Pacific salmon and Pacific herring mortalities in the Fraser River plume caused by river lamprey (Lampetra ayresi)

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Pacific salmon and Pacific herring mortalities in the Fraser River plume caused by river lamprey (*Lampetra ayresi*)

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Abstract: River lamprey (*Lampetra ayresi*) enter the Strait of Georgia from the Fraser River and feed almost exclusively on Pacific herring (*Clupea harengus*) and salmon (*Oncorhynchus* spp.). Although the major prey of river lamprey is Pacific herring, the greater effect of lamprey predation was on the populations of chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon. In 1990 and 1991, river lamprey killed a minimum of 20 million and 18 million chinook salmon, respectively, and a minimum of 2 million and 10 million coho salmon in the same years. 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 because river lamprey also feed in other areas and the abundance estimates are conservative. These high mortality rates indicate that river lamprey predation must be considered as a major source of natural mortality of chinook and coho salmon in the Strait of Georgia.

Résumé : La lamproie à queue noire (*Lampetra ayresi*) quitte le Fraser pour entrer dans le détroit de Géorgie et se nourrit presque exclusivement de hareng du Pacifique (*Clupea harengus*) et de saumon (*Oncorhynchus* spp.). Bien que sa principale proie soit le hareng du Pacifique, c'est sur les populations de quinnat (*O. tshawytscha*) et de coho (*O. kisutch*) que l'effet de la lamproie se fait le plus sentir. En 1990 et 1991, les lamproies à queue noire ont tué respectivement un minimum de 20 millions et de 18 millions de quinnats et un minimum de 2 millions et de 10 millions de cohos. En 1991, les lamproies à queue noire présentes dans le panache du Fraser ont tué l'équivalent d'environ 65 et 25 % respectivement de la production totale canadienne de coho et de quinnat (poissons d'élevage et poissons sauvages combinés). Ces estimations sont probablement faibles, du fait que la lamproie à queue noire se nourrit aussi dans d'autres régions et nos estimations de l'abondance sont conservatrice. Ces taux élevés de mortalité indiquent que la prédation par la lamproie à queue noire doit être considérée comme une source importante de mortalité naturelle du quinnat et du coho dans le détroit de Géorgie.

[Traduit par la Rédaction]

Introduction

Marine mortality for all Pacific salmon species (*Oncorhynchus* spp.) generally exceeds 50% and frequently exceeds 90%. Most of this mortality is believed to occur shortly after the salmon smolts enter salt water (Groot and Margolis 1991; Pearcy 1992), although there is little scientific evidence to support this belief. Predation is the obvious source of the early marine mortality because even if food is scarce, "starving" salmon are believed to be killed by predators, but again there is little scientific support for this hypothesis. It is important to understand the sources of early marine mortality of salmon because the effort and cost of increasing smolt production in fresh water should be assessed with an understanding of how much of this increased production might actually survive in the marine environment.

In an earlier study, spiny dogfish (*Squalis acanthias*) were identified as important predators of young Pacific salmon entering the Strait of Georgia (Beamish et al. 1992). Large numbers of spiny dogfish moved into shallow water at almost the exact time that chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon smolts started moving into salt water. Even though predation rates of spiny dogfish on salmon were small, the large numbers of spiny dogfish were considered to be an important source of early marine mortality of salmon. A second important predator of Pacific salmon and Pacific herring (*Clupea harengus*) in the Strait of Georgia is the river lamprey (*Lampetra ayresi*) (Roos et al. 1973; Beamish 1980).

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The river lamprey has a restricted distribution but because of its abundance and feeding behaviour, it is potentially an important source of marine mortality of Pacific salmon in the Strait of Georgia. Although *L. ayresi* has been reported in the Skeena River (Withler 1955), it is most common in the Fraser River where it has been shown to be the dominant organism by weight in the bottom sediments of the 160 km section of river from the city of Hope to the river mouth (Beamish and Youson 1987). Newly metamorphosed *L. ayresi* enter the Strait of Georgia after the lumen of the oesophagus opens, and the lamprey is able to osmoregulate in salt water (Beamish and Youson 1987). The migration into salt water occurs from April to July during maximum Fraser River discharge. River lamprey begin feeding almost immediately after entering the ocean. In earlier studies (Beamish 1980; Beamish and Youson 1987), we speculated on the impact of lamprey predation on salmon and herring. In this study, we attempt to measure the amount of species specific salmon and herring mortality in the Fraser River plume caused by river lamprey predation.

