Transactions of the American Fisheries Society 121:444–455, 1992

Spiny Dogfish Predation on Chinook and Coho Salmon and the Potential Effects on Hatchery-Produced Salmon

RICHARD J. BEAMISH, BARBARA L. THOMSON, AND GORDON A. MCFARLANE

Department of Fisheries and Oceans, Biological Sciences Branch
Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada

Abstract.—Large numbers of spiny dogfish *Squalus acanthias* moved into the area near the mouth of the Big Qualicum River, British Columbia, at the time hatchery-reared smolts of chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* were leaving the river in 1988 and 1989. A small percentage of the spiny dogfish preyed on the smolts, but the resulting smolt mortality is 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 the Big Qualicum Hatchery was similar to the pattern of survival of other hatchery-produced salmon. We propose that this long-term decline in survival results from predation.

Spiny dogfish *Squalus acanthias* are abundant in the Strait of Georgia. The biomass of the population is about 60,000 tonnes (Fargo and Tyler 1989), representing 35 million spiny dogfish (based on an average weight of 1.7 kg). This small shark is an omnivorous, opportunistic feeder (Ketchen 1986), but its predation on Pacific salmon has rarely been observed. In the most comprehensive published study of feeding habits of spiny dogfish, 27 stomachs containing Pacific salmon were identified from 9,466 examined (Jones and Geen 1977). In three other studies that examined the possibility that spiny dogfish might be important predators of Pacific salmon in the Strait of Georgia (Chatwin and Forrester 1953; Godfrey 1968; Robinson et al. 1982), only one spiny dogfish was found to have fed on salmon (Chatwin and Forrester 1953). This inability to demonstrate substantial predation on young or adult salmon has resulted in the belief that spiny dogfish are not important predators of salmon (Jones and Geen 1977; Ketchen 1986).

In this study we reexamined the role of spiny dogfish as predators of Pacific salmon, particularly hatchery-produced chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch*. We examined the diet of spiny dogfish for 2 years in the Strait of Georgia to determine if spiny dogfish fed on salmon smolts, and we examined production from a hatchery near the spiny dogfish population we sampled as well as other hatcheries in the Strait of Georgia to determine if the pattern of survival could be related to predation.

Methods

Abundance of spiny dogfish.—A swept-area abundance estimate of spiny dogfish in the study area (Figure 1) was made by towing a bottom trawl net at 3.5–5.5 km/h. Surveys were conducted from July 11 to July 17 in 1988 (44 tows) and from July 24 to 28 in 1989 (40 tows). Abundance of spiny dogfish was estimated by dividing the survey area (Figure 1) by the total area fished and multiplying by the total catch of spiny dogfish. Area fished was determined by multiplying the distance swept by the net by the width of the net; the width of the net for each tow was determined according to procedures used by Saunders et al. (1984). The net was assumed to catch all spiny dogfish in its path. Confidence intervals (95%) for the estimate of spiny dogfish abundance, mean length of spiny dogfish, and mean length of ingested salmon smolts were determined with the procedures described by Cochran (1977). Trawl surveys were not conducted during the period of greatest predation on salmon smolts to avoid altering the feeding behavior of spiny dogfish. However, gillnetting was conducted during both the trawl survey and the period of dogfish predation. Spiny dogfish abundance during the period of salmon smolt predation (May and June) was estimated by calculating the average daily catch per standardized gill-net set (catch per unit of gill-net effort or CPUE) during the period of smolt predation, dividing by the gill-net CPUE during the abundance survey and multiplying by the estimated spiny dogfish abundance during the trawl survey. Gill-net CPUE was also used directly as an index of abundance.

