NPAFC
Doc. 1285
Rev. _____

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Submitted to the
NORTH PACIFIC ANADROMOUS FISH COMMISSION

by

CANADA

October 2010

THIS PAPER MAY BE CITED IN THE FOLLOWING MANNER:
Preikshot, D., R.J. Beamish, and R.M. Sweeting. 2010. Changes in the diet composition of juvenile sockeye salmon in the Strait of Georgia from the 1960s to the early 21st Century. NPAFC Doc. 1285. 17 pp. (Available at www.npafc.org).

Changes in the diet composition of juvenile sockeye salmon in the Strait of Georgia from the 1960s to the present

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Abstract

Studies of the diet of juvenile sockeye salmon in the Strait of Georgia over the past 40 years show a trend of decreasing consumption of copepods and increasing consumption of decapod zooea and larvae. Presently, amphipods and decapods are the dominant prey items on the diet, representing approximately 60% of a relatively restricted number of items. The dominance of decapods in the diet appeared to be unique among the diets of juvenile salmon examined in other studies. Amphipods were usually the most common diet item in all examined studies of juvenile sockeye salmon diets. Studies of the diets of juvenile sockeye salmon, including our own, provide patchy information about a critical period in the establishment of brood year abundance. More comprehensive studies are needed that monitor the diets of juvenile sockeye salmon throughout the early marine period in relation to the composition of their zooplankton prey items.

Introduction

In 2009, the return of sockeye salmon to the Fraser River was substantially less than forecasted and was among the lowest in recorded history. In 2010, the opposite occurred and the estimated return of about 34 million adults, among the largest in history, was substantially more than forecasted. These contrasting, and unanticipated, returns prompted us to review the existing literature on the diets of juvenile sockeye salmon in their early marine period.

Studies on juvenile sockeye salmon in the ocean were rare on Canada's Pacific coast prior to the late 1960s (Beamish *et al*. 2003). Before the late 1960s the prevailing view among fisheries scientists was that the recruitment of Pacific salmon was mostly determined in fresh water (Ricker 1958). This view was a not too surprising consequence of the proximity of fresh water to most human observers. Spectacular phenomena like the spawning of millions of sockeye salmon in one river or the calamitous events surrounding partial blockages of the Fraser River in 1913 and 1914 (Thompson 1945) made freshwater appear to be the likely control on Pacific salmon production and, hence, the logical focus for research and management efforts. The importance assigned to the fresh water stage of the life history was emphasized by the construction of fishways, spawning channels and hatcheries.

Studies, in Canada, of Pacific Salmon early in their marine life history have been summarised in Bulletin 3 of the North Pacific Anadromous Fish Commission (Beamish *et al*. 2003). In general, these studies were patchy because they tend to be expensive as they require ship time and associated personnel. Also the results of such studies are of less interest as they usually suggest fewer opportunities for management intervention. Nevertheless, toward the end of the 20th Century there was an increasingly compelling body of evidence suggesting that marine mechanisms were at least as, if not more, important than freshwater processes in explaining production of Pacific salmonids such as sockeye (Beamish and Bouillon 1993, Hare and Francis 1995, Mantua *et al*. 1997 and Beamish *et al*. 1999). There were thus few studies in the late 1950s and 1960s (Foerster 1968). However, by the mid 1970s a cadre of researchers at the Pacific Biological Station in Nanaimo, British Columbia were devoting significant effort to studying the migrations and feeding habits of juvenile Pacific salmon in the Strait of Georgia.

Beginning in 1998, a systematic approach to indexing juvenile Pacific salmon abundance, migratory patterns, and diet was carried out in annual surveys in July and September in the Strait of Georgia (Beamish *et al*. 2000, 2004, and 2008). The extreme contrast in the total returns of sockeye salmon to the Fraser river in 2009 and 2010, Figure 1, indicated that it was timely to assemble all of the diet information on the early marine feeding period of sockeye salmon in the Strait of Georgia. Although previous studies were conducted using different sampling patterns and gears, they can still provide useful qualitative information on the diet of juvenile sockeye salmon. A comparison between these previous studies and our recent studies may provide more evidence that will help explain the extreme contrast in production that most likely resulted from extreme differences in early marine survival.

A comparison of the diets of juvenile sockeye salmon in the Strait of Georgia with diet information from similar studies of juvenile sockeye salmon in other areas throughout their distribution may provide some clues to the process regulating the survival of juvenile sockeye salmon in the Strait of Georgia. An assessment of what is known is also helpful for the design of future studies that most certainly are necessary to improve the ability to forecast adult returns more accurately and to ensure that the critical rearing habitat in the water column of the Strait of Georgia is understood and protected.