Methods

Lamprey that feed on other animals are generally considered to be parasites because their hosts may not be killed by the feeding event. The river lamprey, however, feeds by removing flesh from the host and should be considered to be a predator rather than a parasite. Determining the number of prey of each species killed by river lamprey predation required a population estimate of lamprey in the plume, an estimate of the total number of prey, an estimate of the percentage of each prey species in the lamprey diet, and estimates of the prey mortality that resulted from each lamprey attack. When making these determinations, we ensured that any approximations were conservative. Estimates of prey mortality, therefore, should be conservative.

Abundance of river lamprey, Pacific herring, and salmon

A trawl survey of the surface waters of the Fraser River plume and adjacent waters was conducted in 1989, 1990, and 1991. The trawl net had a 4 × 4 m opening with stretched mesh side panels varying from 9.0 cm at the mouth to 0.5 cm in the cod end (Whitehouse and Levings 1989). The top of the trawl was held at the surface using floats attached to the head-rope. The net was kept open using 1.24 × 0.4 m midwater trawl doors. The net was towed off the stern at a speed of approximately 2 kn for approximately 30 min. All river lamprey captured were counted, measured, and preserved in 10% formalin. Pacific herring and salmon were examined for lamprey wounds and measured. All salmon were preserved in 10% formalin so that their identification could be confirmed in the laboratory using standard taxonomic characteristics.

Comparisons of lamprey catches inside and outside the Fraser River plume were made by standardizing the length of sets to 1 km of water strained and comparing average catch in the two areas. Estimates of fish abundance in the plume were obtained by multiplying the total catch by the plume area and dividing by the amount of water strained. The amount of water strained was estimated by multiplying the width of the net by the total distance trawled. Salinity measurements indicated that the plume varied in thickness from several metres to several centimetres thick. Our nets fished about 4 m deep, but we used surface area fished rather than volume because the variation in the thickness of the plume made it impractical to estimate the depth of the plume during the study. We assumed that the net caught all fish in the path of the net opening.

June is the period of maximum discharge of the Fraser River and the time when most young juvenile river lamprey enter the Strait of Georgia (Beamish 1980). The shape, depth, and area of the plume is influenced by Fraser River discharge, tide, and wind and is continuously changing (St. John et al. 1992). Because of the changing shape of the plume and because it is not possible to obtain area estimates daily, we estimated the plume's average size from the generalized surface salinity pattern determined by Waldichuk (1957) for June 1950. In 1950, the total annual discharge was about average for this century (Beamish et al. 1994) and less than in 1990 and 1991 (Environment Canada 1990). Harrison et al. (1991) identified the plume area as having a surface salinity from 10 to 15%. We selected a salinity of 10% as the boundary of the plume to ensure we used a conservative estimate of the average size of the plume in June.

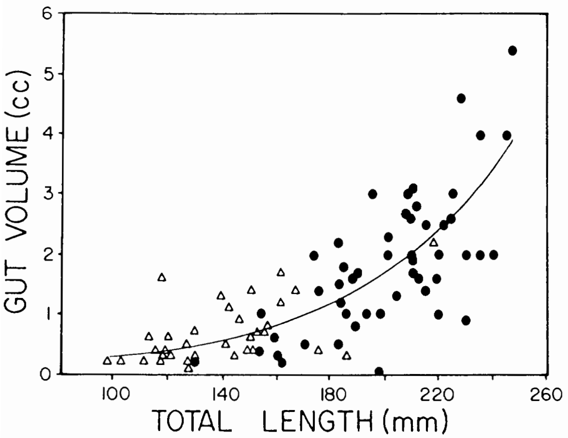
In 1989 and 1990, sets were made randomly throughout the plume, and a smaller number were made just outside the plume boundary. The survey design was modified to a random stratified design in 1991. Fewer trawls were set in the centre of the plume, which had lower, more consistent catches of river lamprey in the previous years, and more trawls were made just inside the outer boundary of the plume. This area had higher, but more variable, catches of river lamprey in previous years. A small number of trawls were made immediately outside the plume boundary, which could usually be distinguished by the abrupt transition from silty plume water to the clearer water of the Strait of Georgia. Temperature and salinity were measured at the end of each set to verify our position within the plume. The abundance of Pacific herring and salmon in the plume in 1990 and 1991 was estimated using the swept-area procedure used for river lamprey.