Predation study.—Chinook and coho salmon from the Big Qualicum Hatchery are released into the Big Qualicum River, British Columbia, approximately 1.5 km from the Strait of Georgia (Figure 1). The estuary of the river is small, less than 600 m by 450 m, and salmon smolts move

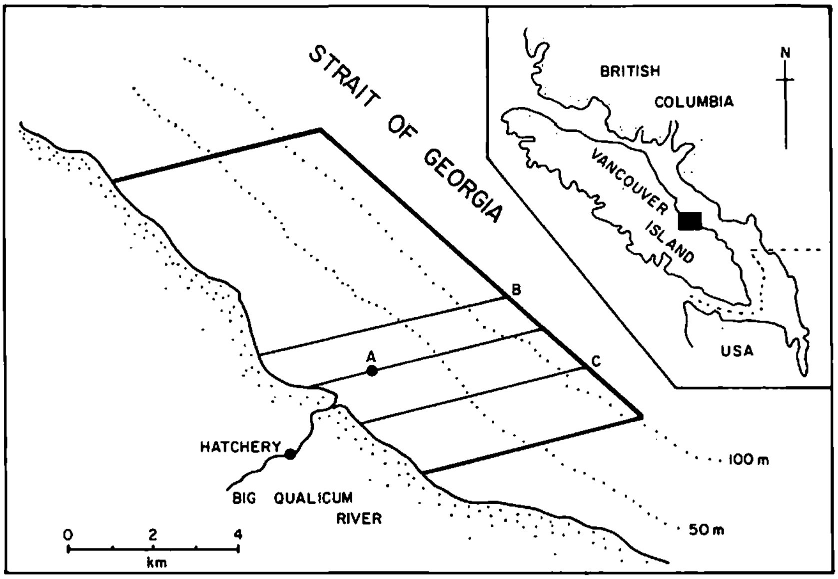

FIGURE 1.—Big Qualicum River study area. Thick lines enclose the bottom trawl survey area. A is the standard gill-net fishing site used in 1988; it is located on the gill-net transect formed by Loran C line 5990-Y-29325. B is the gill-net transect on Loran C line 5990-Y-29330, and C is the gill-net transect on Loran C line 5990-Y-29320.

quickly into the surrounding waters of the Strait. We conducted our predation study in these surrounding waters and in the estuary (Figure 1).

In 1988, we fished at one location (Figure 1, site A) about 1 km from the mouth of the river at a depth of 10 m. From May 16 through July 22, 1988, we set gill nets (90 m × 4 m, 13–15-cm stretched mesh) every 2 d. All sets were on bottom, alternating between morning sets (0500–0700 hours) and evening sets (2200–2400 hours). In most sets, one 90-m net was set for 1 h. If more nets were set or if the duration extended beyond 1 h, catches were standardized to one 90-m net/h. At the same time, we set longlines with about 70 size-12/0 "mustad" halibut hooks on bottom and vertically from the surface. Hooks were baited with Pacific herring *Clupea pallasi* or chinook salmon smolts. After the first 2 weeks we found that all gear types caught spiny dogfish almost exclusively; therefore, we concluded that spiny dogfish would be the major predator in the area. Because catches were highest in the morning and stomach contents of fish caught then were more easily identifiable than the stomach contents of fish caught in the evening, we fished only in the early morning with gill nets after the first 2 weeks. Catches from the 13-cm stretched-mesh gill nets were used in this analysis because this mesh size caught the most fish and was the only mesh size used later in the study (Figure 2).

From December 1988 to March 1990, we fished along three transect lines including site A fished in 1988 (Figure 1). Gill-net sets were at depths of 5 m, 10 m, 20 m, 35 m, and 55 m, although not all depths were fished on the same date. All spiny dogfish captured in gill nets were measured for total length (tip of snout to tip of tail) and sex was determined.

Hatchery releases.—Salmon are released from the Big Qualicum Hatchery by opening barriers, allowing access to the river. Salmon move passively into the river over a period of about 4 weeks. Once in the river, most are believed to migrate the short distance to salt water in less than 1 d (Mace 1983). Release dates are determined by the hatchery manager.

In 1988, 5.6 million chinook salmon were released on May 10 and 1.2 million coho salmon on May 14. Hatchery staff estimated that 5% (279,000) of the chinook salmon smolts in this release had entered salt water by May 19, 50% by June 1, and 90% by June 8. No chinook salmon smolts remained in the hatchery after June 15. Half of the coho salmon smolts had left the hatchery by May 25 and 90% by June 4; all had entered salt water by June 18. In 1988, about 24,000 coho salmon were released directly into salt water about 6 km offshore. A second group of about 12,000 coho salmon was transported directly to a net-pen about 0.5 km offshore.