Methods

The historic data for this analysis was from three summaries, (1) field surveys done by Barraclough and colleagues in the late-1960s, (2) field surveys reviewed by Healey in the mid-1970s, and (3) field work done by Haegele in the early 1990s. The recent juvenile Pacific salmonid survey work is part of an ongoing project being conducted by Beamish and colleagues. The data from these surveys were averaged over monthly time periods with particular interest in work done during June and July. These monthly averages for prey species or taxa were aggregated into seven groups: terrestrial insects (mostly flies and social insects), fishes (including larvae and eggs), euphausiids (all life history phases), decapods, (crab zooea and megalopae), amphipods (mostly gammarids and hyperids), copepods (mostly calanoids, pseudocalanoids, and harpacticoids), and ‘other zooplankton’ (including chaetognaths, ctenophores, oikopleura, polychaetes, and ostracods).

Barraclough and Colleagues conducted trawl surveys on juvenile fishes in the Strait of Georgia in 1966, 1967, 1968, and 1969 (Barraclough and Phillips 1978). Although the focus of these surveys was Pacific salmon, juveniles of other fish species were included in the analysis. The trawl net was towed at the surface between two vessels at approximately 5.6 km/hr and was 6.1 m wide by 3 m deep. Trawls were conducted for either 10 or 15 minutes during daylight hours and all were conducted in the Southern Strait of Georgia (Barraclough and Phillips 1978). Figure 2 shows the approximate geographic extent of these surveys. Of these surveys four were conducted during a June and July of their respective years; June/July 1966 (Barraclough 1967 and Barraclough and Fulton 1967) and June/July 1967 (Robinson *et al*. 1968 and Robinson 1969). Stomach contents were reported in frequency occurrence along with lengths of individual diet items. To make these data comparable to volume data reported in all other work, lengths were transformed using a simple cubic relationship. All diet items are assumed therefore to have the same length weight relationship. Diet items were reported to the species level and we aggregated them into seven groups described above.

Healey (1978) summarised juvenile Pacific salmon survey work done by himself and others in 1974, 1975 and 1976. Pacific salmon juveniles were sampled with purse seines of varying sizes mounted on three separate vessels; Caligus – 218 fm (399m) seine, Tahlok – 150fm (274m) seine, and R.D. 104 – 100 fm (183m) seine. July surveys were available for 1975 and 1976. Samples for these surveys were obtained throughout the Strait of Georgia but the vast majority of juvenile sockeye samples in July 1975 were from waters near the southern Gulf Islands, (Figure 3). Data reported from 1976 also was in the southern Gulf Islands area but includes juvenile sockeye sampled from mid-May, Late June and early July. Diet data were reported as percent volume and was thus in our preferred form for comparison with other surveys.

Juvenile sockeye salmon diet data from the early 1990s were collected in a juvenile Pacific herring survey reported in Haegele (1997). Because these surveys were designed to sample juvenile Pacific herring, sampling was done at night, when Pacific herring move to surface waters to feed. Fish were sampled using a 220m long by 27m deep purse seine operated by any one of three vessels. In his summary of diet compositions, Haegele (1997) provides frequency occurrence data for prey grouped at the species level. He also includes size conversion factors, for groups of prey taxa, which were used to convert diet constituents to a volume equivalent. The Pacific herring samples were collected on a survey grid sampling the east coast of Vancouver Island and portions of the central and northern Strait of Georgia (Figure 4).

Juvenile sockeye salmon diet data from July 1998 to July 2009 was obtained from specimens collected in a juvenile Pacific salmon trawl survey conducted in the Strait of Georgia. The survey is conducted on a sampling grid that encompasses most Strait of Georgia Waters (Figure 5). The trawl net is 30m wide by 15m deep and pulled at 2.6 m/s for 30 minutes. Trawls are conducted with the head rope at the surface, 15, or 30 m depth (Beamish *et al*. 2008). Diet from these surveys is recorded as percent volume.

After diet data from the aforementioned surveys were either converted to, or transcribed from, percent volume composition all prey contributions were averaged over the month of June or July. The two exceptions are the Healey (1976) and the Haegele (1997) data which are reported as an average of May to July inclusive for the former and June to July for the latter, with none of the original data available for parsing into separate months.

Results

Figures 6, 7, and 8 contain different visualisations of the changes in juvenile sockeye diets in the Strait of Georgia during early summer between 1966 and 2009. Figure 6 shows how contributions from the seven major taxa have changed relative to each other. Figure 7 has individual graphic representations of changes in diet volume contributions from the six most important prey taxa; amphipods, decapods, copepods, euphausiids, fish and ‘other’ zooplankton. Figure 8 shows these trends after being converted to ordinal rankings of diet volume contributions, from 1 (most important) to 7 (least important).