We speculated that natural mortality of lamprey had only minor effects on our abundance estimates because they were made about midway during the lamprey feeding period. There is no estimate of natural mortality of lamprey in salt water and therefore, we chose an annual natural mortality of $M = 0.4$. This mortality rate, commonly observed for marine fishes, was applied to the time remaining in the feeding period after the lamprey population size was estimated.

Intestinal contents of river lamprey

In 1991, the percentage of salmon and Pacific herring in the diet of river lamprey was estimated from the intestinal contents. Intestinal contents were determined in the laboratory from a random sample of 103 of 786 lamprey that were collected in 1991 and preserved in 10% formalin. The body weight and length of the preserved lamprey were measured before dissection. The entire intestine was then removed and weighed separately. Intestines with contents

Fig. 1. River lamprey gut volume versus gut length for 1976 (●) and 1991 (Δ). Line fitted to combined data sets is gut volume + $e^{(2.94 + 0.174 \times \text{length})}$.



less than 0.1 g were considered to be empty. Scales from the intestines were identified as salmon, Pacific herring, or not identifiable.

Table 1. Species and numbers captured in the Fraser River plume during 1989, 1990, and 1991 trawl surveys.

	1989	1990	1991
River lamprey	181	518	899
Chinook salmon	43	84	205
Chum salmon	2	49	141
Coho salmon	21	15	61
Sockeye salmon	8	47	130
Pink salmon	4	23	6
Pacific herring >100 mm	262	632	4062
Pacific herring ≤100 mm	558	2756	1528
Stickleback	13	94	53
Sandlane	11	13	130
Starry flounder	0	11	3
Smelt	64	7	17
Other	4	12	36

Wounding studies

All herring and salmon caught during the trawl surveys were examined for lamprey wounds. In 1990, wounds were recorded and in 1991 wounds were counted and scars (healed wounds) were recorded. In both years, the percentage of the catch of each species with wounds was calculated. The wounding percentages for the various salmon species was used to estimate the species specific mortality. The type of wound was important because a high percentage of scarred prey would indicate that prey survived the lamprey feeding events, where as a high percentage of fresh wounds probably resulted when some prey escaped in the trawl.

Number of prey attacked

In the plume, very few scarred prey were found, indicating that the relatively large wounds caused by lamprey were fatal to the hosts. Therefore, we assumed that an average feeding event would ultimately cause the death of the host. Because we could not observe feeding behaviour in the wild, we estimated the number of hosts attacked by estimating the minimal number of feeding events required for river lamprey to grow from the average size when they entered salt water to the estimated terminal size.

The average size at first feeding was 12 cm and 1.8 g (Beamish 1980), and the terminal size was approximately 25 cm and 34 g. This is the size of the only known river lamprey captured during its return to the spawning ground in the Fraser River and is very similar to the average terminal size of 27 cm and 34 g of river lamprey fed in the laboratory (Beamish and Williams 1976; Beamish and Scarsbrook 1979). We used a conversion rate of 29% (Brett and Groves 1979) to estimate the amount of flesh consumed for an average lamprey to grow to 34 g. This high conversion rate was for young, fast-growing, well-fed fish. The rate is less than the 39% conversion rate determined by Farmer (1980) for the landlocked sea lamprey (*Petromyzon marinus*). The 29% conversion rate was selected because the river lamprey feeds by consuming tissue, similar to the fish studied by Brett and Groves (1979), whereas the sea lamprey consumes body fluids. Consumption of body fluids would result in a lower faecal energy loss than the consumption of tissue (Farmer 1980). Beginning at 12 cm and 1.8 g, we estimated the average intestinal volume for this length from Fig. 1. Twenty-nine percent of this volume would be added to the weight (assuming 1 cc (1 mL) of flesh weighs 1 g). Using the length–weight relationship, $W = 1.44 \times 10^{-3}$ L (cm)$^{2.978}$ (Beamish 1980) we estimated the new length and repeated the calculation for the second feeding event. We continued our calculations until the terminal size of 34 g was reached. The number of feeding events was summed and considered to be the minimum average number of hosts that would be attacked.