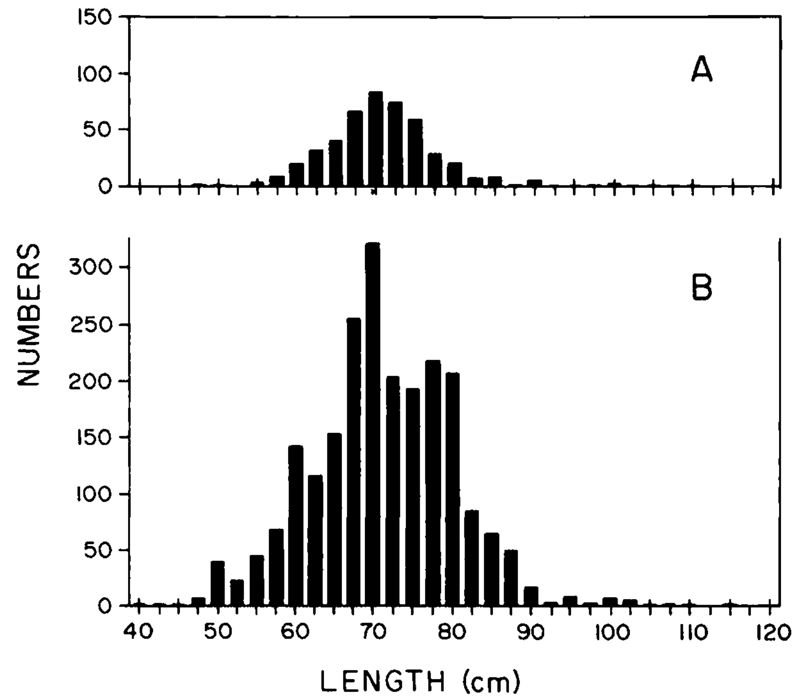

FIGURE 2.—Length-frequency distributions of spiny dogfish caught (A) by gill net and (B) by bottom trawl in 1988. Lengths are shown at 2.5-cm intervals.

In 1989, 0.6 million chinook salmon smolts were released from the hatchery on May 10, 3.1 million were released on May 25, and 2 million chinook were released from June 7 to June 11. The first release of coho salmon smolts (0.5 million) occurred on May 7; 0.2 million coho salmon were released on May 11, and the remaining 0.76 million were released from May 25 to June 8.

Stomach contents.—Contents of stomachs from spiny dogfish captured in gill nets were visually classified into broad taxonomic categories. Salmon were identified to species and preserved. All salmon identifications were confirmed in the laboratory according to standard taxonomic criteria. The state of digestion was categorized according to the results of the digestion study (below; Table 1) as freshly ingested (skin present on at least one side of the body and head parts intact; in stomach less than 12 h), partially digested (skin missing on both sides and soft parts of head digested, about 25% digested; in stomach less than 24 h), and digested (pieces of muscle present, about 50% digested; in stomach more than 24 h).

About 70 spiny dogfish, caught in the Strait of Georgia on April 14, 1989, on longlines baited with herring, were transported live to the Pacific Biological Station and held in two large tanks (50,000 L) supplied with aerated, flowing water at ambient temperature (9–11 °C). On April 18 and April 24, we tagged the spiny dogfish and force-fed them one coho salmon each by placing a smolt head first as deeply as possible into the shark's throat. Five force-fed spiny dogfish were left in the tank for each of six time periods (6, 12, 18, 24, 36, or 48 h). After the designated digestion period, spiny dogfish were removed, killed, measured and dissected to examine their stomach contents. Condition and length of salmon in the gut were recorded; then the salmon were photographed and preserved in 10% formalin.

Hatchery production.—We examined survival of chinook and coho salmon released from the Big Qualicum Hatchery and from all hatcheries that release salmon into the Strait of Georgia to determine if survival appeared random among brood years[1] or followed some pattern. Hatchery release and survival data were obtained from the Salmon Enhancement Program and Kuhn et al. (1988). Releases included chinook salmon fry, chinook salmon smolts, and coho salmon smolts reared in

[1] In northwestern salmon terminology, "brood year" means a year-class of salmon, referenced to the year in which eggs were fertilized.