In absolute terms, copepods appear to decrease in importance, particularly after the 1960s, when they were often more than 20% of diet by volume. Since the 1960s copepods were rarely more than 10% of diet. The declining trend in copepods through the 1970 and 1990s is more obvious when examining the ranked values, Figure 8. Decapod contributions to diet composition appear to have continuously increased in importance from the 1960s to the 1990s (Figures 7 and 8). Euphausiids diet contributions appear to decline in the 21st Century after a peak in the early 1990s. Amphipods were almost absent in diet compositions in the 1960, were very important (more than 50% of volume) in the 1970s. Amphipods decreased between 1990 and 1993, but have been a large contributor in recent years often comprising a third, or more, of diet volume. Despite these changes in absolute values, however, after the 1960s amphipods have always been among the top 3 diet items, Figure 8.

Terrestrial insects and fishes were significant diet items in the 1960s, when they comprised a third to two thirds of diet volume, but both have been a very small portions of diet volume since the 1970s. This observation may be a result of the rather limited geographic extent of sampling in the 1960s surveys which were concentrated near the Fraser River plume. The 'other' zooplankton group has no obvious trend and varies greatly in the reported data, though this group usually has made up about 10% of the volume of juvenile sockeye diets, it has also been as large as 40% or as small as 1%. After the 1960s three groups, amphipods, decapods and euphausiids consistently form about 75% of diet volume.

Discussion

Two long-term trends appear in these data. There is a continuous decline in the contribution by copepods to the diet of juvenile sockeye salmon and a concomitant increase in the contribution by decapods between 1966 and 2009. The 1960s stand out because of the singular importance of insects, and fish in juvenile sockeye salmon diets derived from those surveys. Over the same period euphausiids seem to have increased to the early 1990s then declined somewhat through to 2009. Thus, the variation in contribution of certain diet items varies on not only an obvious annual scale but also decadally. Amphipods appear to be a preferred item in all decades although this role may be supplanted by decapods if trends in this analysis continue.

The existence of this variation suggests that while these fish have clear preferences for a half a dozen items, there appears to be a certain degree of opportunistic foraging that reflects prey availability. Such opportunism was first suggested by Healey (1980) when comparing his mid 1970s diet data to that of Barraclough and colleagues from the 1960s. If this diet variation is linked to bottom-up type changes in ecosystem production a better understanding of why sockeye diets have changed, and how this influences early marine survival, may help explain mechanisms underlying observed changes in Pacific salmon production (Beamish *et al*. 2004 and Peterman *et al*. 2010).

Though juvenile sockeye diets are relatively restricted in all reviewed studies, spatial and temporal variation can be seen in prey selection. Off the coast of Washington and Oregon Brodeur and Pearcy (1988) developed an index of diet importance and found that euphausiids and chaetognaths were equally important as diet items compared with fishes, particularly smelts and unidentified fish larvae. Using similar methodology Landinham *et al*. (1997), sampling in Northern British Columbia and Southeast Alaska found that fishes and amphipods were overwhelmingly the most important diet items for juvenile sockeye, comprising approximately 40% of the importance index each, with euphausiids and copepods about 10% each. The apparent importance of smelts and chaetognaths in the diets of juvenile sockeye of the Oregon and Washington coast is a contrast to the predominance of amphipods in Southeast Alaska, which is similar to Strait of Georgia data.

Auburn and Ignell (2000) sampled sockeye salmon throughout the Gulf of Alaska, describing feeding habits in near-shore, shelf, slope, and oceanic areas. In describing diet items in percent wet weight (similar to percent volume) they found that in all habitats the most important contributors to diet were different proportions of amphipods, euphausiids, fishes and copepods. Auburn and Ignell (2000) found that in the near-shore habitat unidentified fish species were 46% wet weight of diet and euphausiids were 27%. In the shelf habitat copepods were 73% and euphausiids were 25%. In the slope habitat euphausiids were the largest contributor to diet 40%, with the other three groups from 10 to 20%. In the oceanic habitat euphausiids were the largest component of diet 71%, while copepods were 18%. Although the diet data from the Gulf of Alaska near shore habitat might be expected to be most similar to data from the Strait of Georgia it is not.

In the eastern Bering Sea Farley *et al*. (2007) examined diet, by % mass, of age 1.0 (freshwater age 1, oceanic age 0) and 2.0 (freshwater age 2, oceanic age 0) juvenile sockeye in 2000 – 2003. They found that age 0 pollock and sand lance were the largest component of diet. In some years they observed that euphausiids were a large component of diet but only for the age 1.0 sockeye. All other zooplankters, including amphipods and copepods, were rarely more than 10% of diet. In the western Bering Sea, Naydenko *et al*. (2007) found that amphipods were the most important component of the diet of juvenile sockeye salmon. In some areas of the Western Bering shelf, euphausiids (30% in the central region) and pteropods (10% in the south), were also significant portions of the diet. The diet data from the western Bering Sea thus appears to be more similar to diet data from the Strait of Georgia than that of the eastern Bering Sea.

