lake Washington in Washington State, USA. Within the Fraser River about 18 different stocks were represented, indicating that small numbers of juvenile sockeye from a relatively large number of stocks remain in the Strait of Georgia in July.

Sockeye smolts have rarely been caught in the inner estuary and delta habitats of the Fraser and So-mass rivers, even though these systems are major producers of sockeye salmon (Levy et al. 1979; Morris and Leaney 1980). Sockeye smolts have been found in the outer Nitinat estuary, and the outer regions of other estuaries during their downstream migration, but the catches were considered small in comparison to the number of downstream migrants (Kask and Parker 1971; Barraclough and Phillips 1978). It therefore appears that sockeye smolts move quickly to nursery areas outside their natal estuaries. However, sockeye races from the Fraser River that migrate downstream as fry have been found within estuary habitats during April–June. They have been seen to migrate into the river plume after this time, where some remain until September (Healey 1980b).

Greer et al. (1980) examined the distribution of fish species on Roberts and Sturgeon Banks recorded in seine and trawl surveys. Levings and Kotyk (1983) carried out two trawling surveys for juvenile salmonids (chum, pink, coho, chinook and steelhead) in Discovery Passage and nearby channels in the northern Strait of Georgia. This was part of a sampling program established to examine the dispersal of wild chinook fry and juvenile marked chinook from release experiments at Quinsam hatchery into the Campbell River (Fig. 1) estuary. Chum salmon dominated the catches and peaked in abundance in late June, as did pink. Most chum salmon were probably from the Fraser River system. Chinook and coho salmon were less abundant and were primarily fish from the Quinsam hatchery. Steelhead trout and sockeye salmon were uncommon.

Argue et al. 1986 reported on habitat utilization and dispersal of juvenile coho and chinook from the Cowichan River estuary based on three years (1973, 1975, 1976) sampling with various net gears. Juvenile chinook and coho (ocean age 0) utilized the estuary from early April through June. Chinook then moved to deeper water at the head of Cowichan Bay, just past the estuary drop off, and to nearshore waters

around the perimeter of the bay. Coho smolts were not common on the estuary at any time, but were abundant near the drop off and at nearshore stations around the edges of the bay. Neither species was abundant at deep water stations (> 45 m) in the middle of Cowichan Bay. Juvenile chinook abundance outside Cowichan Bay in nearshore habitats peaked in July and August. Coho smolts were most abundant at outside sites when purse seine sampling started in June. Coded-wire tagged juveniles from the Cowichan River were recovered in the Bay through to the end of sampling in October. For coho smolts, there was evidence that later migrants from fresh water dispersed less from Cowichan Bay than earlier migrants.

Macdonald et al. (1988) examined the habitat utilization by juvenile salmonids in the Campbell River estuary. In this study, the authors wanted to characterise the microhabitats occupied by salmon by defining the physical features such as water velocity, salinity and temperature, and to investigate the importance of inter- and intra-specific aggression on micro-habitat selection. They found that water velocity, temperature, and salinity were the variables most important in characterising differences among micro-habitats. Coho salmon were observed in regions of higher salinities and water velocities than chinook salmon. Hatchery chinook salmon were found in lowest water velocities of all.

Macdonald et al. (1988) evaluated the importance of estuaries to juvenile chinook salmon survival. In late April of 1983–1985, 140,000 marked chinook salmon smolts were transported by helicopter from Quinsam hatchery to four release sites: riverine, estuarine, transition and marine, near Campbell River, British Columbia. At the marine site, fish were released directly into seawater. Beach seine data for four months after release showed that fish released directly into marine waters rarely dispersed to the Campbell River estuary. Fish released immediately adjacent to the mouth of the estuary (transition zone) had the widest immediate dispersal pattern, with many of them returning to the estuary. Estuarine zone fish displayed the most restricted distribution. Fish released to the river and estuary remained in the sampling area for a longer period (34–47 days) than those released in the marine or transition zone (20–23 days). Overall, fish released into the estuarine zone showed many signs of delayed seaward migration. They dispersed at lower rates, they travelled shorter distances immediately after release and were thus recaptured in greater numbers than chinook salmon deprived of estuarine residence.

Levings et al. (1983) carried out some preliminary marking experiments with juvenile chum and chinook salmon in May and June 1981 at three low tide refuges on Roberts and Sturgeons Banks at the

Fraser River estuary. They used spray marking with fluorescent grit. Residency periods of up to two days were documented. These experiments were part of a larger study investigating the juvenile salmonid use of foreshore habitats on Sturgeon and Roberts Bank in the Fraser River estuary. Preliminary results from this study suggested that the two species, chinook and chum salmon, may have different habitat preferences.

In summary, coho, yearling chinook and sockeye salmon all tend to rear to a large size in fresh water and spend little time in estuaries. Pink salmon migrate to the coastal ocean when very small and quickly move across the intertidal marshes and inner estuaries. Chum and sub-yearling chinook salmon, however, have much longer residence time in estuaries (Levy et al. 1979; Healey 1982a; Levy and Northcote 1982). Chum salmon are abundant in estuaries for two months in early spring, and chinook salmon throughout the spring, summer and fall. Pink and sockeye salmon spend very little time in estuaries. Habitats occupied by each species vary with fish size, tidal stage and time of year. The favourite habitats appear to be tidal creeks to marshes, the junction of major and minor tributaries in the intertidal zone, and the delta front.

Movement Patterns into Coastal Oceans

Peak migration of smolts into estuaries occurs in the spring and migration into the open ocean occurs in the late spring and early summer. Parsons et al. (1969a, b) and Stephens et al. (1969) suggested that the timing of movement into nearshore areas of the Strait of Georgia might be related to zooplankton abundance. The juvenile salmon that leave protected nearshore waters, inlets, and estuaries of the north-eastern Pacific enter the open coastal waters in large numbers by June (Healey 1980a, b). Most juvenile sockeye, chum and pink salmon spend several months in coastal "corridors" of around 30–40 km width, as they migrate northwards and westwards along the Gulf of Alaska. Some stocks of coho and pink salmon spend all of their marine life in coastal waters (Argue et al. 1983; Hartt and Dell 1986; Fisher and Pearcy 1987, 1988). However, juvenile steelhead generally migrate offshore into oceanic waters of the Gulf of Alaska, and are rarely found close to shore (Pearcy and Masuda 1982; Hartt and Dell 1986).

Pink salmon fry upon entering the sea at Bella Coola are initially shore oriented and form a narrow band extending into Burke Channel (Parker 1969b). With growth, they appear to move away from the shoreline and the fingerlings occupy more pelagic positions. At the end of May the fingerlings formed tight schools which were observed to migrate out of coastal waters to the more exposed waters of the Queen Charlotte Sound. Barraclough and Phillips

(1978) found that migration of fish across the Strait of Georgia could be rapid. Current velocities associated with discharge from the Fraser River could exceed 2.7 km/hr, which would mean that it would take only a few hours for juvenile salmon to cross the Strait. Groot and Cooke (1987) suggested that sockeye smolts move 6–7 km/day in the Strait of Georgia (i.e. about 0.7 to 0.8 body lengths per second at an average smolt length of 10 cm). Data from Parker (1965) and Healey (1967) suggest that pink salmon fry took 20–30 days to migrate about 70 km down Burke Channel in central British Columbia (i.e. about 0.6 to 0.8 body lengths per second). Healey (1989) used a default rate of 1 body length per second for sockeye, pink and chum salmon in his model of the coastal migration of salmon through Hecate Strait. Movements of coho and chinook were believed to be slower as movement of these species was thought to be more of a gradual dispersal than a directed migration.

Ocean type chinook enter the ocean at around 70–80 mm fork length, usually during their first summer, and these fish generally remain in coastal waters throughout their oceanic life (Healey 1982b; Healey and Groot 1987). Stream type chinook enter the ocean at a larger size and, after spending one year in fresh water, are also found in this band of juveniles migrating northwards. Healey (1983) suggested that stream and ocean type chinook salmon were different races. Information on ocean distribution and migration patterns of chinook also was recorded by Argue (1970). He found stream type chinook in their first ocean year in test troll catches throughout Juan de Fuca Strait during September and October, possibly indicating they were migrating to offshore waters. Stream type chinook migrate far offshore whereas ocean type chinook remain in coastal waters throughout their life. Ocean type chinook occur only in spawning populations south of about 56° N, but dominate in virtually all river systems from this latitude to the southern extremity of their range in California (Healey 1983). For example, Healey (1980a, b) reported high catches of juvenile ocean type chinook salmon in the southern Strait of Georgia during the period June to November, after which catches declined. Immature ocean type chinook salmon in their second ocean year were also abundant in the Strait of Georgia as demonstrated by sport fishery catches (Argue et al. 1983). Timing of seaward migration of stream- and ocean- types was similar. Stream type chinook smolts migrated in April and May, slightly later than recently emerged ocean type fry migrants, but before the downstream movement of ocean type smolts (Healey 1980a and unpublished data). First ocean year stream type chinook were present in the Strait of Georgia for about two months following downstream migration. Ocean type, however, remain abundant in the Strait of Georgia

throughout their first and second years of ocean life. (The patterns of scale or otolith growth zones are used to identify the particular life history type).

Argue et al. (1983) found that most emigration of coho from the Strait of Georgia took place prior to December of their first ocean year, as indicated by several years of marine tagging data covering all calendar months. There is, however, evidence that some coho continued to move out through Juan de Fuca Strait during winter and spring months in their second year (Argue 1970). In contrast, chinook tagging results showed modest levels of exchange at all ocean ages between the Strait of Georgia and the west coast of Vancouver Island.

Fraser et al. (1982) suggested that significant numbers of chinook salmon probably remained in the Strait of Georgia through to maturity, as indicated by substantial local sport and commercial troll fisheries and recoveries from many Strait of Georgia tag releases (Argue et al. 1983). A portion of the Fraser River chinook juveniles migrated out of the Strait of Georgia in a northwesterly direction through Johnstone Strait. This northwesterly direction had been proposed to be a dominant migratory route for many salmon stocks (Mason 1965). It was believed that these stocks remained relatively close to shore because of the rich feeding grounds off the continental shelf. According to Mason (1965), the highly productive troll fishery off the British Columbia and Alaska coasts, capturing primarily immature, feeding chinook salmon has confirmed this.