TABLE 1.—States of digestion of coho salmon force-fed to spiny dogfish.

Digestion period (h)	Typical state of digestion
12	Fins and skin partially digested; soft parts of head partially missing
18	Skin missing; soft tissue of head digested; fins missing; stomach wall partially digested
24	Head digested in most samples; stomach wall missing
36	Only large pieces of muscle remain
48	Only small pieces of muscle and otoliths remain

hatcheries. From 1972 to 1981, the hatchery release estimates included a relatively small number of coho salmon released before smolting. The number of chinook salmon fry released in the autumn was not included; however these releases were small compared to spring releases. The hatcheries that released chinook salmon into the Strait of Georgia and were included in our analysis were Big Qualicum, Chemainus, Little Qualicum, Puntledge, Sechelt, Indian, Lions Bay, Vancouver Bay, Englishman River, Oyster River, Seymour, Quinsam, Capilano, Tenderfoot, Nanaimo, and Cowichan. Hatcheries, special projects, or public involvement projects producing coho salmon were Big Qualicum, Tenderfoot, Quinsam, Puntledge, Capilano, Sechelt, Rosewall, Vancouver Bay, Seymour, Indian Arm, Sliammon River, Lower Campbell River, Noons Creek, Cowichan River, Horseshoe Bay, and the West Vancouver Laboratory.

Results

Spiny Dogfish Abundance

In 1988, 2,248 spiny dogfish were captured in the trawl survey (Figure 1). The estimated abundance in the survey area was 173,000 fish (95% confidence interval, ±110,000 fish). Lengths ranged from 42 to 116 cm (Figure 2) and averaged 72 cm (±0.4 cm). The difference of 0.8 cm (±0.9 cm) in mean lengths between spiny dogfish caught in the trawl and gill-net surveys was not statistically significant ($P > 0.05$), indicating both methods sampled a similar population. In 1989, 1,464 spiny dogfish were captured. The estimated abundance was 126,000 fish (±87,600 fish). Lengths ranged from 46 to 110 cm and averaged 74.7 cm (±0.4 cm).

On May 19, 1988, the gill-net catch of spiny dogfish in a 1-h period (CPUE) was 70.0 fish/h (Figure 3). Gill-net CPUE averaged 39.3 spiny dogfish/h for the period May 19 to June 15, then declined to an average of 10.7/h by late June and 4.0/h in July (Figure 3). In 1989, the combined gill-net CPUE for all depths increased abruptly from 6.6 spiny dogfish/h in April to 21.6/h by early May (Figure 3). At depths less than 20 m, CPUE averaged 28.6 spiny dogfish/h between May 15 and June 21 (Figure 4). Maximum average CPUE occurred on May 10 at 43.6/h (Figure 3). The CPUE declined in late June to 13.2 spiny dogfish/h (Figure 4); it averaged 7.2/h during July and 3.8/h for the remainder of the year. At the time of the 1988 and 1989 trawl surveys, the average gill-net CPUEs were 2.1 and 4.2 spiny dogfish/h, respectively. Using these average CPUEs as relative indices of abundance, we estimate that

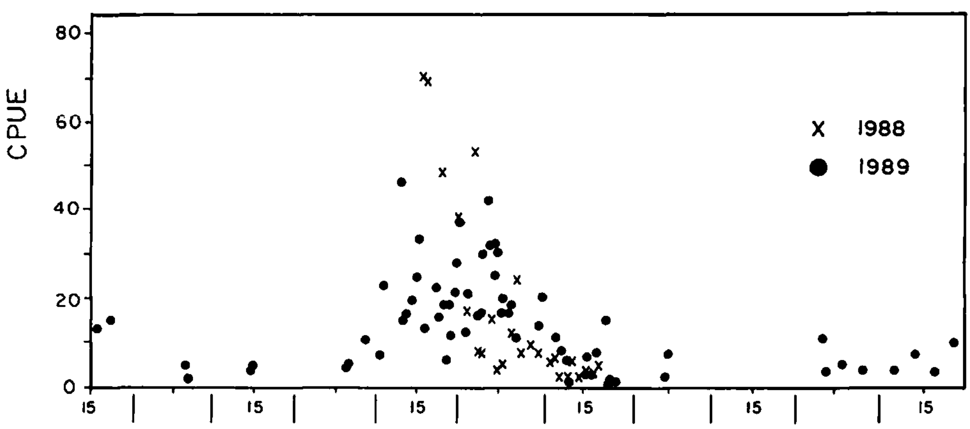

FIGURE 3.—Average standardized catches per unit effort (CPUE, fish per 90-m net per hour) by day of spiny dogfish caught by gillnetting during 1988 and 1989.