Karpenko *et al*. (2007) summarised decadal variation in juvenile and adult Pacific salmon diet in the Northwest Pacific in the 1960s, 1970s, and 1980s. For juvenile sockeye salmon they suggested that amphipods were the most important diet item by weight in all decades; 43%, 48% and 35%, respectively. Juvenile fish were significant in the 1960s and euphausiids in the 1970s and 1980s. These trends in fish and euphausiids diet contributions are a surprising parallel to the Strait of Georgia diet trends as is the dominance of amphipods in all decades.

It is interesting to note that in no other diet studies do decapods appear to play as important a role in the diet of juvenile sockeye as they do in the Strait of Georgia, particularly after the start of the 21st Century. In general, fish appear to be more important diet items elsewhere than in the Strait of Georgia. In all regions euphausiids and amphipods often appear to be the second or third most important diet item. This suggests that throughout the North Pacific the production of euphausiids and amphipods has a profound impact on juvenile sockeye salmon diet. This illustrates the importance of zooplankton surveys in understanding ecosystem effects on growth and survival of sockeye salmon early in their marine life history. Our results and the other research described above shows that juvenile sockeye salmon do not consume a variety of food resources but can make large diet shifts within their limited range, depending on prey availability.

Diet changes could be linked to juvenile sockeye salmon growth and survival in the marine environment via: (1) competition, with other Pacific salmon and different fish species for prey resources, (2) changes in the gross abundance of different prey resources, and (3) changes in the timing of the appearance of prey resources. Any of these three mechanism could be manifested as the observed diet changes we at annual and decadal scales and over different area scales in the north Pacific for sockeye salmon. A better understanding of what causes these shifts in the composition of prey will help better understand changes in marine survival and production, not only of sockeye, but also other Pacific salmon. Examining annual and decal changes in diet is a fundamental step towards helping understand and manage Pacific salmon in their marine and fresh water ecosystems.

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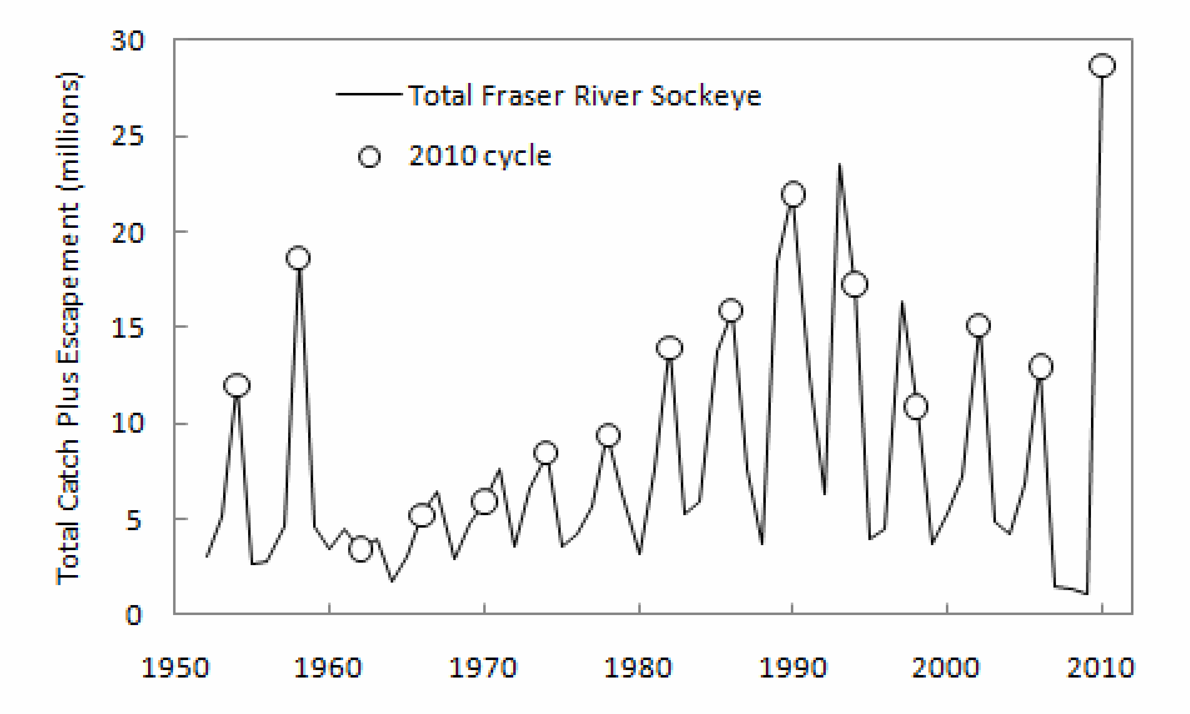

Figure 1: Total returns (catch plus escapement) of adult sockeye salmon to the Fraser River from 1952 to 2010. Data for 2010 represents the in-season count from the Pacific Salmon Commission as of the time of the preparation of this report (October 2010). Other return totals of the 2010 cycle line are shown as open circles.