Healey (1967) examined the orientation of pink salmon during early marine migration from the Bella Coola River (Fig. 1) system for one summer only in 1966. He stated that the Bella Coola River and Burke Channel (Fig. 1) was a unique system in which to study the early marine migrations of Pacific salmon because they remained relatively distinct for much of their journey through the Channel. He noted that the movements of pink salmon fry down Burke Channel were saltatory: short periods of active migration were interspersed with longer periods when the juveniles did not migrate and accumulated in bays. Fry were sampled from these aggregations and their ability to orient using celestial cues was examined. During the early morning fry tended to prefer directions at right angles to their direction of migration, but at other times of the day they preferred the direction of migration. The preference for direction of migration was strongest at mid-day. Fry were better oriented on clear days than on cloudy days. These data indicate that the fry may use celestial cues to find directions during their oceanic migrations.

Healey and Groot (1987) compared the short migrations of ocean type chinook with the long distance migrations of sockeye to try to assess the sophistication of the direction finding mechanisms

required for each type of migration. During outward migration as juveniles to oceanic feeding grounds, both species apparently used compass orientation. During the homing migration, however, both species use a combination of compass and bicoordinate orientation until near the home stream mouth (at which time they use local environmental cues).

Sockeye salmon in southern British Columbia typically migrated seaward after one year in fresh water (Foerster 1968). Hartt (1980) and Hartt and Dell (1986) showed that juvenile sockeye, pink and chum salmon in the eastern Pacific migrate northward along the coast in a narrow band after leaving their natal river. This narrow band extends 1,800 km from southern Vancouver Island to Yakutat in Alaska and persists for about three months. Chinook are also found in this band but are stream type rather than ocean type (Healey 1983).

Sockeye salmon from the Fraser River can follow two routes out of the Strait of Georgia, either south through Juan de Fuca Strait or northwest through Johnstone Strait. Most juvenile sockeye salmon are thought to leave via the northern route (Groot and Cooke 1987). Upon leaving the Fraser River estuary, most smolts proceed along the mainland coast northward but some are flushed west across the Strait of Georgia by the Fraser River plume and tidal currents towards the Gulf Islands. Once among the Gulf Islands, these smolts turn north and migrate diagonally back across the Strait to join up with the smolts that have moved directly north from the river mouth (Groot and Cooke 1987). Groot and Cooke (1987) estimated that sockeye smolts migrated through the Strait of Georgia, a distance of about 200 km, in 30 days. To do this they had to travel 6–7 km per day. Johnson and Groot (1963) and Groot (1972) examined the rates of travel for sockeye smolts from Babine Lake (Fig. 1) (5–8 km/hr), with individual schools travelling at rates of 24.5–30.0 cm per second during active migration. At this rate, the smolts must swim for 6–8 hours per day. During their first summer in the Gulf of Alaska, juvenile sockeye salmon continued to travel rapidly along the coast of North America. Hartt (1980) estimated that to cover the distances of 1,150 and 2,770 km between the Fraser River mouth and the tagging sites in southern Alaska, the fish must have travelled 13.7–25.9 km/day. The average fork length at tagging was 20.8 cm. Thus, travelling at an optimum swimming speed of about two body lengths per second (Brett 1965), they must have swum on a direct course for 9–17 hr/day to get to the tagging site.

Healey and Groot (1987) concluded that ocean type chinook salmon remain in the region of their natal stream during their first summer at sea and then, during their first winter at sea, migrate northwards and establish a distribution along the coast within a

few hundred to 1,000 km of their natal stream. They maintain a relatively fixed coastal distribution throughout their ocean life, and migrate rapidly along the coast from the ocean feeding area to their home stream once mature. In contrast, sockeye salmon undertake a directed migration either north or northwest soon after entering the ocean. The following Spring, they migrate south and west into open waters of the Gulf of Alaska more than 1,000 km from their natal stream. Following their first winter at sea, they move continuously in a wide circle around the Gulf of Alaska throughout their ocean life and migrate rapidly from the open Gulf of Alaska directly to their home stream when mature.

Locally, returning chinook salmon congregate in particular areas as indicated by concentrations of fishing vessels during chinook salmon fisheries. The fact that chinook tend to occur at depth rather than near the surface (Argue 1970) suggests that the areas in which they aggregate may be characterized by bottom topographic features or oceanographic features below the mixed layer, that serve to congregate potential prey. Different size fish may also have different habitat requirements, a possibility suggested because the size composition of the catch changes dramatically along the west coast of Vancouver Island (Healey 1986). Also, chinook salmon from each brood year that are destined to mature at an older age appear to occupy the most northerly parts of a stock's geographic distribution.

Immature sockeye are distributed far offshore and appear to migrate actively throughout their life in the ocean. Their seasonal movements carry them in a large circuit off the Gulf of Alaska once each year. Their migration as immature fish may be a response to the seasonal movements of greatest ocean plankton production and thus serves to keep the sockeye in regions of good feeding. What is clear is that these fish are constantly on the move once they enter the ocean. In contrast, chinook salmon, once they have established a coastal distribution, appear to be relatively sedentary.

Little is known about what happens to immature sockeye after October or November of their first ocean year, when they have reached Kodiak Island. Because they are found well to the south in the Gulf of Alaska the following spring, French et al. (1976) concluded that there is a movement south and southwest in autumn and winter. Groot and Cooke (1987) examined the migration routes of juvenile and adult Fraser River sockeye salmon into and out of the Strait of Georgia. The purpose of their study was to determine if adults returned to the Strait of Georgia and Fraser River by retracing the same route taken by juveniles during their seaward migration. They suggested that the ability to predict the proportion and migratory routes of the Fraser River sockeye return-

ing to their home stream through Johnstone and Juan de Fuca straits would contribute significantly to the solution of international problems related to management. Migratory routes were determined by seining and trawling during 1982–1984. They noted that sockeye salmon returning to the Fraser River from their ocean feeding grounds migrated either via a northern or southern route around Vancouver Island with the proportion taking the northern route varying annually from 2 to 80% between 1954 and 1987. Sockeye smolts leaving the Fraser River on their way to the ocean were also seen to follow either route around Vancouver Island. This information, together with results of previous studies, showed that most juveniles left inland water by moving north by one of two patterns. In one migration, smolts leaving the Fraser River immediately turned north and continued to travel along the mainland coast. A second pattern was observed as a movement of smolts across the Strait of Georgia towards the Gulf Islands, a northward movement along the east side of these islands and then diagonally northward through the strait to join the smolts migrating across to the mainland shore. This suggested that Fraser River sockeye smolts have a north to northwestern directional tendency. The movement from the river mouth across the Strait of Georgia towards the Gulf Islands was assumed to result from a combination of strong river outflow and tidal currents. Comparison of the migratory patterns of the juveniles and the adults suggested that they were not related and the authors were unable to substantiate their hypothesis that the outward migration of the juveniles determines the inward migration of adults. They suggested that the smolts perform a one directional compass orientation (north to northwest) and that the adults show goal orientation homing to the Fraser River from their ocean feeding grounds by either following a northern or a southern route around Vancouver Island.

Diet and Growth Studies

Feeding within estuaries

Healey (1980a, b) examined the relationship between foraging success and residency in estuaries. He stated that the residence of chum fry was related to the seasonal abundance of their principal prey species, the copepod *Harpacticus uniremis*, in the Nanaimo River estuary. Estimates of amount of *H. uniremis* eaten by chum salmon was of the same order as estimates of its production, leading to the speculation that the abundance of chum was potentially limited by the production of this copepod (Healey 1979; Sibert 1979). The data indicated that food consumption by chum salmon was lowest when fish were most abundant in the estuary, and that emigration of the

majority of the chum coincided with a major decline in the population of *H. uniremis*.

Healey (1978) tried to establish a relationship between migration and food limitation. He found that movement of salmon juveniles away from the estuary did appear to be related to disappearance of their dominant food. But for the entire Strait of Georgia, he was unable to demonstrate food limitation. He suggested that demonstrating food limitation may be impossible because plankton samples generally have not revealed an abundance of the types of food that are in the stomachs of young salmon (Barraclough 1967; Barraclough and Fulton 1968; Barraclough et al. 1968; Robinson et al. 1968).

This absence of a relationship between movement away from shore and stomach contents may be an indication that food resources were adequate in most habitats to allow for successful foraging. Distribution of fish may be controlled by another need such as avoiding predators, or taking advantage of relatively warm nearshore water temperatures to maximize growth efficiency (Brett and Higgs 1970). The growth rate of juvenile pink, chum and chinook salmon during their first few weeks is very rapid (Healey 1979, 1980a, b) suggesting that food is not directly limiting at this time. After 15 June, when stomach contents declined, the fish began to show distributional patterns related to foraging success. Healey assumed that food resources were low enough that the fish had to seek out the best feeding areas to satisfy their food requirements. For pink, chum and sockeye salmon, which are largely planktivorous, this meant that they had to leave the Strait of Georgia. However, coho and chinook salmon, which are largely piscivorous, were able to satisfy their food requirements without migration.

Manzer (1956) examined diurnal variations in feeding intensity of pink, chum and coho salmon from June 8 to July 18 in Chatham Sound (Fig. 1) and adjacent waters. He noted diurnal variations in feeding intensity: pink, chum and coho salmon apparently did not feed with equal intensity from dawn to dusk, and their feeding rhythms during this time were not similar. Pink salmon fed relatively heavily during early morning and late afternoon and more lightly during 12:00 to 14:00 hours and possibly in the late evening, suggesting a bimodal diel feeding cycle. Parker and Vanstone (1966) found that juvenile pink salmon in central coastal British Columbia in late May fed most intensely in the afternoon and least intensely during the early morning. With chum, as with pink salmon, food consumption in Chatham Sound declined through the morning to a low between 12:00–14:00 hours. After that, food consumption increased in late evening (Narver 1968; McDonald 1973; Doble and Eggers 1978). Coho salmon, in contrast, appeared to consume food at about the same level of intensity

during the day, except possibly in late evening when feeding may have been reduced. Juvenile sockeye salmon are apparently crepuscular feeders.