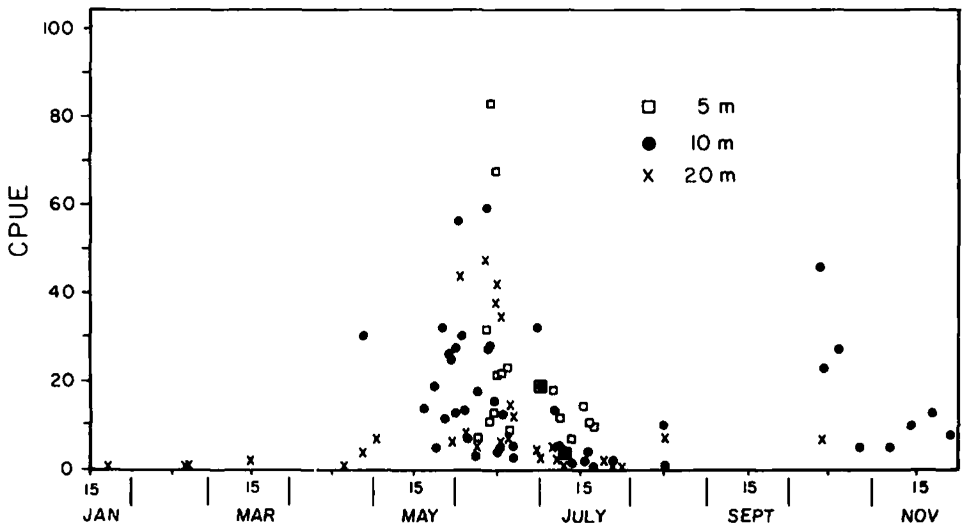

FIGURE 4.—Average standardized CPUE by day of spiny dogfish caught along Loran C line 5990-Y-29325 at 5 m, 10 m, and 20 m by gillnetting during 1989.

up to 1.4 million spiny dogfish were in the study area at the time most hatchery-reared salmon entered salt water (mid-May to mid-June) in 1988 and that 1.0 million spiny dogfish were present in 1989.

The abundance of spiny dogfish increased close to shore in October and November (Figure 4). Spiny dogfish at this time were feeding on larger salmon.

Predation Study

The extent of digestion of the salmon force-fed to spiny dogfish was used to assess the length of time salmon had been in the stomachs of spiny dogfish caught in the gill nets. There was some variation in the amount of digestion at each time period but the states of digestion at 12, 24, 36, and 48 h were quite distinct (Table 1). Skin, fins, and soft parts of the head of the coho salmon smolts were digested first. After 18 h, the stomach wall was digested; after 24 h, the head was missing from four of the five coho salmon. After 36 h, only large pieces of muscle remained. At 48 h, smaller pieces of muscle were left and one spiny dogfish had no fish remains.

In 1988, predation on chinook and coho salmon smolts occurred in the spring and early summer. Although gillnetting started on May 16, 1988, the standardized gill-net sets did not begin until May 19. In 1988, 1,161 spiny dogfish were captured from May 19 to July 22. Young chinook and coho salmon occurred regularly in the stomachs of some spiny dogfish caught in gill nets set up to June 15 (Figure 5). After June 15, spiny dogfish that had eaten salmon were caught in only two sets. The percentage of spiny dogfish with chinook and coho salmon in their stomachs was highest (21.7%) in mid-May, suggesting that some predation occurred earlier (Figure 5). Because salmon were first released from the hatchery on May 10 it is probable that predation occurred from May 10 to May 16. Thirty-eight percent of the 558 spiny dogfish captured from May 19 to June 15, 1988 had empty stomachs. Of the 344 spiny dogfish with stomach remains, 69 contained chinook and coho salmon smolt remains; 41 stomachs contained smolts that appeared to have been ingested less than 24 h previously, according to our digestion study. The amount of predation, therefore, appeared to increase rapidly to a maximum about 1 week after the hatchery began to release salmon. Over the next 6 weeks there was a gradual decline in the amount of predation.