We used a second method to estimate the number of hosts attacked that did not fix the growth rate but fixed initial and terminal sizes. We used the average daily growth determined from laboratory feeding studies to estimate the number of days it took lamprey to grow from the size at entry into salt water to their terminal size (27 cm and 34 g). Assuming that a lamprey feeds once a day (Beamish and Williams 1976), we considered the number of days to represent the average number of hosts attacked and killed and used this second estimate to check the first estimate that we considered to be more reliable.

Feeding studies

River lamprey were collected from the southern Strait of Georgia during June 1988. They were transported to the Pacific Biological Station, Nanaimo, British Columbia, and held in aquaria at ambient temperature and supplied with continuously flowing salt water (28%). Rock and gravel substrate was placed in the bottom of the tanks to provide the lamprey with areas of shelter. Live Pacific herring were placed in the tanks as a food source.

An experiment, to study growth of river lamprey, was conducted from August 9 to September 20, 1988. Eighteen

Table 2. Numbers and percentages of lamprey wounds on Pacific herring and salmon.

	1990			1991		
	Catch No.	Wound No.	Wound (%)	Catch No.	Wound No.	Wound (%)
Pacific herring ≥100 mm	632	123	19	4062	641	16
Chinook salmon	83	11	13	205	23	11
Chum salmon	51	8	16	141	13	11
Coho salmon	17	1	14	61	13	9
Sockeye salmon	44	0	0	130	15	21
Pink salmon	22	1	5	6	1	17
Total salmon	217	21	10	543	65	12
Total	849	144	17	6585	706	11

river lamprey were measured and weighed and then placed in a 350-L tank with 50 Pacific herring. Dead Pacific herring were removed and replaced daily. The herring were measured for fork length, and the number of the lamprey wounds were recorded. Lamprey remaining at the termination of the experiment were measured for length and weight.

Results

River lamprey density and abundance

Estimates of the abundance of river lamprey were made using 1990 and 1991 data. The 1989 survey captured 181 lamprey in 85 sets. We used this information to design the 1990 and 1991 surveys and not for population estimates because the sampling locations in 1989 were selected as part of another study and did not sample the plume effectively. From July 4–26, 1990, 63 sets inside the plume caught 518 lamprey, and 8 sets outside the plume caught 5 lamprey or 7.9 and 1.0 lamprey/km, respectively. From June 10 – July 12, 1991, a total of 87 sets inside the plume resulted in a catch of 899 river lamprey or 10.3 lamprey/km, and 5 sets outside the plume resulted in a catch of 4 lamprey of 1.4 lamprey/km. In 1990 and 1991, the ratio of river lamprey in the Fraser River plume and outside the plume was 7.9:1 and 7.4:1, respectively.

Abundance estimates were calculated for the Fraser River plume using the total catch for the total area surveyed of 0.26 km^2 in 1990 and 0.35 km^2 in 1991. The number of lamprey caught within the survey area was then calculated for the area of the plume of 1506 km^2 (about 22% of the total area of the strait). The abundance of lamprey in the plume in 1990 and 1991 was 3 million (± 700 000) and 3.9 milion (± 963 000), respectively.

Catches of fishes other than lamprey

Pacific herring and all five species of Pacific salmon in the Strait of Georgia were caught in the trawls (Table 1). Other species were much less abundant. Catches of Pacific herring from the 1989, 1990, and 1991 surveys were the largest of all species captured (Table 1). Catches of Pacific herring were separated into two length-classes because Pacific herring less than 100 mm tended to be young-of-the-year (40–90 mm, average 77 mm) and more susceptible to damage from the trawl net, making it difficult on occasion to distinguish between net damage and lamprey wounds.

Table 3. Number of wounds on Pacific herring and salmon in 1991.

	Single wound	Multiple wound
Pacific herring (≥100 mm)	552	89
Pacific salmon (all species)	61	4

All salmon except pink salmon were more abundant in the catches in 1991 than in 1990 (Table 1). The average catch rate of all five species in the plume in 1990 and 1991 was 3.46 and 6.03 salmon/km, respectively. This compares to an average catch rate of 0.27 and 2.11 salmon/km outside the plume in 1990 and 1991, respectively. In 1991, the catch of herring >100 mm (average 144 mm) was almost five times higher than in 1990 (average 133 mm). The average lengths of Pacific salmon caught during 1990 were as follows: chinook, 110 mm (±31); coho, 144 mm (±30); chum, 109 mm (±15); pink, 102 mm (±14); and sockeye, 68 mm (±15). The average lengths in 1991 were as follows: chinook, 89 mm (±22); coho, 130 mm (±47); chum, 103 mm (±20); pink, 78 mm (±13); and sockeye, 68 mm (±18).