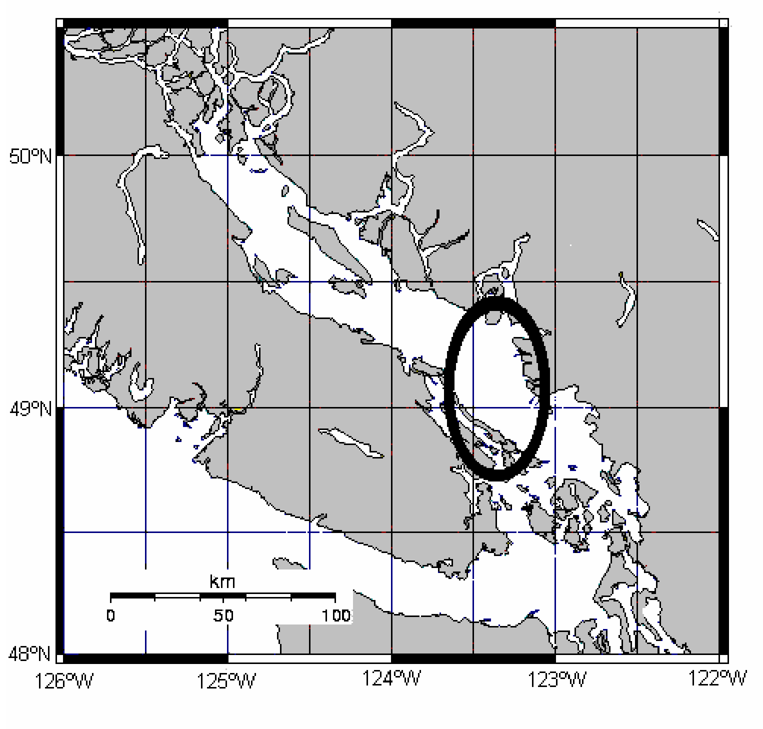

Figure 2: Approximate extent (black ellipse) of juvenile fish surveys described in Barraclough and Phillips (1978).

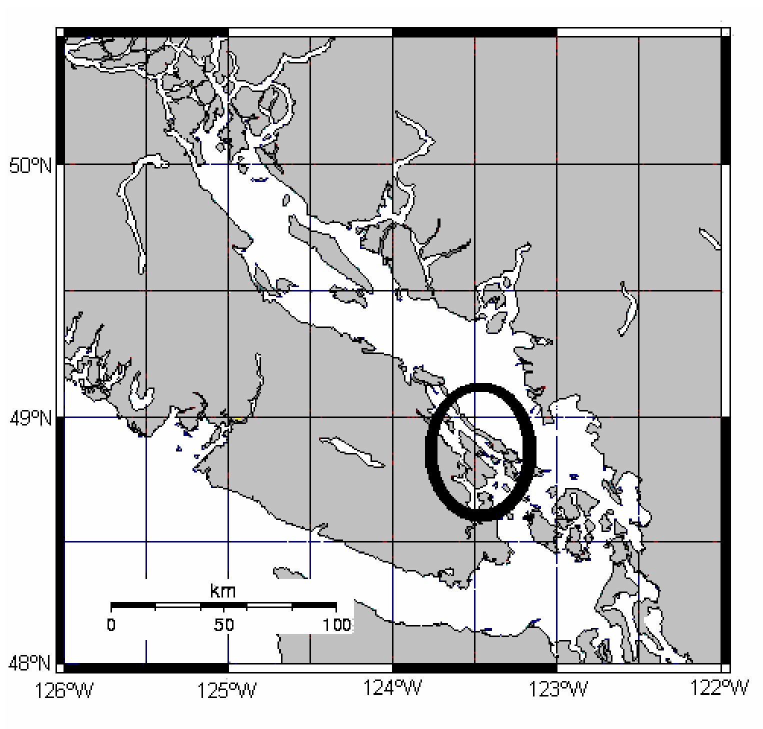

Figure 3: Approximate extent (black ellipse) of juvenile salmon surveys described in Healey (1978).