Coho salmon predominated in the stomachs initially and chinook salmon later (Table 2). There were 31 coho salmon, 63 chinook salmon, and 15 unidentified salmon in the 41 stomachs that contained salmon in the less-than-24-h digestion category, an average of 2.7 salmon smolts per stomach. Five stomachs contained both chinook and coho salmon. One spiny dogfish had eaten 17 salmon smolts. One coho salmon contained a coded wire tag identified with the Big Qualicum Hatchery.

Chinook and coho salmon in the stomachs had average estimated fork lengths of 8.6 cm (±0.5

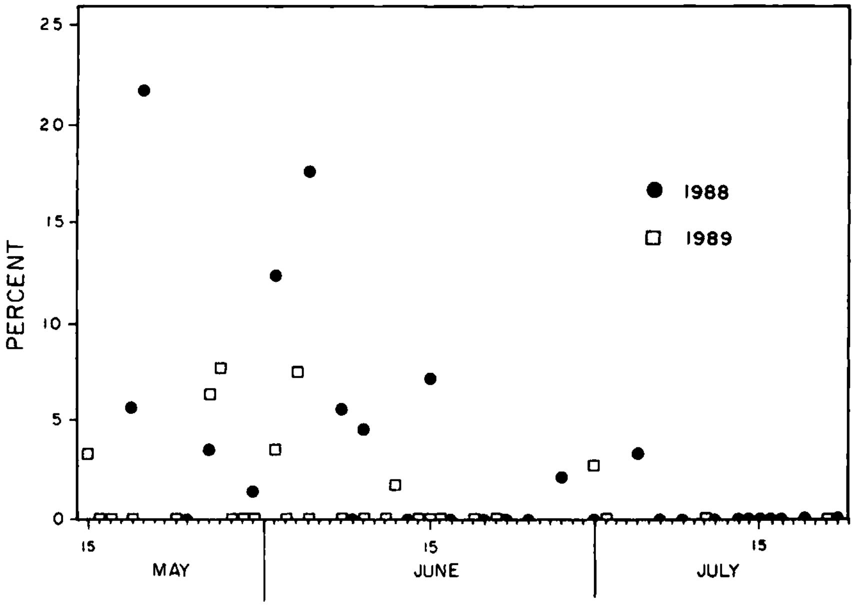

FIGURE 5.—Percentages of the daily catches of spiny dogfish caught by gillnetting that had salmon smolts in their stomachs in 1988 and 1989.

cm; range, 7–13 cm) and 13.6 cm (±0.5 cm; range, 12–15 cm), respectively. The average sizes of chinook and coho salmon released from the hatchery in 1988 and 1989 were 7 and 18 cm, respectively.

In 1988, the direct release of coho salmon 6 km offshore attracted large numbers of spiny dogfish within several hours, and the sharks were observed feeding on the salmon. Twenty-four hours after other coho salmon were released directly into a saltwater net-pen, 18 spiny dogfish were found feeding on salmon inside the net. An underwater examination indicated that spiny dogfish had apparently "chewed" through the net meshes.

In 1989, most predation on salmon occurred from May 15 to June 21. Of the 1,470 spiny dogfish captured between May 15 and June 21 at the site fished in 1988, 988 had been feeding and 20 of these had remains of young salmon in their stomachs; 14 of the 20 contained the remains of 42 salmon that had been in the stomachs less than 24 h.

In 1989, 5,078 spiny dogfish were caught along the three transect lines at depths less than 10 m over the period May 15 to June 21. Only two of 717 spiny dogfish sampled after June 21 contained salmon smolts in their stomachs. The largest catches of spiny dogfish feeding on salmon occurred on May 26 and 27 (Figures 3, 5). Of the 5,078 spiny dogfish caught in 1989, 3,577 had stomach contents and 44 contained salmon smolt remains, 34 of which contained remains of 67 salmon that had been in the stomach less than 24 h: 21 coho salmon, 18 chinook salmon, and 28 unidentified salmon, an average of 2.0 salmon per stomach.