LeBrasseur and Parker (1964) showed that the growth rate of juvenile pink salmon is extremely rapid during their first few months at sea. Phillips and Barraclough (1978) examined the early marine growth of several juvenile Pacific salmon species in the southern Strait of Georgia and Saanich Inlet using samples taken with a two boat surface trawl from April to July 1966–69, 1973, and 1975. Growth rates calculated from change in average size with time showed that pink salmon grew at rates of 3.5–4.0% body weight per day, and chum salmon at rates of 4–5% per day over the weight range of 0.5–10.0 g. Growth rates could not be calculated for sockeye, chinook or coho salmon because these fish did not show a consistent increase in size with time.

LeBrasseur and Parker (1964) found that young pink salmon grew at a rate of 6.35% body weight/day for their first 40 days, falling to a rate of 3.50%/day for the following 30 days. This study identified an average range of 3.5–5.0% body weight/day for Strait of Georgia pink salmon. Healey et al. (1977b) described comparable rates of 4.7–6.4% body weight/day for chum salmon in the Nanaimo River estuary during early marine residence. This was similar to rates of 4–5% body weight/day observed for chum in the open waters of the Strait of Georgia. He did not, however, find significant differences in growth rate between early and later estuarine residence. LeBrasseur and Parker (1964) also determined a reduction in size of sockeye with time in the open waters of the Strait of Georgia. They likened the offshore migration of young pink salmon at fork lengths of 60–70 mm to true smolting behaviour as exhibited by sockeye. Because sockeye are larger when they enter the marine environment, they do not spend much time in nearshore waters. Early emigration of large fish and continual addition of smaller downstream migrants may mask growth and account for the observed reversal in size of the offshore samples. It would also be possible that size selective mortality accounted for the observed changes. Chinook, coho and sockeye salmon had different size groups too, depending on how long the different races within a species reared in fresh water before entering the ocean.

Fish captured offshore appeared to grow at a greater rate than those captured inshore. Data for juvenile pink salmon captured by LeBrasseur and Parker (1964) indicated that larger fish tended to move offshore earlier than the rest of the population. Argue et al. (1986) reported similar findings for coho and chinook juveniles dispersing from Cowichan Bay. Thus, these larger fish would be most available to the surface trawl, leading to possible overestimation of mean size from offshore samples. Conversely,

the growth rate of the remaining nearshore fish may be artificially depressed due to loss of large fish to offshore areas and to recruitment of smaller downstream migrants or fish from areas closer inshore.

Parker (1971) found that a large part of the early mortality of pink and chum salmon was due to predation by coho smolts. He showed that there was greater selectivity by the predator for smaller prey resulting from late entry into the estuary, from slower growth rates, or from a preference for pink rather than chum salmon. He suggested that rapid growth might be important for survival of pink and chum salmon because that would allow them to grow out of a size class in which they were susceptible to predation.

Larkin (1988) examined the evidence for compensatory growth and mortality of sockeye salmon. Average total mortality of sockeye salmon at sea is around 90%, but varies from stock to stock and from year to year. Large smolt productions in sockeye have been associated with higher rates of marine mortality, e.g. for Cultus Lake (Foerster 1954) and Chilko Lake (Henry 1961). Mortality has also been shown to be lower when smolt size is larger. For pink salmon, a large production of seaward migrants may be associated with smaller adults returning (Davidson and Vaughan 1941; Hoar 1951; Neave 1953; Peterman 1978).

Diet composition

Diets have been described for salmon from a number of estuaries (LeBrasseur et al. 1969; Levy and Levings 1978; Sibert and Kask 1978; Fedorenko et al. 1979; Healey 1979, 1980b; Levy and Northcote 1981; Argue et al. 1986). The main conclusion from these studies is that salmon diets vary seasonally, geographically and annually. Thus salmon are opportunistic feeders and capable of exploiting a variety of taxa.

Parker (1969a) examined the diet of pink salmon fry. He noted that the pink fry entering the estuary fed incessantly, with diet consisting mainly of smaller zooplankters such as nauplii of copepods and barnacles, and oikopleura. With growth, the diet became mainly (80%) calanoid copepods. The pink salmon grew quickly (7% weight increase per day) and had catholic tastes, suggesting they are opportunistic feeders. The pink salmon fry appeared to leave the estuarine environment when food availability declined. He noted an afternoon maximum in feeding as indicated by relative stomach fullness.

Levy and Levings (1978) sampled the fish community of the Squamish River estuary during the period October 1975 to September 1976, using beach seines, gillnets and tidal creek enclosures. Juvenile salmonids used the estuary during spring and summer months (except for sockeye salmon). The salmonids

fed on estuarine crustaceans and insects, especially the mysid *Neomysis mercedis* and the amphipod *Anisogammarus confervicolus*.

Argue et al. (1986) sampled juvenile coho and chinook on the Cowichan River estuary and in Cowichan Bay using tow nets and pole, beach and purse seines. Estuarine benthic organisms and insects were most common by weight in the stomach contents of chinook and coho from March through May. Stomach contents of juveniles of both species caught from June onwards were dominated (content weight) by larval and juvenile fish (principally Pacific herring).

Healey (1980b) reported that the diets of chinook were similar over the course of the two years, with feeding on harpacticoid copepods important in March and early April, decapod larvae and amphipods in April and May, and mysids and insect larvae in May–July. Outside the intertidal area of the estuary, fish larvae, mainly herring, dominated the diet of juvenile chinook salmon from May to August, whereas calanoid copepods, decapod larvae and insects were occasionally important. Thus a change from a predominantly invertebrate diet to a predominantly fish diet occurred as young chinook salmon dispersed away from the intertidal area of the estuary. Using weights of stomach contents as an index of feeding conditions, he found that there was substantial variability from year to year. Poorest feeding conditions occurred in 1976 and the best conditions were in 1975 when population densities were the highest. There was a concomitant decline in the volume of stomach contents at these high juvenile densities.

Healey (1982a) summarized information on abundance, food requirements and production of the five major species of Pacific salmon in two estuaries in southern British Columbia and compared some of these features among seven other estuaries. He stated that the major prey of juvenile salmon in estuaries tends to be detritus feeders, suggesting that the food web supporting juvenile salmon is detritus based. Adult insects (mainly Diptera) were also a common occurrence in diets. Decapod larvae were important in the diet from seven of the nine estuaries considered in this report. Harpacticoid copepods, decapod larvae and cladocera were common in diet of chum salmon from several estuaries in southern British Columbia (Healey 1979 and unpublished data; Levy and Northcote 1981). Sibert and Kask (1978) compared diets of coho and chinook salmon among estuaries and among habitats within estuaries and concluded that each species had a distinctive feeding habit within an estuary but there was little similarity between estuaries. They said coho salmon had a narrow diet spectrum and their diet did not overlap with that of other species. Chinook salmon had a wider spectrum. Levy and Northcote (1981) compared chum and chinook salmon from marsh habitats of the

Fraser River estuary and concluded that chum salmon diet varied less from place to place than did chinook salmon diet. Thus, Healey (1982a) suggested that the range of feeding specificities among juvenile salmon correlated with the degree of dependence of the species on estuarine habitats. Chinook salmon, having great dependence on estuaries, appear less restricted in the types of food they can exploit. He also suggested that all the juvenile salmon, but particularly chinook and chum, appear to depend greatly on prey animals living near to or on the bottom, particularly in the inner estuary. He found that more pelagic forms were taken in the outer estuary but benthic food was still most important.

Kask et al. (1988a, b) examined the nearshore epibenthos of the Campbell River estuary and Discovery Passage, in relation to juvenile chinook salmon diets. Specifically, 284 epibenthic sled samples were collected from ten sites, which included established areas and newly created islands in the estuary as well as sites in the transition area immediately off the river mouth and in the marine zone. The epifauna was counted and compared to the food organisms present in juvenile chinook collected in the same areas. Comparisons were also made of the epibenthos and the diets of juvenile chinook in all three zones from 1982 to 1984. In the estuary, both wild and hatchery chinook relied on marine calanoids most likely transported in with the salt wedge (Brown et al. 1984) and freshwater cladocera flushed downstream from the lake and river habitat. The epibenthos (amphipods, harpacticoids, isopods, and cumaceans) contributed to the diet but usually comprised less than 15% of the total diet for either group. Once into the transition zone, the juvenile chinook salmon consumed mainly epibenthic amphipods and harpacticoids. These two groups alone made up 64–91% of the total diet. Calanoids made up a much smaller percent of the diet than in the estuary. The 14 wild fish analysed from the marine zone had eaten mainly harpacticoids (62%), barnacle cypris (24%) and decapod larvae (8%). Animals of benthic origin formed part of the diet in all three zones. They were most important in the transition zone followed by the marine and estuarine areas. Kask et al. (1986) compared the diet of juvenile salmon in the estuary and nearshore areas to that of previous studies and found differences in prey items between years and areas. In 1983, diets of all the chinook salmon analysed in all three zones changed from that recorded in 1982, demonstrating the opportunistic nature of chinook feeding preferences.

Following an experimental rehabilitation of the Campbell River estuary in 1981 to 1982, a program was established to monitor the use of the new, as well as the established, habitats of juvenile salmonids, particularly wild and hatchery chinook salmon. The

role of each of the nearshore habitats in providing food for the young fish was also monitored using an epibenthic sled (Kask et al. 1986). From March to December 1982, 146 nearshore samples were collected from three different habitat areas: estuary, transition and marine. Copepod nauplii, nematodes and harpacticoids dominated the estuarine and transition zones whereas harpacticoids, copepod nauplii and amphipods dominated in the marine zone. Densities of nearshore epibenthos were highest in the marine zone and lowest in the estuarine zone. Overall mean density of harpacticoids was almost 40 times greater in the marine zone than in the estuary. The epibenthic nearshore populations appeared to be most important in the diet of the juvenile chinook salmon in the transition zone, followed by the estuarine and marine zones. The transition and marine zones seemed to have the highest food potential, the dominant prey organisms occurring in the greatest densities in these nearshore areas. Epibenthic organisms never constituted more than 40% of the salmon diet in the estuarine zone. The proportion of epibenthos in the diet increased to over 99% in the wild chinook and 74% in marked chinook salmon (mainly harpacticoids and copepods). These fish also began to prey on pelagic euphausiids. Once in the marine zone, they reduced reliance on epibenthic harpacticoids and increased consumption of decapods (megalops and zoea) and pelagic amphipods. Pelagic calanoids, mainly *Neocalanus plumchrus*, were consistently present in stomachs of juvenile chinook in all three zones and often dominated their diet. Even in the estuarine zone, marine calanoids transported in with the salt wedge formed a major part of the food in both wild and marked fish. Amphipods were also important in all three zones.