Lamprey wounds on Pacific herring and salmon

Wounds caused by lamprey attacks were easily separated from other marks. Lamprey wounds ranged from circular depressions to longitudinal gouges. There was a loss of scales at the edges of the wound, and occasionnaly there were puncture holes anterior of the position of first attachment. Other marks, which were rare, were not associated with such extensive descaling and with the loss of flesh.

The combined percent of Pacific herring and salmon with wounds was similar in 1990 and 1991 (Table 2). Wounding percentages for chinook, coho, and chum salmon were slightly lower in 1991 than in 1990, but those for sockeye and pink salmon and Pacific herring were higher in 1991 than in 1990. In 1991, multiple wounds were found

Table 4. Estimated numbers of salmon (by species and total) and Pacific herring killed in the Fraser River plume by river lamprey in 1990 and 1991.

	1990 (millions)	1991 (millions)
Chinook salmon	20	18
Chum salmon	15	10
Coho salmon	2	10
Sockeye salmon	0	12
Pink salmon	2	1
Total salmon	39	51
Pacific herring	156	203

on 4 salmon or 6% of those with wounds and on 89 Pacific herring or 14% of those with wounds (Table 3). Only one salmon and nine herring had more than 2 wounds in the 1991 sample. Scars (healed wounds) were rarely observed. In 1991, only 28 or 0.7% of all Pacific herring caught had scars and 6 or 0.9% of all salmon caught had scars.

Laboratory feeding studies

In the feeding experiment to study lamprey growth, the average size of lamprey increased from 15.4 cm (±2.7) and 4.1 g (±2.2) to 23.1 cm (±3.7) and 17.8 g (±10.6) in 42 d. One lamprey died after 6 d and one after 8 d; it was unlikely that they had fed. These lamprey were not replaced and not included in the estimate of average growth in length. In this 42-d period, 128 Pacific herring were killed or had severe wounds that would likely result in death. Almost all of these herring had multiple wounds.

Lamprey intestinal contents

The intestinal contents of the lamprey contained some scales and portions of the internal organs of their prey. Of the 103 intestines examined, 25% were empty and 75% contained food. Of the intestines with food, 43 (56%) had contents that were not identifiable and 34 (44%) contained scales or pieces of scales. Pacific herring scales were found exclusively in 20 intestines, and salmon scales were found exclusively in 8 intestines. The remaining six intestines contained both salmon and herring scales, but in all cases herring scales represented >75% of the scales. These intestines were classified as containing Pacific herring because the percentage of salmon remains was small and our estimate of the percentage of herring and salmon attacked is an approximation. Thus, 26% of the intestinal contents that could be identified were from salmon. In the study by Beamish and Williams (1976), salmon remains were found in 14% of the intestinal content of lampreys. The average of these two studies, therefore, indicated that lamprey prey were 20% salmon and 80% herring and other species. Because very few species other than salmon and herring were caught (Table 1), and only a few had lamprey wounds, we considered the prey to consist only of salmon and Pacific herring.

The volume of intestinal contents from this study and from Beamish and Williams (1976) was compared to lamprey length (Fig. 1). This relationship was needed to estimate the amount of flesh consumed in the methods used to determine the number of prey killed.

Average number of prey killed

The two methods used to estimate the number of prey killed produced very similar estimates. In the first method, using a conversion efficiency, we started with a weight of 1.8 g. Using this method we estimated that it would take 65 feeding events for a lamprey to grow from 1.8 g to its average terminal size of 34 g.

Our second estimate of the number of prey killed, based on the results of the laboratory feeding study, indicated that in 42 d the average lamprey increased in size from 15.4 to 23.1 cm. Knowing that it took 42 days to grow from 15.4 to 23.1 cm, we calculated by linear extrapolation that the average time it would take to grow from 12–25 cm was 74 days. Assuming one prey was killed per day, 74 prey would be killed.

The two methods, therefore, produced estimates of 65 and 74 prey killed. To be conservative, we used the estimate of 65 prey killed.