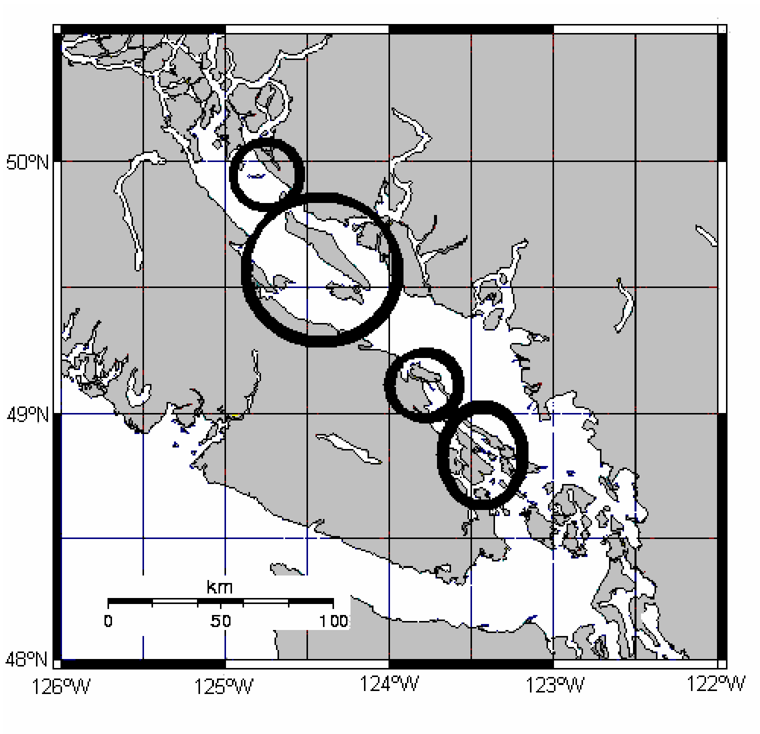

Figure 4: Approximate extent (black ellipses) of juvenile herring surveys described in Haegele (1997).

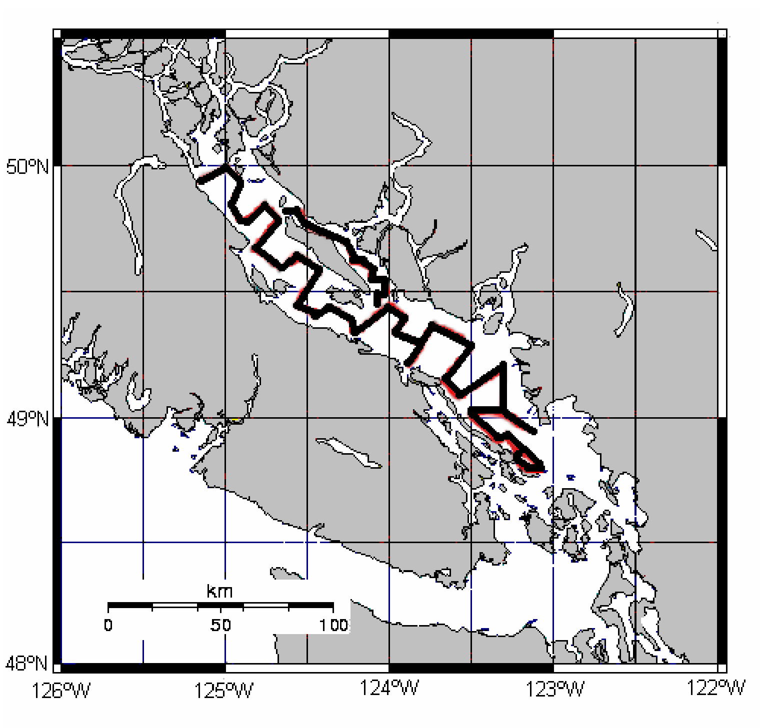

Figure 5: Transects used in July 1998 – 2009 juvenile salmonid surveys, adapted from Beamish *et al*. (2008).