Levings (1994a) continued the examination of feeding behaviour of juvenile salmon and the significance of habitat during the estuarine and early sea phases. He evaluated feeding success by using the Forage Ratio (FR), which is the ratio of weight of food in the stomach of a fish compared to the weight of the fish. Both forage ratios and food consumption have been found to vary between habitats and with environmental conditions. Post-smolt chum in British Columbia showed higher forage ratios in estuarine habitats (FR = 1.84) than in offshore areas (FR = 1.48) in the Strait of Georgia. The same trend was shown by post-smolt chinook salmon in the same area (Healey 1982b).

Bravender et al. (1996) surveyed the fish populations, juvenile salmon diets and epibenthic invertebrates in the Englishman River estuary in 1993. Chinook and chum salmon found between March and July were rearing in several low tide refuges. Most of the chinook salmon juveniles were hatchery fish from Big Qualicum River stock and reared in a side

channel in the Englishman River by Habitat Enhancement staff in Nanaimo. Diet analysis for chinook showed that insects dominated the diet. Forage ratios calculated for juvenile chinook were similar for those recorded for both the Nanaimo River and Campbell River estuaries.

Feeding outside of estuaries

Manzer (1956) examined the diet of young pink, chum, sockeye and coho salmon between June and August 1955 in Chatham Sound, in northern British Columbia. In general, food spectra were similar but the degree of importance of different groups varied. In general, pink and chum salmon were planktophagous, with copepods and oikopleura spp. being most important. Coho were mainly piscivorous (herring larvae and sandlance (*Ammodytes hexapteras*) most frequent). Sockeye salmon overlapped these two groups somewhat in their diet. They fed mainly on plankton but fish were also important. Samples of cohabiting pink and chum salmon showed that either all or many of the individuals consumed copepods, but this item made up a greater fraction of the food of pink salmon.

Godfrey (1968) presented data on the diets of chinook, coho and chum salmon captured in June 1965 in the Gulf Islands, Fraser River plume and central Strait of Georgia. He found that juvenile chum salmon consumed much smaller organisms than juvenile chinook and coho salmon. All three species fed on fish, zooplankton and terrestrial insects. Some chinook and coho salmon fed on sandlance, but this was not found in chum stomachs. He suggested that the frequency of occurrence of terrestrial insects indicated that surface feeding was of some importance to each of the three species.

Godin (1981) examined the stomach contents of pink salmon fry in the littoral zone of Departure Bay and Hammond Bay, Nanaimo, British Columbia. Stomach analyses showed that pink salmon fry fed mainly during daylight hours in May. Although the diurnal pattern of feeding differed slightly between the two bays, maximum mean prey biomass in the stomachs of the pink salmon occurred near or at dusk in both bays. The fry consumed similar items in both bays, but in differing proportions. Harpacticoid copepods, copepod nauplii, and barnacle larvae collectively comprised 93.1 and 86.2% of the diets of Departure Bay and Hammond Bay fish, respectively. About 38% of the diet of Departure Bay fish and 51% of the Hammond Bay fish consisted of epibenthic prey, mainly harpacticoid copepods. These data provided additional support for the importance of the detritus-microbe-consumer type food chain supporting the production of pink salmon during their early period of marine residency. In contrast to the diets

listed here, the diets of larger juvenile pink salmon in more offshore waters consisted mainly of larger, planktonic prey species (Barraclough and Fulton 1967, 1968). Chum salmon fry also fed on epibenthic invertebrates, mainly harpacticoid copepods, in nearshore marine habitats (Mason 1974; Feller and Kaczynski 1975; Sibert et al. 1977; Healey 1979). These fry fed mainly during daylight hours and little or no feeding occurred at night.

Healey presented some of the most detailed observations of diet of juvenile salmon, from within the Strait of Georgia, from Saanich Inlet, as well as in Hecate Strait (as part of the Hecate Strait program), and in the Barkley sound region (as part of the MASS project). Healey (1980b) provided an extensive summary of the diets of juvenile salmon in the Strait of Georgia from studies carried out by himself and various other authors from 1966–1977. Different items appeared to be important in different years. In 1966, sockeye smolts caught in the plume fed on insects, euphausiids and copepods. In 1967, they fed on copepods, insects and fish larvae. In late summer they fed on amphipods and insects. In 1975, sockeye salmon smolts fed on crab larvae and fish larvae, whereas in 1976, copepods and ctenophores were important. He suggested that overall sockeye smolts prefer copepods and insects, but also eat amphipods, euphausiids and fish larvae when available.

Phillips and Barraclough (1978) found evidence that there was an inverse relationship between abundance and size. Pink salmon captured in Fraser River plume in 1966 and 1968, years of high abundance, were smaller on average than those caught in 1967 or 1969, when abundance was low. To grow at a rate of 7% of body weight per day, pink salmon juveniles must eat almost continuously. While in transit to nearshore nursery areas, pink salmon fed on calanoid copepods in April and May in the Fraser River plume. However, in nearshore nursery areas during the same months, they fed on epibenthic prey, with harpacticoid copepods being the major food item (Kaczynski et al. 1973; Healey unpublished data). In late May, when pink salmon moved offshore, they again fed on zooplankton. Data provided by Healey (1980b) for Saanich Inlet for early June 1966 and 1968 were also typical of diets in the Strait of Georgia at that time. Pink salmon fed mainly on copepods in 1966. Of secondary importance in the diets were amphipods, insects, chaetognaths and the larvacean oikopleura. In 1968, euphausiid eggs dominated the diet, with oikopleura, insects, euphausiids, and copepods being of secondary importance (Barraclough and Fulton 1968; Barraclough et al. 1968). In late summer, pink salmon that remained in the Strait fed on amphipods and insects, with crab larvae, euphausiids and copepods being of secondary importance.

The diet of juvenile pink, chum and coho salmon

from the same samples taken in Saanich Inlet were compared by Healey in 1966 and 1968. The relative contribution of various food organisms changed in the same direction between years for all species. It appeared that copepods were less available in 1968 than in 1966, and because of this, pink salmon turned their attention to the next most available and preferred prey, which was euphausiid eggs. The belief that this was a choice, rather than a result of the eggs being overwhelmingly abundant, was indicated by the relatively low abundance of euphausiid eggs in the diet of chum and coho.

Healey (1980b) suggested that small food items are particularly important for pink salmon, including harpacticoid copepods during their residence in near-shore areas, and calanoid copepods and euphausiid eggs in late May and June before they leave the Strait. The importance of amphipods and insects in late summer was thought to reflect the scarcity of copepods at that time, as well as the large size of the remaining pink juveniles in the Strait of Georgia.

Healey (1980b) suggested that stomach contents give a good indication of success of feeding conditions. In Nanaimo River estuary areas the stomach contents increased with time: in April, stomach contents averaged 1–2% of body weight, whereas by late May they increased to 4–5% of body weight. Stomach contents of fish caught over deeper water ranged from 2–3% for most of April and May, increased to 3.5% in early June, and then dropped to less than 0.5% at the end of June. In July the stomach contents averaged about 1% of body weight. Clearly, fish left nursery areas and entered a depth zone where the foraging success was lower. Healey also found that the majority of pink salmon left the Strait of Georgia when foraging success was very poor. Barraclough et al. (1968) reported that stomach contents were poor for a brief period at the end of June 1968 in Saanich Inlet. Thus, movement of pink salmon away from beaches does not appear to be a response to poor feeding conditions but the movement of fish out of the Strait of Georgia in late June and early July may be a response to poor feeding conditions.

The average increase in the fork length of chum salmon from samples taken in the Fraser plume was 0.80 mm/day in 1966–69 (Phillips and Barraclough 1978) and from samples taken monthly in the Gulf Islands in 1976 was 0.72 mm per day. In nearshore nursery areas and estuaries, chum salmon fed mainly on harpacticoids (Kaczynski et al. 1973; Healey 1979), although Dunford (1975) found that chum in the upper Fraser marshes fed mainly on chironomid larvae and cladocera. In 1966 and 1968, chum that moved offshore fed mainly on oikopleura. This was also a dominant food item in the chum diet in the Nanaimo area during June 1975 (Healey unpublished data), and Chatham Sound in northern British Co-

lumbia (Manzer 1969). Chum salmon also appeared to prefer polychaetes and chaetognaths. They generally took larger prey than pink salmon and were less attracted to euphausiid eggs than pink salmon were.

Healey (1979) reported on regional diet differences found in the late summer of 1975. The regional comparison suggested that chum salmon prefer euphausiids over other items such as crab megalops. In 1975 and 1976 he recorded stomach content weights. In the Nanaimo River estuary, average contents varied from 1.2 to 5.9% body weight between March and June. There was no apparent seasonal trend, but stomach contents did tend to be low when chum were most abundant in the estuary. However, there were more chum salmon rearing in the estuary in 1975 than in 1976, and their stomach contents were greater on average in 1975, which suggested a relationship between carrying capacity of the estuary and food supply (Healey 1979). Similar changes in stomach contents were seen over time, as e.g. with pink salmon, but chum salmon tended to have more food in their stomachs. Seasonal changes suggested that the best feeding conditions for chum were in May. As with pink salmon, they left nearshore areas when feeding conditions were improving, and entered the pelagic zone where their feeding success appeared lower. Their departure from the Strait of Georgia in late June was associated with the lowest recorded stomach contents. Chum salmon also showed reduced stomach contents at this time in Saanich Inlet in 1968 (Barraclough et al. 1968).