Estimated mortality of Pacific salmon and herring

Our estimate of lamprey abundance in 1990 was made after about one-third of the average growth had occurred. Thus, there were about 45 d of feeding left until the average lamprey reached the average terminal size. Using our estimate of natural mortality of $M = 0.4$, the total mortality during the remaining feeding period was approximately 144 000 lamprey. A similar estimate for 1991 indicated that approximately 188 000 lamprey would die as a result of natural factors. Because our estimates of lamprey abundance must be considered approximate and because the mortality estimates are relatively small, we chose to use the lamprey abundance estimates without correcting for natural mortality before and after the abundance estimates were made.

The number of salmon killed was determined as the lamprey population × 65 prey killed × 0.2% of the prey. An estimated 39 million Pacific salmon of all species were killed in 1990 and 51 million salmon were killed in 1991 (Table 4). Using the wounding percentages for each salmon species (Table 2) as an indication of the relative deaths for each species, we estimated the total mortality for each species of salmon (Table 4). In both 1990 and 1991, more chinook salmon were killed than any other Pacific salmon species. Chum salmon deaths were also high in both years. In 1991, both coho and sockeye salmon deaths were considerably higher than in 1990. Pink salmon deaths were the lowest, especially in 1991 when there were few smolts leaving the Fraser River. In 1990 and 1991 there were an estimated 156 million and 203 million Pacific herring larger than 100 mm killed directly or indirectly by river lamprey (Table 4).

Discussion

Relative importance of lamprey predation

In this study we 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 with approximately 20 million killed in 1990 and 18 million killed in 1991. These estimates can be put into perspective by comparing them with hatchery releases. In 1990 and 1991, all the Canadian hatcheries releasing chinook salmon directly into the Strait of Georgia and into the Fraser River and then into the Strait of Georgia produced a total of approximately 33 million and 34 million smolts, respectively. The mortality caused by river lamprey in the Fraser River plume in 1990 and 1991 is equivalent to approximately 62 and 53%, respectively, of these releases. There is evidence that the numbers of wild and hatchery reared chinook smolts that entered the Strait of Georgia at this time may have been about equal (R.J. Beamish, Pacific Biological Station, Nanaimo, BC V9R 5K6, unpublished data). If this approximation is correct, the mortality in the plume by river lamprey accounts for about 25–30% of the total marine mortality of all chinook salmon entering the Strait of Georgia from Canadian sources.

The mortality estimates of coho for the same period were not as consistent as those for chinook salmon. The 1990 estimate was approximately 2 million coho and the 1991 mortality estimate was approximately 10 million coho. In 1990 and 1991, all Canadian hatcheries that released coho salmon directly or indirectly (from the Fraser River) into the Strait of Georgia produced 7.6 million and 7.7 million smolts, respectively. Again, very preliminary evidence is that the abundance of hatchery and wild coho was about equal when they first enter salt water during the study period (R.J. Beamish, unpublished data). Thus, in 1990, coho mortality in the plume is equivalent to 26% of the total hatchery release into the Strait of Georgia or about 13% of all coho smolts entering the Strait. Coho mortality in 1991, in the plume only, is equivalent to 130% of the total hatchery release into the Strait of Georgia or about 65% of the total mortality of all coho smolts entering the Strait of Georgia.

Estimates of chum salmon smolt production entering the Strait of Georgia are difficult to determine. However, if we use escapements to the Fraser River and other rivers entering the Strait of Georgia of 650 000 and 1.3 million for 1989 and 1990, respectively (Salmon Stock Assessment Data Base, Pacific Biological Station, Nanaimo, BC V9R 5K6), a sex ratio of 1:1, average egg production of 3350 (Salo 1991), and egg-to-smolt survival of 10%, then approximately 108 million and 214 million chum smolts were produced in 1990 and 1991, respectively. Our estimates of chum salmon mortality in 1990 and 1991 of approximately 14.9 million and 10.1 million smolts would represent 13.7 and 4.7% of the total smolt production of chum salmon from the rivers flowing into the Strait of Georgia, and therefore, would not be considered to be a major source of early marine mortality.