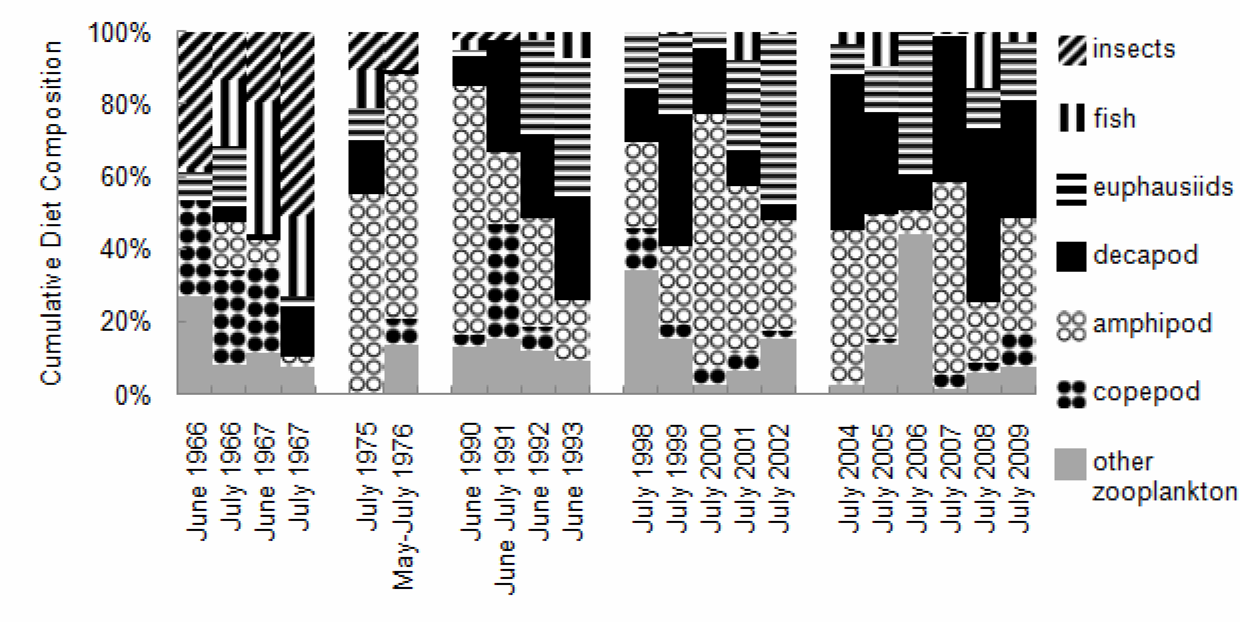

Figure 6: Monthly-averaged diet data for juvenile sockeye salmon in the Strait of Georgia from 1966 to 2009.

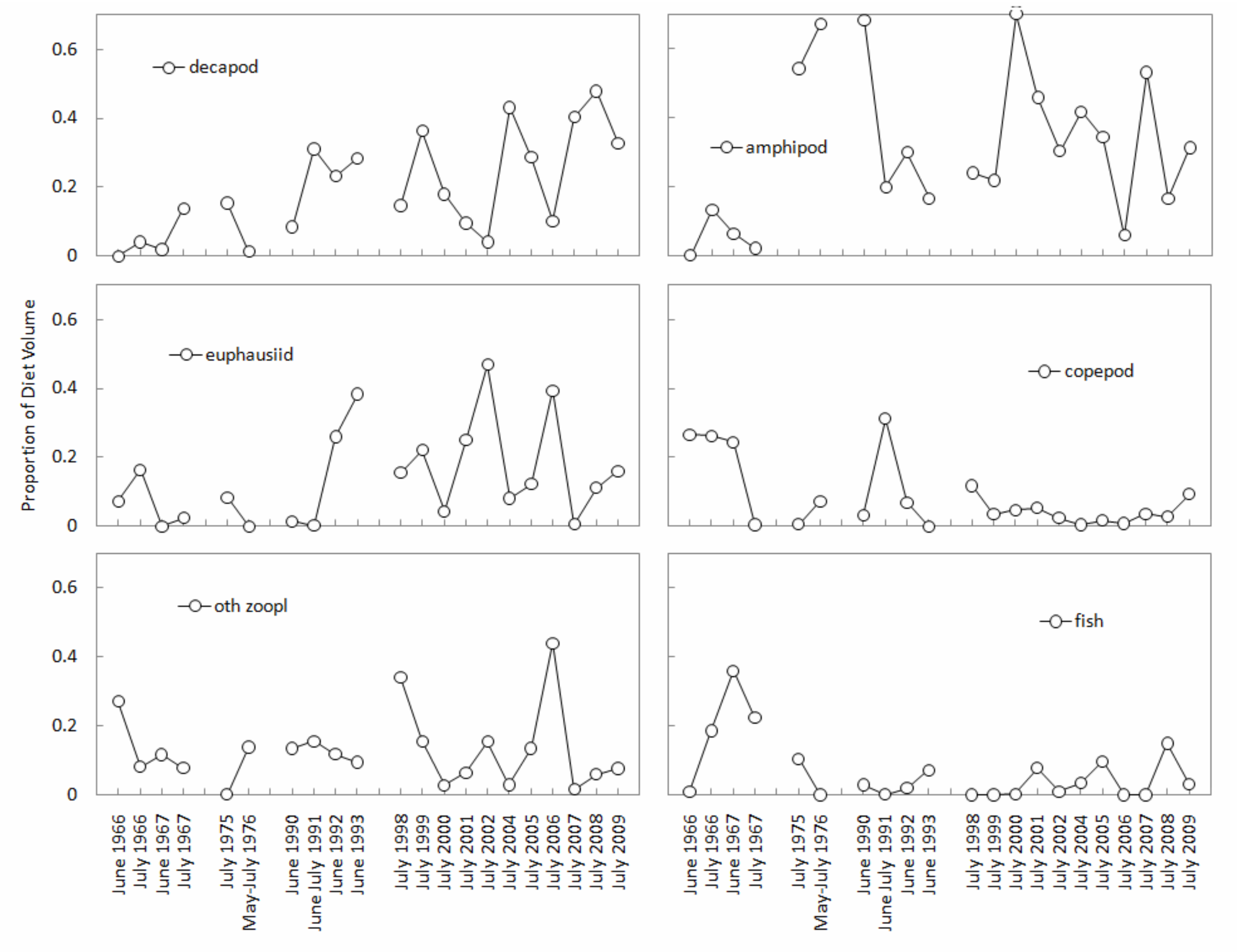

Figure 7: Monthly-averaged diet data trends for the six major prey groups for juvenile sockeye salmon in the Strait of Georgia from 1966 to 2009.