Euphausiids dominated the diet of juvenile coho caught in Saanich Inlet in June of 1966 and 1968. Since diets of pink and chum salmon suggested that euphausiids were less abundant in 1966 and 1968, their predominance in the diet of coho suggests that they are a preferred prey. Coho salmon did show flexibility in the importance of secondary items, probably as these are taken with respect to availability. Coho also showed regional differences in diet. They showed a positive correlation between abundance and the amount of food in their stomachs in late summer 1975 and 1976, leading to apparently greater numbers remaining in the Strait in 1975, when feeding conditions were better.

Chinook salmon show a complex size distribution in the Strait (Healey 1980a, b). In the estuary, they were seen to feed on a wide variety of invertebrates and were much less dependent than chum salmon on small copepods. Chinook juveniles ate insect larvae and adults, amphipods, decapod larvae and calanoid copepods (Sibert and Kask 1978; Healey unpublished data). Upon leaving the estuary, larval and juvenile fish were the dominant prey of juvenile chinook, and invertebrates were a diet choice of secondary importance (Godfrey 1968; Beamish et al. 1976; Healey unpublished data). Prey such as

crab megalops, euphausiids and amphipods made up the invertebrate fraction. Diet was seen to change from year to year depending on availability of various organisms. Overall, chinook salmon appeared to prefer fish, particularly Pacific herring, but also liked larger invertebrates and appeared to have similar food preferences to coho. Healey (1980b) also found a relationship between chinook salmon abundance and feeding conditions similar to that for coho and chum salmon.

The way that the young salmon use nursery areas in the Strait of Georgia suggests resource partitioning (Healey 1978, 1980b). Pink, chum and chinook salmon that migrate downstream as fry spend most of their first month in the ocean in very shallow water close to shore. Chum and chinook salmon coexist in estuaries and pink and chum salmon in high salinity nurseries. All three species are opportunistic feeders, and often have the same diet components when they coexist. However, when dominant food items are the same, they generally are found in different proportions in the diets and the choice of secondary items differs. Chinook, particularly, feed on different things than chum salmon during estuarine residence. Harpacticoid copepods and shrimp larvae are dominant items for chum feeding, but chinook feed on harpacticoids for only a few days after migrating downstream, and after that concentrate on amphipods, insect larvae and adults, and mysids. Pink and chum salmon do feed on the same things but in different proportions.

The major concentration of juvenile pink and sockeye and possibly chum salmon, occurs around the Gulf Islands (Healey 1978, 1980b). Thus, just a small area of the Strait of Georgia was originally believed to support the bulk of the juvenile salmon population. Offshore movement appears to be unrelated to food abundances, and is apparently not timed to correspond to plankton blooms in the Strait of Georgia, as these blooms are beginning to decline in May. Juvenile pink, chum and sockeye salmon that are foraging over deep water in May and June may experience food shortages as their demands increase with growth. Thus it is hardly surprising that this is when the greatest differences in diets occurred: chum feed mainly on oikopleura, pink on small copepods and invertebrate eggs, and sockeye on copepods, amphipods and insects (Healey 1978). Stomach volume was low, perhaps indicating that these species leave the Strait of Georgia in response to poor feeding conditions (Healey 1980b, 1982a). After these juveniles left, feeding conditions appeared to improve for the young-of-the-year sockeye salmon entering the Strait. Juvenile sockeye salmon fed well and grew rapidly at the food densities found during July and August.

Healey (1980b) suggested that coho and chinook salmon do not depend as much on invertebrate food

resources as chum, pink and sockeye, and thus they face a different situation. In fact, a significant proportion of coho and chinook salmon remained within the Strait of Georgia to rear. Chinook stomach contents did not decline in late June, as did those in pink and chum salmon (Healey 1978, 1980b). Both coho and chinook salmon fed on larger invertebrates as well as fish: e.g., while pink and chum salmon in Saanich Inlet ate copepods, euphausiid eggs and oikopleura, coho fed on euphausiid adults and insects. In late summer, both coho and chinook salmon concentrated on amphipods, crab megalops and fish. Because of their preference for fish and large invertebrates, coho and chinook may not compete with pink, chum and sockeye salmon but may compete with each other.

Bravender et al. (1996) compared the diets of juvenile salmonids in the Englishman River estuary with the diets recorded for the Nanaimo River estuary by Healey (1980a) and the Campbell River estuary (Kask et al. 1986, 1988a, b; Macdonald et al. 1988). Juvenile chinook in the Englishman River estuary fed primarily on insects, mainly dipteran adults, but also other adult insects and larvae. In the Nanaimo River estuary, juvenile salmon fed on five taxonomic groups which changed in importance as the fish grew over the spring, with the salmon progressing from feeding on harpacticoid copepods in early spring, to decapod larvae, amphipods, mysids and insect larvae in early summer. In the Campbell River estuary, freshwater cladocerans and copepods were the most important components of the diet.

Healey (1991) also examined the diets and feeding rates of juvenile pink, chum and sockeye salmon in Hecate Strait during July and August 1986 and 1987, as part of the Hecate Strait program. The objectives of this study were to describe seasonal and species-specific patterns of feeding and to test assumptions and predictions of models relating feeding success of juvenile salmon during their first summer at sea to survival and recruitment. A wide variety of taxa was consumed by all three species, but only a few taxa made up most of the fishes' daily food intake. Diet composition was more similar among species within sampling periods than within species among sampling periods, although there were some apparent species-specific feeding preferences. Patterns of changing diet composition with increasing time and distance between samples were consistent with expected mesoscale patterns of plankton patchiness in coastal waters. Juvenile salmon fed selectively on larger sized taxa in the plankton community and larger salmon fed on larger prey. Young salmon did not switch to larger prey later in the summer, however. Weights of stomach contents and estimated daily ration were small enough to limit growth rates, and the hypothesis that limitation of growth during

early ocean life affects survival and recruitment cannot be rejected.

Haegele (1997) collected information on herring, salmon and plankton abundance in the Strait of Georgia from 1990 to 1994. Purse seine and plankton tows were made on ten transects, each with five stations, around the perimeter of the Strait of Georgia during two weeks in both the late spring and late summer. Haegele found that juvenile chinook, coho and chum salmon were much more common in late spring than late summer. He did not catch any juvenile pink or sockeye salmon. Major plankton species were copepods, crab larvae and euphausiids which were also the major prey of juvenile herring and chinook and coho salmon. Larvaceans and amphipods were of lesser abundance in the plankton but were targeted by the juveniles of chum, sockeye and pink salmon. Haegele (1997) reported that there was no obvious correlation between plankton density and juvenile Pacific herring or salmon abundance. Both juvenile chinook and juvenile coho salmon ate mainly crab larvae, but they both also ate fish, mostly Pacific herring larvae and 0+ herring, along with amphipods, euphausiids, and insects. Chum salmon ate different things in different years: overall larvaceans were most common in spring, and amphipods and euphausiids and crab larvae in the summer. Sockeye and pink salmon juveniles had the most cosmopolitan diet feeding on all the above prey as well as ostracods. These results were similar to those of Healey (1978) except that Healey considered fish to be more important in the diet of chinook and coho salmon juveniles than did Haegele (1997). Generally, salmon juveniles did not appear to target copepods, the principal prey of herring.

Perry et al. (1998) examined spatial variations in feeding and condition of juvenile pink and chum salmon feeding on the Vancouver Island continental shelf during the early summer of 1992. They found that juvenile pink salmon off northern Vancouver Island had more food in their stomachs, and were in better condition, than pink salmon off southern Vancouver Island. Juvenile chum salmon in the north also had more food material in their stomachs, and the authors suggested that these variations were associated with variations in zooplankton biomass, since they found more plankton in the north. There was a significant positive relationship between amount of food in pink salmon stomachs and their condition factor. However, no difference was found in the condition factor of chum salmon between northern and southern regions and there was no relationship between stomach contents and condition factor for chum salmon from the south. Using a bioenergetics model, the authors showed that pink salmon in the north had higher potential growth rates than those in the south, but chum salmon did not respond in the

same way. They suggested that chum salmon in the south were food limited.

Using diet comparisons, King and Beamish (2000) indicated that there could be a competitive interaction between ocean age 0 chum and coho salmon. Trawl surveys were carried out in the Strait of Georgia in June/July and September of 1997 and 1998. Onboard stomach analyses were done on 2,230 ocean age 0 coho and 1,558 ocean age 0 chum salmon. In June/July 1997, the three most abundant food items for coho were decapods, teleosts and euphausiids, while decapods, teleosts and amphipods were the top items for chum. In September 1997, amphipods replaced decapods for coho and ctenophores replaced teleosts for chum. In June/July 1998, the top three items for coho salmon were decapods, amphipods and teleosts, and for chum salmon were decapods, amphipods, and euphausiids. In September 1998 the top three items for coho were amphipods, euphausiids and decapods, and for chum were amphipods, euphausiids and ctenophores. The authors concluded that in early summer, chum are potential competitors of coho salmon in the Strait of Georgia, whereas by late summer, the chum were still competitors but also began to feed on gelatinous zooplankton. There was almost complete diet overlap between hatchery marked and unmarked coho.

Neville and Beamish (1999) compared the diets of ocean age-0 hatchery and wild chinook salmon from the Strait of Georgia between 1996 and 1998. Salmon were identified as hatchery or wild using otolith microstructure. Diet items were summarised into nine main categories and by percent volume and frequency of occurrence. Diet overlap was determined using a modified Morisita Index. There was a significant overlap in diet of hatchery and wild ocean age 0 chinook and this overlap persisted even with differences in size of the two types. The dominant diet items for both were amphipods, euphausiids, decapods and teleosts.