We are uncertain why there was an absence of sockeye salmon mortality in 1990 and a large estimate of mortality in 1991. It may appear that we misidentified chum and sockeye salmon, but our identifications were confirmed in the laboratory using standard taxonomic measurements thus we concluded that misidentifications were not the explanation. A possible explanation is that because the abundance of smolts in 1991 was greater than in 1990 (Salmon Stock Assessment Data Base, Pacific Biological Station, Nanaimo, BC V9R 5K6), we did not have a large enough sample to observe the presence of wounds.

The relative importance of lamprey predation on sockeye smolts can be estimated by calculating the approximate number of smolts that went to sea in 1991 from the Fraser River. If we use an egg-to-smolt survival estimate of 10.09% (Foerster 1968), a sex ratio of 1:1, and an average egg production of 3274 (Foerster 1968), the 3 million sockeye salmon (Salmon Stock Assessment Data Base, Pacific Biological Station, Nanaimo, BC V9R 5K6) that escaped to spawn would produce about 511 million smolts in 1991. Our estimates of sockeye salmon mortality in 1991 of approximately 11.7 million is 2.3% of the estimated smolt production in the Fraser River. Lamprey predation on sockeye, therefore, does not appear to be a major source of early marine mortality in the Fraser River plume.

Virtually all pink salmon spawn in odd years in the Fraser River drainage, with the young pink going to sea in even years (Neave 1966). The estimated number of pink salmon deaths were low relative to the other species, even though in even numbered years pink salmon smolts may be the most numerous of all the species of salmon smolts. We conclude that our study did not identify lamprey predation as a major source of pink salmon smolt mortality in the Fraser River plume.

During the spawning season, Pacific herring move into the Strait of Georgia from offshore (Taylor 1964; Hourston and Haegele 1980). In recent years, the estimated average biomass of spawning Pacific herring has been about 50 000 t (range from about 30 000 to 70 000 t (V. Haist, Pacific Biological Station, Nanaimo, BC V9R 5K6, personal communication). Assuming eight herring weigh about 1 kg (Hart 1973), there would be about 500 million spawning fish. The estimates of Pacific herring mortality (larger than 100 mm) were 156 million in 1990 and 203 million in 1991. This mortality is mainly on 1 year olds, not the spawning 3 year old and older fish. Nevertheless, the estimates of herring mortality caused by lamprey are sufficiently large to conclude that lamprey predation could be an important source of marine mortality of Pacific herring in the Strait of Georgia.

In this study, we examined the mortality in the Fraser River plume only. We observed feeding outside the plume and we know that feeding river lamprey occur elsewhere in the strait (Beamish 1980). Abundance estimates of river lamprey were made in two earlier studies. In the 1976 study, the abundance of river lamprey was estimated using the area fished by a purse seine. Minimum and maximum abundance estimates were made based on the minimum and maximum area that could be fished by a purse seine. The maximum abundance estimate was based on the area of the seine when the lamprey would be unlikely to swim through the meshes (Beamish and Williams 1976). The maximum population estimate in 1975 was 6.2 million river lamprey and the minimum was about 10% of this number.

A second estimate of abundance was made in 1979 using gear that captured young lamprey in the Fraser River as they moved into salt water (Beamish and Youson 1987).

This method was based on the volume of river discharge strained and produced a population estimate of 6.5 million river lampreys. The two estimates in this study of 3 million in 1990 and 3.9 million in 1991 are lower than the earlier estimates but are for the plume area only. Considering the difficulty involved in estimating the abundance of any fish and particularly an eel-shaped fish that is difficult to catch, the four abundance estimates are quite similar, even though the 1990 and 1991 estimates are for the plume only. We have no reason to conclude that the abundance of lamprey is constant from year to year, but we can conclude that the mortality estimates based on the population of lamprey in the plume only, will be conservative, possibly accounting for approximately one-half to two-thirds of the actual deaths.

The problem of lamprey predation is not unique to the Strait of Georgia. The landlocked sea lamprey has been a source of mortality for salmonids in the Great Lakes and considerable effort has been expended to reduce the impact of lamprey-caused mortality (Smith and Tibbles 1980). Reduction of lamprey abundance in the Great Lakes has increased the abundance of salmonids and it is possible that a program to reduce river lamprey abundance could improve the natural survival of chinook and coho salmon in the strait. Any program that attempted to control river lamprey abundance should include studies of the other key factors that regulate the abundance of chinook and coho in the strait so that the effect of a control program can be evaluated.

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