Coho salmon occurred more frequently than chinook salmon in stomachs at the beginning of the 1989 predation period. The average size of the chinook salmon in spiny dogfish stomachs was 7.2 cm (±1.0 cm; range, 5.5–12.0 cm). Coho salmon in stomachs averaged 11.9 cm (±0.4 cm; range,

TABLE 2.—Numbers of salmon smolts, by species, eaten within the previous 24 h by spiny dogfish collected in the 1988 gill-net sampling.

Date	Spiny dogfish caught[a]/spiny dogfish with salmon remains	Number of smolts in spiny dogfish stomachs			
		Coho salmon	Chinook salmon	Unidentified salmon	Total salmon smolts
May 19	70/4	2	2	0	4
May 20	69/15	24	10	0	34
May 26	114/5	2	26	1	29
Jun 1	57/7	2	8	6	16
Jun 4	17/3	0	8	0	8
Jun 7	107/6	1	6	8	15
Jun 9	41/1	0	3	0	3
Total		31	63	15	109

[a] Does not include catches from gill-net sets in which salmon predation did not occur.

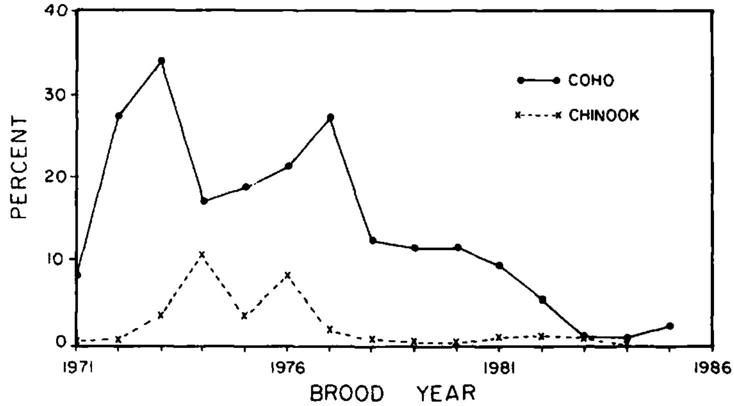

FIGURE 6.—Survival (%) of chinook and coho salmon from Big Qualicum Hatchery, British Columbia, between 1971 and 1985.

9.5–13.2 cm). Only two spiny dogfish had both coho and chinook salmon in their stomachs. Seven ingested coho salmon and two chinook salmon had been tagged with coded wires at the Big Qualicum Hatchery.

The impact of this predation on the survival of smolts released from the Big Qualicum Hatchery was estimated from the daily predation estimates and the size of the spiny dogfish population. In 1988, an average of 7.3% of spiny dogfish caught from mid-May to mid-June had salmon smolts in their stomachs. If the population of spiny dogfish was about 1.4 million, as estimated, and the average number of salmon in the stomachs less than 24 h was 2.7, then the number of salmon smolts killed in the study area in 4 weeks could have been about 7.7 million (approximately equivalent to the total 1988 release). In 1989, at the site fished in 1988, an average of 1% of the spiny dogfish caught between May 15 and June 21 had an average of 3.0 salmon smolts in their stomachs. Based on the 1989 population estimate of 1 million spiny dogfish, we estimate that approximately 1.1 million salmon smolts were consumed. Alternatively, a lower estimate of 0.5 million salmon smolts killed is obtained if we use the catches from the three transect lines, in which 0.7% of the spiny dogfish caught had an average of 2.0 salmon smolts in their stomachs.

Pieces of larger salmon, 15–50 g, were found in spiny dogfish stomachs throughout the year but were more common in fall and winter (September–March). Spiny dogfish were predominantly caught at deeper depths at this time. Flesh color, skin color, and scale pattern confirmed that the flesh pieces found in the spiny dogfish stomachs were from larger salmon.