Beamish et al. (2001b) examined the hypothesis that during some ocean conditions, Pacific herring could also be a competitor of juvenile coho salmon. Traditional views were that the survival of coho might be linked to the abundance of herring as prey. Beamish and co-workers proposed that the abundance of coho salmon might also be linked to herring through diet overlaps, resulting in reduced coho growth and consequent higher winter mortalities. The critical size and critical period hypothesis of Beamish and Mahnken (1998, 2001) proposed that, during the first marine summer, coho must grow at a rate that would enable them to survive the first marine winter. The diets of ocean age 0 coho showed a preference for small fish, while Pacific herring age 1+ and 2+ preferred copepods and small eggs of invertebrates. However, decapods, amphipods, and euphausiids

were prey that were common to both diets. Beamish et al. (2001a) showed that there was no relationship between herring abundance and coho abundance, ruling out a direct linkage between coho and herring, either as prey or competition. However, once it is known that slower growing coho do not survive through the first marine winter as well as their faster growing siblings, then Beamish et al. (2001a) argued that it was possible that competition from herring contributed to the aggregate of factors that reduced growth of coho in their first marine year below a critical minimal level.

HATCHERY STUDIES

Most work regarding juvenile hatchery fish in the ocean has been 1) examination of interactions in estuaries by workers such as Levings (Levings 1985, 1986; Levings et al. 1986, 1987, 1989a, b; Levings 1990, 1991; Levings and Macdonald 1991; Levings 1993a, b, 1994a, b, c; Bravender et al. 1996; Levings and Bouillon 1997; Bravender et al. 1997a,b; Korman et al. 1997; Levings 1998; Bravender et al. 1999) and 2) determination of abundance and survival of hatchery fish in the Strait of Georgia (Beamish et al. 1998b, 2000a; Sweeting et al. 2003). Korman et al. (1997) analysed juvenile salmon population growth and abundance data collected in the Campbell River estuary in 1994 to describe chinook habitat use, residency timing, growth, and potential competitive interactions between wild chinook fry, hatchery chinook and other salmon species. The authors found that wild chinook fry densities were highest in estuarine zone sites, while hatchery chinook densities were generally higher than wild densities between the nearshore and deeper water habitats. Habitat type significantly affected the density of wild chinook in the estuary where their densities were greatest at riparian and intertidal island sites. Hatchery and wild chinook juveniles showed different patterns in their seaward emigration timing. The timing of peak abundance of hatchery chinook in the estuary coincided with the peak abundance of wild fry. This was considered a likely period of strong competitive interaction between hatchery and wild chinook salmon. Wild and hatchery juveniles were generally larger at transition zone sites compared to those from the estuarine zone. Growth rates of wild chinook tended to be slightly higher than growth rates of hatchery chinook. The inverse relationship between wild chinook fry size and total salmon biomass, assessed in mid-May, was similar to that established with earlier data, supporting the conclusion that growth of wild chinook in the Campbell River estuary may be density dependent.

McAllister and Brown (Pacific Biological Station, Nanaimo, BC, Canada, personal communica-

tions) also examined the use and residency of hatchery and wild chinook fry and juveniles in the Campbell River estuary. They examined these issues from 1982–1986 and in 1989, and concluded that the hatchery juveniles affected the growth and size of wild chinook fry in the estuary and that increases in rearing capacity resulting from the intertidal islands may also have reduced competitive effects on wild chinook growth. They concluded that wild chinook fry appeared to move seaward more rapidly in years of high total salmon biomass in the estuary than in years of low biomass, which could potentially lead to greater exposure of smaller chinook to larger predators outside the estuary.

Levings et al. (1986) examined the differential use of the Campbell River estuary by wild and hatchery-reared juvenile chinook salmon. Juvenile chinook were sampled by beach seine between March 1982 and December 1983 in the Campbell River estuary and adjacent waters of Discovery Passage to examine estuarine use by wild and hatchery fish. Wild juvenile chinook entered the estuary as migrant fry and were present in the estuarine zone mainly in late April to June, in the transition zone mid-May to July and in the marine zone in July. Maximum catches of wild stocks were similar in the estuarine and transition zones, but maximum catches of most hatchery stocks were higher in the transition zone. For both wild and hatchery chinook, catches in the marine zone were much lower than in the estuarine and transition zones. Wild fry resided in the estuary for 40–60 days, while most hatchery fish used the estuary for about one half of this time. Residency and growth rates of wild fish were similar to those recorded for wild fish in the Nanaimo estuary, where there were no hatchery fish (Healey 1980a). The potential for interaction between wild and hatchery fish was greatest in the transition zone, where hatchery fish were most abundant and because hatchery releases occurred when catches of wild fish were highest in this foreshore area. This study allowed some preliminary analysis of diet differences between hatchery reared and wild salmon. Comparisons of the percent numerical composition of the dominant taxa in stomachs were made from a number of established and new sites. Chi squared analysis showed significant differences at all stations in both years, with a predominance of marine calanoids in the hatchery fish diet, and an abundance of harpacticoids, calanoids, insects and freshwater cladocerans in the diet of the wild fish. Higher rates of growth were seen in the hatchery fish with earlier release dates and smaller mean sizes. These results indicated that chinook food limitation and interspecific or intraspecific interactions may be most significant in the transition zone. Here, catches of hatchery groups were highest, and in both 1982 and 1983,

large numbers of hatchery fish were released when the main migration of wild stocks to the transition zone was occurring (late May to early June). Using estimated peak biomasses for the two different groups, Levings and co-workers were able to estimate, based on size of fish, that hatchery chinook could consume up to four times as much food as wild fish. In late June the transition zone also supported high densities of pink and chum juveniles, many of which may be Fraser River outmigrants (Levings and Kotyk 1983). These two species could impose a food demand almost equivalent to that of the wild and hatchery chinook and their peak biomasses also occurred in mid to late June. Wild chinook fry in the Campbell River area in 1989 comprised a total of 55% of the total catch of young salmon in the estuary but appeared to consume only 28% of the total rations required by the young salmon. Chinook and coho smolts from the Quinsam hatchery were found to take the largest fraction of rations in the estuary (approximately 65%) even though they were found to make up only 28% of the average numbers caught. Hatchery chinook and coho salmon also dominated food consumption in the transition zone immediately outside of the estuary, consuming approximately 63% of the total.

This major study of the importance of estuaries for salmon showed that in two of the three years of the experiment, fish that experienced the estuary survived best (Levings et al. 1989b). There was evidence of changing ocean conditions in the third year and final conclusions remain to be published. Their unpublished summary appears to show that the total return of all age classes of chinook salmon, in all brood years, was a function of both estuarine and open ocean conditions. The survival experiments and the hatchery-wild interaction studies showed that the factors affecting chinook salmon survival in estuary and ocean habitats are likely not independent. Levings et al. (1989b) suggested that if wild chinook salmon are to be maintained, habitat space in the estuaries needs to be maintained or enhanced and interactions with hatchery fish need to be minimized. A very important conclusion was that the size and health of the fish as established in the estuary may affect their survival later in the ocean.

Beamish and staff had carried out a survey to determine juvenile coho abundance and distribution in the Strait of Georgia and in Puget Sound in 1997 (Beamish et al. 1998a). In addition, the survey provided data that enabled estimates of hatchery and wild coho to be determined prior to any fishery (Sweeting et al. 2003). These marked coho and catches from surveys in June/July and in September indicated that the proportion of juvenile hatchery coho salmon within the Strait of Georgia ranged from 76–79%. If estimates of smolts from enhanced adults

(i.e. hatchery fish spawning in the wild) were included as hatchery releases, estimates of hatchery percentages in the catch could be as high as 87%. Both hatchery and wild juvenile coho salmon remained in the Strait of Georgia until after September, several months after coho left Puget Sound. There was no difference in the fork length of coho with or without the left pelvic fin.

Beamish and Sweeting (1999) examined the patterns in the recapture rates among release locations of coded-wire tagged (CWT) juvenile coho salmon in the Strait of Georgia. Analysis of CWT recoveries from research surveys during 1995 to 1998 indicated that, in September, the production from Fraser River hatcheries dominated the recaptures. However, recaptures from the Fraser River hatcheries also tended to exceed the expected adult returns, indicating that early marine survival was higher for Fraser River stocks than for coho salmon juveniles released on the opposite side of the Strait. The relative proportions of CWTs from the nine major hatcheries seen in the September surveys generally persisted until the next fall, which indicated that the fall/winter mortality was non-selective across all of the hatcheries.

Zhang et al. (1995, 1998) found that otolith microstructure exhibited characteristic differences between hatchery reared and wild chinook salmon from the Cowichan River. The daily growth increments that formed in the otoliths of the hatchery-reared salmon after exogenous feeding were more regular in width and contrast than those in the otoliths of wild chinook salmon. Also, hatchery fish otoliths often showed a check when the fish were released from the hatchery. Samples were collected in early summer, late summer and late fall in 1995, 1996 and 1997. The percentage of wild fish dropped from 71.5% in late summer to 36.8% in the late fall of 1995, and more dramatically from 61.4% in the late summer to 19.2% in the late fall of 1996. There was also a general decrease in lengths of each rearing type from the 1995/1996 samples to the 1996/1997 samples, suggesting that ocean conditions were possibly less favourable for growth in 1996/1997. Hatchery fish were not found to be moving into the Strait of Georgia in the fall, and thus, differential mortality and/or utilisation of these waters accounted for this shift to a reduced percentage of wild juveniles.

EARLY MARINE GROWTH

Relationships between Marine Mortality and Environmental Correlates

Early studies focussed on the influence of fresh water factors on production of salmonids (Pritchard 1936; Davidson and Hutchinson 1943; Davidson et al. 1943; Pritchard 1947a, b; Neave 1949; Neave and

Wickett 1948; McKernan et al. 1950; Brett 1951; Wickett 1951, 1952; Neave 1953; Smoker 1954; Wickett 1954; Silliman 1970). However, examination of the relationship between ocean factors and survival of Pacific salmon began in the late 1950s. Vernon (1958) found that year class strength of pink salmon in the Fraser River was negatively correlated with the temperature encountered by juveniles when entering the Georgia Strait. He also showed that there was an inverse relationship between sea surface temperature in the Strait of Georgia during the seaward migration stage (April to August), and pink salmon catches (total run or percentage survival) of the following year. However, this apparently only held for the 1935–1957 data and not later data. Vernon (1956) suggested that the negative relationship between temperature and pink salmon survival might not be due to lethal temperatures, but due to warm surface waters forcing young fish to move to deeper strata where food may be less suitable or predation more intense. He suggested that because the Fraser River and its estuary are near the southern limit of the range for pink salmon, their abundance might be inversely related to sea temperature. Overall, low temperatures and high salinity appeared to be most favourable for survival. Wickett (1958) found that low sea surface temperatures along the coast in June were associated with reduced survival of pink salmon in central British Columbia.