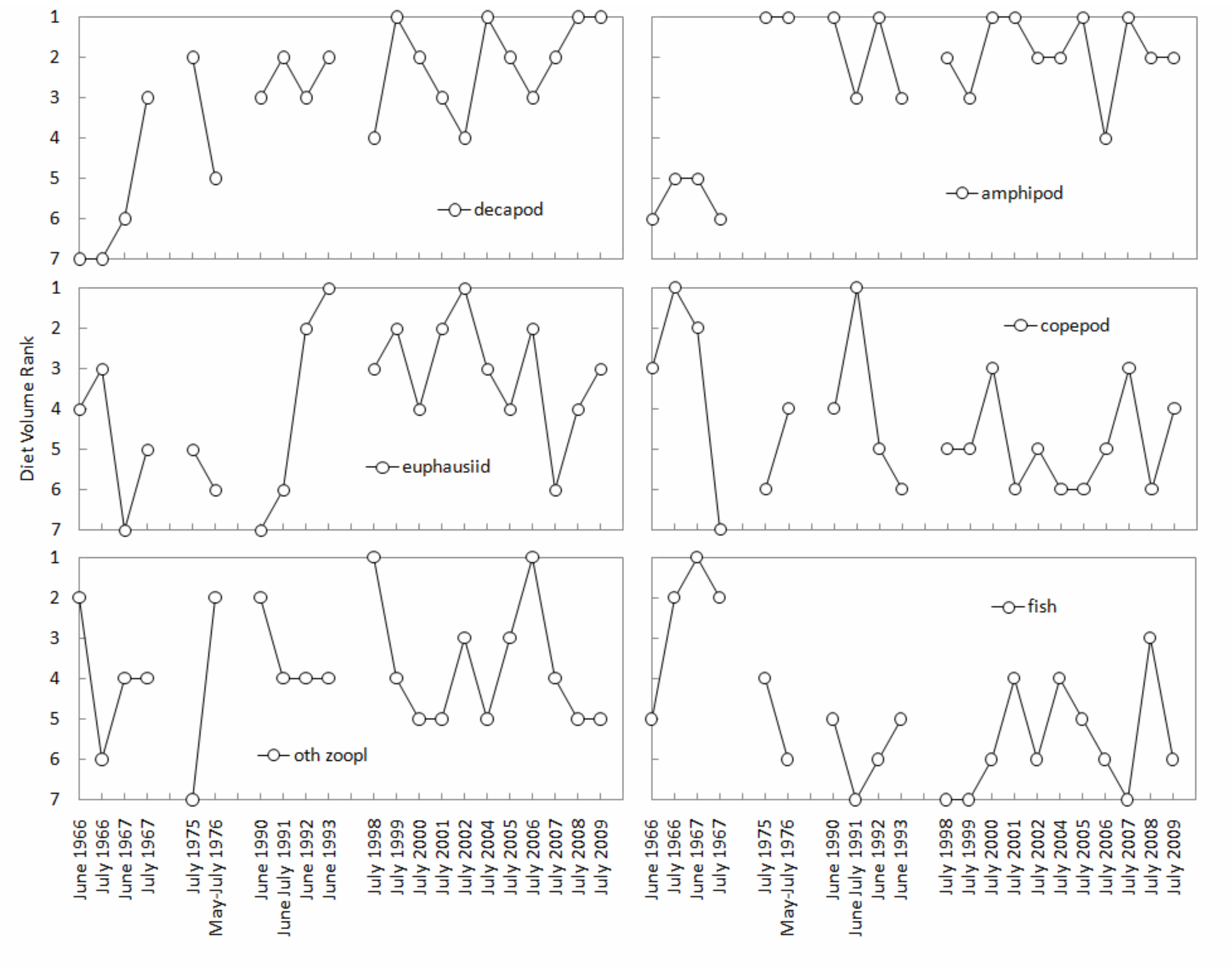

Figure 8: Monthly-averaged diet data trends for ordinal rankings of the six major prey groups for juvenile sockeye salmon in the Strait of Georgia from 1966 to 2009 with a rank of 1 denoting the most important diet item that year and 7 denoting the least important.