Hunter (1959) examined the effects of temperature, stream discharge, sex ratio and population density in relation to egg to fry survival of pink and chum salmon in the central coastal region of British Columbia between 1947–1956. Within the limits of this study, temperature, stream discharge and sex ratio did not appear to affect the population, but population density was important. The density of spawners in preceding years also affected the survival in subsequent years. Predation was an important factor in keeping fry density low. Ocean survival, including the effect of fishing mortality, varied from 5.2% down to 0.7% for pink salmon, and from 2.6% to 0.85% for chum salmon. Ocean survival for pink salmon before fishing mortality ranged from 10.8% down to 1%. The combination of freshwater and ocean survival rates indicated that a variation of up to 190 times the lowest rate recorded was possible.

Holtby and Scrivener (1989) examined correlations between coho smolt survival at Carnation Creek, British Columbia and environmental factors. They found negative correlations between sea surface temperatures (SST) and smolt survival in the year of migration for coho salmon and also showed lower smolt survival during years of higher temperatures and low salinity. They suggested that variability in smolt survival was associated with variations in SST during the first few months of ocean residence. Holtby et al.

(1990) found positive correlations between salmon growth rates and upwelling. Holtby (1988) found that smolt size can be an important factor in determining smolt survival and that a size selective mortality agent was acting during some of the years in his study. Overall, he concluded that smolt survival was size dependent during years when smolt survival was poor, and when herring abundance was low, which is consistent with the hypothesis that variation from smolt to adult survival of the coho salmon of Carnation Creek resulted from changing predation intensity.

Holtby et al. (1990) examined the influence of smolt size and early ocean growth on marine survival of coho salmon over a 17-year period at Carnation Creek. Comparisons of overall marine survival were made both between years, using two smolt groups of different age and of different mean sizes, and within years, using observed smolt size distributions and smolt size distributions back calculated from the scales of returning adults. Large size did not give a consistent survival advantage, but large smolts did survive better in years when marine survival was relatively poor. Marine survivals were correlated with early ocean growth as estimated by the spacing of the first five ocean circuli on the scales of returning adults. Marine survival and early ocean growth were positively correlated with ocean conditions indicative of strong upwelling along the northwest coast of Vancouver Island. Neither smolt survival nor early ocean growth was correlated with regional coho smolt production. The authors suggested that interannual variability in smolt survival was driven by ocean conditions that determined smolt growth rates, which subsequently affected the susceptibility of smolts to a size selective predator. The authors also found that marine survival and early ocean growth were positively correlated, which suggested that marine survival of Carnation Creek coho salmon was closely related to ocean conditions off the west coast of Vancouver Island during the first four months of life. Conditions favourable to upwelling and subsequent transport of upwelled water onto the continental margin may have been conducive to fast growth for juvenile salmon migrating up the coast. Relatively fast growth was in turn associated with relatively high survival. They also found covariation of survival of coho salmon smolts and Pacific herring, suggesting some common underlying factor.

The marine survival of chum salmon was also correlated with sea surface salinity for April or for the spring months at Amphitrite Point, British Columbia (Scrivener 1987). This salinity was taken to be an indicator of the distribution of predators and of areas of upwelling and high plankton productivity in the nearshore zone off the west coast of Vancouver Island (Fulton and LeBrasseur 1985). In years of very low salinities, the plankton-rich subarctic boundary

between the Alaska Gyre with its coastal current and the California Current shifted northward. Very low survivals were obtained for chum salmon juveniles that entered the ocean during those springs. The marine survival of chum salmon was also related positively to fry size and the timing of movement into salt water (Scrivener 1987, Holtby and Scrivener 1989). Both were affected by logging.

Predation Studies

Parker (1969b) examined the predator-prey relationships among pink and chum salmon fry and coho salmon smolts in a central British Columbia inlet. For brood years 1961 to 1963, 56, 61 and 32 million pink fry, respectively, were estimated to have entered the sea. During the first 40 days of sea life, he estimated that 43, 34 and 19 million fish were lost to the populations, representing losses of 77%, 55% and 59%. Parker suggested that these losses were mainly due to predation by coho salmon smolts.

Parker (1971) suggested that pink salmon survival was higher than chum salmon due to a shorter life history and a faster growth rate. Parker (1971) proposed that selective predation on pink was responsible for enhancing and maintaining this superiority. He tested his hypothesis in the laboratory using coho as predators. Original and terminal length frequencies of both prey and predators were recorded. Populations were maintained until the numbers of prey were reduced. On the basis of experimental evidence, Parker (1971) concluded that coho salmon were size-selective when preying on both juvenile pink and chum salmon during early sea life. Hargreaves and LeBrasseur (1985) re-analyzed these data and calculated the expected number of pink and chum salmon fry remaining in each aquarium at the end of Parker's experiment if predation had been non-selective. They then compared these estimates with the actual number of pink and chum fry remaining, using the χ^2 goodness of fit test. Parker had reported in his paper that coho salmon predation was size selective for the smaller fish, regardless of species. Hargreaves and LeBrasseur's calculations suggested that there were fewer pink salmon fry remaining at the end of the experiment than the number expected if coho salmon predation had not been species selective. Hargreaves and LeBrasseur concluded that coho preferred pink salmon as prey which corroborated the results of their own field experiments.

Dunford (1975) implicated the Pacific staghorn sculpin as an important predator of juvenile salmon. Levy and Levings (1978) found that this sculpin was the most dominant fish in the Squamish River estuary. On several occasions in their study, staghorn sculpins were observed preying on juvenile chum salmon in tidal creek enclosures. The importance of this predation remains poorly understood. Slaney et al.

remains poorly understood. Slaney et al. (1985) suggested that because migrant juvenile sockeye salmon are fairly large, predation on them by other smaller juvenile salmonids in estuarine and marine environments is unlikely. Chum salmon fry, however, are preyed on by other larger juvenile salmonids during their short freshwater migration, in estuaries, and in their early marine rearing phase (Bakkala 1970). In addition to coho and chinook smolts, they are eaten by steelhead and cutthroat trout (*S. clarki clarki*) and Dolly Varden (*Salvelinus malma*) char. Although steelhead smolts prey on salmonid fry in both fresh water (Hunter 1959) and estuaries, they are seldom numerous enough to influence chum stocks (Slaney et al. 1985). Like coho smolts, resident and anadromous cutthroat trout have been considered major predators on chum fry (Pritchard 1936; Hunter 1959), but they are seldom as numerous as coho salmon, Dolly Varden or sculpins and few quantitative data on their impact on chum populations were found. In estuarine and marine habitats, steelhead trout and chum salmon are present at the same time, and they also may move through estuaries and offshore at the same time.

Coho, chinook, steelhead, cutthroat and Dolly Varden are all recorded as predators of pink salmon fry (Pritchard 1936; Hunter 1959; Parker 1965). Parker (1971) reported that coho smolts began to prey on pink fry soon after the fry emerged. The coho salmon followed the pink salmon fry downstream through the estuary and for the first weeks of their marine life. Using a series of multiple mark recapture experiments conducted as pink salmon fry moved out of the Bella Coola river and seaward along Burke channel, Parker calculated that fry losses were between 59 and 77% in the first 40 days after emergence, and that most of these losses were due to predation by coho smolts. Hargreaves (Pacific Biological Station, Nanaimo, BC, Canada, personal communication) also observed coho salmon predation on pink salmon fry in Masset Inlet, and suggested that coho salmon were the main cause of pink salmon fry losses in their early marine life. Models of coho salmon smolt predation on pink fry were developed by Bailey and Anderson (1974), Belford (1978), Peterman and Gatto (1978). They suggested that coho salmon predation can significantly affect pink salmon fry survival and that the extent of predation can be influenced by the duration of exposure.

A number of experimental approaches have indicated that smaller Pacific salmon suffer the highest mortality during early sea life (Hager and Noble 1976; Bilton et al. 1982a, b). Healey (1982c) found more direct evidence, showing that mortality of juvenile chum was strongly size selective over the size range of 45–55 mm fork length. Predation is generally considered to be the most likely cause of size

selective mortality of juvenile salmon.

Hargreaves and LeBrasseur (1985) examined predation on juvenile pink and chum salmon by yearling coho salmon in marine enclosures in Masset Inlet, on the north end of Hecate Strait, British Columbia. They used two net enclosures, each containing 1,500 chum and 500 pink salmon, and added yearling coho to each enclosure. However, the coho salmon had been used prior to this experiment as predators on juvenile pink salmon only as prey. In these experiments, pink salmon were always significantly larger than chum salmon. For the first half of the experiment coho salmon consumed more pink than chum, and more chum than pink during the latter half. They suggested that the change from feeding on pink salmon fry to feeding on chum was because the chance of encountering a pink salmon was much lower than encountering a chum salmon. Also the remaining pink salmon may have reached a size range in which they could not be eaten. In Parker (1971), whose data they reanalysed, the coho also chose pink over chum when the pink were significantly smaller than the chum. Overall then, there appears to be a preference for pink over chum salmon fry.

Withler (1955) reported what he considered was the first record of a young salmon being attacked by a young river lamprey (*Lampetra ayresi*). Roos et al. (1973) reported that river lamprey feed on young juvenile salmon and herring in the Strait of Georgia. Williams and Gilhousen (1968) also found that Pacific lamprey (*L. tridentata*) preyed on Pacific salmon.

Beamish and Williams (1976) examined the effects of river lamprey (*Lampetra ayresi*) predation on salmon and herring stocks in the Strait of Georgia. The numbers and potential importance of river lampreys were unknown until the surface waters of the Strait were fished with a small mesh purse seine. Beamish et al. (1976) carried out a study of the fishes inhabiting the surface waters of the Strait of Georgia during July and August 1974. River lamprey from 14 to 28 cm total length were commonly captured throughout the survey. There was evidence that some young salmon had been attacked by river lamprey. Numerous spiny dogfish also were captured in the surface waters, but most of these were feeding on ctenophores and did not appear to be competing with or feeding on the young salmonids. River lamprey and chinook salmon were found in equal numbers and chinook salmon comprised approximately 20% of the total number of young salmon captured. River lamprey were sufficiently common in the surface waters of the Strait of Georgia to be an important predator of young herring and salmon (Beamish and Youson 1987; Beamish and Neville 1995). Feeding adult lamprey entered the Strait of Georgia from the Fraser River in late spring or early summer and concentrated

in nearshore areas especially in the Gulf Islands. They actively fed on Pacific salmon and Pacific herring in the summer, and preferred Pacific herring. Laboratory studies indicated that one river lamprey could kill an average of one small fish per day. Using this feeding rate and an approximation of the population size, it was estimated that between 60 and 600 million fish could be killed by river lamprey during the active feeding period. Beamish and Neville (1995) determined that in 1990 and 1991, river lamprey killed a minimum of 20 million and 18 million chinook and a minimum of 2 million and 10 million coho salmon. In 1991, river lamprey in the Fraser River plume killed an equivalent of approximately 65 and 25% of the total Canadian hatchery and wild production of coho and chinook salmon, respectively. These estimates are probably low as these river lamprey feed in other areas and the abundance estimates are conservative. Beamish and Neville (1995) estimated that river lamprey predation in the Fraser River plume killed 39 million salmon in 1990 and 51 million salmon in 1991. Chinook salmon were preyed upon in the highest numbers followed by coho.

Estimates for chum salmon smolt production are difficult to determine: estimates of chum salmon mortality in 1990 and 1991 of 14.9 and 10.1 million smolts would account for 13.7 and 4.7 % of the total smolt production of chum from the rivers flowing into the Strait of Georgia and would thus not be considered a major source of early marine mortality. In 1991, juvenile sockeye mortality due to lamprey predation was 11.7 million or 2.3% of the estimated smolt production in the Fraser River. River lamprey left salt water by fall, returning to the Fraser River in preparation to spawn the next spring. Lamprey scars and wounds on all species of juvenile salmon in the Strait of Georgia were also routinely observed in the surveys conducted in the Strait of Georgia by Beamish and staff, confirming that both river lamprey and Pacific lamprey were predators of Pacific salmon.

Beamish and Smith (1976) carried out 129 mid-water trawls, 32 bottom trawls, and 184 purse seine sets resulting in examination of over 100,000 spiny dogfish in the Strait of Georgia during the 1970s. The spiny dogfish were found to feed almost exclusively on planktonic invertebrates, such as euphausiids and ctenophores. Predation on other fishes was rare. Juvenile dogfish occupying the off bottom waters of the Strait of Georgia were found in association with Pacific hake (*Merluccius productus*), wall-eye pollock (*Theragra chalcogramma*), salmon, Pacific herring (*Clupea pallasii*), northern smooth-tongue (*Leuroglossus stilbius schmidti*), myctophids and several other species of small midwater fishes. During the summer, they were routinely captured in association with young salmon. At this time of year, young Pacific salmon of all species and Pacific her-

ring fed almost exclusively on euphausiids. Juvenile spiny dogfish captured in association with these Pacific herring and salmon also fed on euphausiids, but primarily on ctenophores: never on salmon and seldom on Pacific herring. Thus there was virtually no predation on young Pacific herring and salmon and very little competition for the same food source.

A Pacific Biological Station update reported preliminary results of the Beamish predation study near the Big Qualicum hatchery (1989 Pacific Biological Station science updates: July Aug Sept No. 9 Field work for the ocean salmon program mortality). He showed that predation rates on juvenile salmon declined dramatically in early July, coincidental with the appearance of large concentrations of juvenile herring. Virtually all species of predators switched to juvenile herring, although there was a low incidence of predation by dogfish and hake on juvenile chinook. It was suggested based on this observation that this information could be used to determine the correct timing of hatchery releases to increase survival of juvenile chinook salmon. Beamish et al. (1992) noted that large numbers of spiny dogfish moved into the area near the mouth of the Big Qualicum River, BC, at the time hatchery-reared chinook and coho salmon smolts were leaving the river in 1988 and 1989. A small percentage of the spiny dogfish preyed on the smolts, but the resulting smolt mortality was believed to have been large because of the large numbers of spiny dogfish in this area. Spiny dogfish also fed on adult salmon in the fall. The long-term decline in survival of chinook salmon produced at this hatchery was similar to the pattern of survival of other hatchery-reared salmon. Thus, they proposed that predation contributed to the decline. Jones and Geen (1977) found that 27 stomachs of 9,466 spiny dogfish contained Pacific salmon. In three other studies examining the role of spiny dogfish as predators of Pacific salmon (Chatwin and Foerster 1953; Godfrey 1968; Robinson et al. 1982), spiny dogfish were not found to be important predators of Pacific salmon (Chatwin and Foerster 1953).

Beamish and Neville (2001) examined the impact of predation-based mortality on juvenile chinook, coho and chum salmon in the Strait of Georgia using an Ecopath model of the ecosystem. Apart from lamprey and dogfish, which these authors had shown in the past to be important predators of juvenile salmon during the early marine period, the other predators of juvenile salmon in the Strait of Georgia did not appear to be major predators of juvenile salmon. Spiny dogfish predation has been shown to be highly variable, accounting for between 1.4 to 100% of hatchery releases of coho and chinook salmon from the Big Qualicum hatchery (Beamish and Neville 1992). In addition, both lamprey and spiny dogfish reduce predation on juvenile salmon by late summer. The re-

duction in predation by these species, and the general lack of potential predators in 616 survey tows in 1998 and 1999, indicated that predation mortality is probably not the only mechanism that regulates the numbers of mature fish that return. Beamish and Neville (2001) have suggested that the total natural mortality is made up of both an early predation-based mortality and a later carrying capacity mortality. They suggested that their inability to show that predation in the early marine period regulates the number of returning salmon is because the carrying capacity mortality occurred later in the year when the slower growing, smaller fish were unable to survive the first marine winter. The combination of predation and carrying capacity mortality determines the total mortality.

CONCLUDING THOUGHTS

Early studies tended to be based on individual interest rather than on a plan to test ideas about the factors regulating salmon abundance. Early workers (such as Foerster, Neave, Milne and Ricker) believed that the factors that limited survival occurred in fresh water. These beliefs lasted until the mid-1990s. The belief that freshwater factors limited salmon production meant that fishing and freshwater habitat were the factors that limited abundance. This resulted in the theory that stocks could be rebuilt and sustained at levels, perhaps double the historic average catch. The emphasis on increasing the "resource base" began in the 1960s and early 1970s as catches declined, despite the improving management. Bill Ricker's paper in 1976 "Two mechanisms that explain why stocks cannot be rebuilt to historic levels" is evidence that theories of salmon management were becoming inadequate (Ricker 1976). The most intensive effort to understand the early marine phase of Pacific salmon occurred in the 1990s with the MASS program, the Strait of Georgia program, and the High Seas program.

In general, it appears that there have been extensive studies of juvenile Pacific salmon. There is variation in the items eaten and in the proportion of these items. However, there are some consistent preferences. Pink salmon prefer small items, chum salmon prefer oikopleura, and coho and chinook salmon consume more fish species than the other salmon species. Rates of growth are rapid in the early marine period, but there is considerable uncertainty in the measures of these rates. There does appear to be a relationship between these rates of growth and movement, but the relationships probably are not simple. There also is evidence that the early rates of growth are related to marine survival.

Research eventually showed that the abundance of salmon can be limited in the ocean. This means that we need to know how the ocean affects produc-

tion to interpret fishing impacts correctly and to make effective use of enhancement. This new view is captured in a recommendation to Fisheries and Oceans Canada from the Pacific Fisheries Resource Conservation Council that reads "Now more than ever, information on the ocean life stage is required to understand what is happening" (Pacific Fisheries Resource Conservation Council (PFRCC) 2001). When the new millennium started, it was generally accepted that the final abundance of salmon was related to ocean conditions. The continued low catch of salmon remained an overriding concern. However, there was an abrupt change in abundance levels about 2000/2001 that clearly demonstrated the immediate impact of climate and climate change (PFRCC 2001).

FUTURE ISSUES OR QUESTIONS

1. Are estuaries necessary as nursery areas? Are there specific nearshore habitats that are critical to the survival of juvenile salmon? If so, how will climate change and sea level rise affect salmon production? Will the estuary of the Fraser River still be present?
2. Is the abundance of salmon determined only by predation in the first few months in salt water, or is brood year strength a combination of growth-related mortality and predation mortality?
3. Do additions of artificially reared juveniles into the ocean affect the survival of wild juveniles of the same species and the survival of other salmon species? What are the impacts of Atlantic salmon culture on Pacific salmon?
4. How do juvenile salmon survive their first marine winter when temperature is low and prey is less abundant?
5. How do juvenile salmon partition their estuarine and open ocean habitats so that the various species do not compete directly?
6. Where do stocks of juvenile salmon rear in the ocean and why do some stocks of each species survive better than other stocks?
7. What causes the fluctuations in survival in the ocean?
8. Which stocks remain on the shelf and what defines the area of the shelf that forms their marine feeding grounds?
9. When and how much mortality occurs on juvenile salmon between fresh water emigration and migration into deep coastal waters.
10. How can we use the information from past, present and future early marine studies to improve our forecasts of adult returns? Can biophysical models be developed?
11. How will global warming affect salmon on Canada's West Coast?
12. Why have the migration patterns of coho and sockeye salmon changed in the late 1990s?

RECOMMENDATIONS

We know that climate will change and in Canada, for example, we know that the Fraser River is the southern limit for a substantial amount of salmon production. Therefore, we need to have a plan to adapt to the impact of climate change and changed ocean conditions on the production of salmon. As a part of this plan, an international team could be set up to revise the plan, as new information becomes available. This team could be supported through NPAFC and would identify the questions relating to the impact of the ocean on salmon production. As many of these questions as possible might be addressed with the information from the material in this report. The remaining questions could be the focus for research by each country, with the intent of continued sharing of results. Team discussions would occur at the interim and annual meetings in order to minimize costs. A commitment of co-operation and support from team members and from national agencies should provide the ingredients for success.

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