Between December 1988 and March 1989, 367 spiny dogfish were caught at depths of 40–60 m. Of the 138 (37.6%) that had been feeding, 11 (8.0%) contained pieces of larger salmon. Between September 1989 and March 1990, 642 spiny dogfish were caught at depths of 40–60 m, 429 (66.8%) of which had been feeding. Of these, 68 (15.9%) had been feeding on larger salmon. One spiny dogfish contained the fresh remains of a whole, early maturing (jack) salmon.

Survival of Hatchery Produced Salmon

The Big Qualicum Hatchery started production in 1971. Percent survival for chinook and coho salmon released that year was low (Figure 6). Percent survival for chinook salmon increased to 10.5% in the mid-1970s then declined. Fish of the 1984 brood year (released in 1985 and all returned by 1989) had the lowest survival (0.1%). Coho salmon survival was highest (33.8%) for the 1973 brood year (released in 1975). Percent survival was high (average, 23.1%) for brood years from 1973 to 1977 but declined with the release of the 1978 brood year in 1980. The survival of the 1985 brood year was 2.3%. Brood years of the mid-1970s, when releases were smaller, provided the greatest returns. The trend to a maximum return as releases increase can be modelled by a Ricker-type stock–recruitment relationship. According to the calculated relationship for chinook salmon

$$R = 0.064\,Pe^{(-7.31 \times 10^{-7})P},$$

$r^2 = 0.72$, where R is the number of adults returning from a smolt release equal to P, the maximum returns would occur at releases of about 1,400,000 smolts (Figure 7A). For coho salmon,

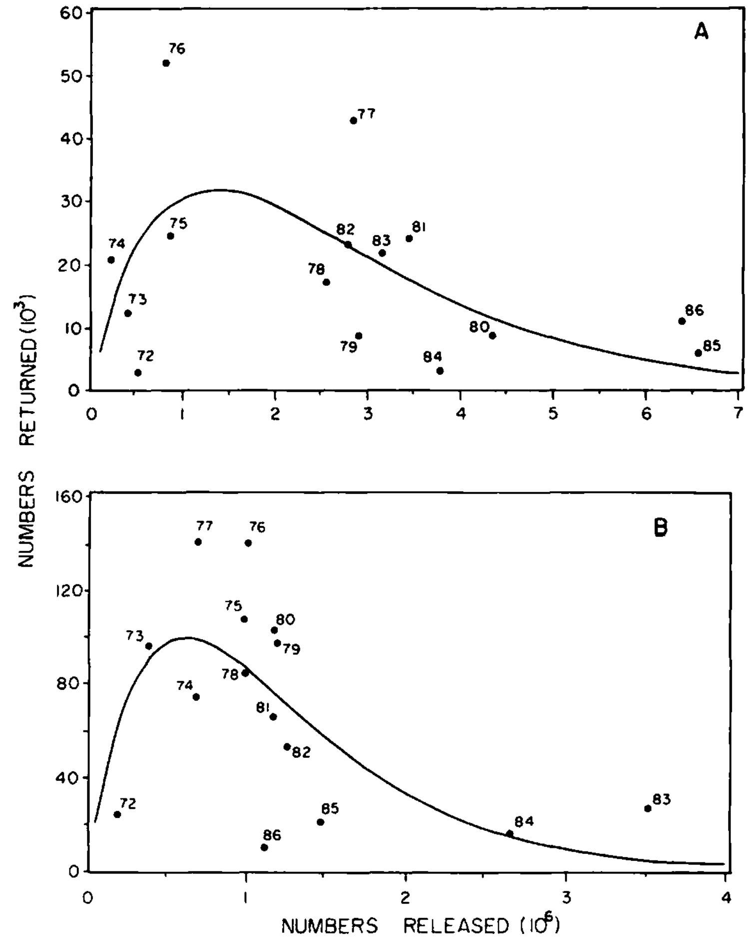

FIGURE 7.—Returns of adults compared to the releases of fry, smolts, or both from the Big Qualicum Hatchery for each brood year of (A) chinook salmon fry and smolts, brood years 1972–1986, and (B) coho salmon smolts, brood years 1972–1986. Solid lines are fitted Ricker curves.

$$R = 0.451\ Pe^{(-16.5 \times 10^{-7})P},$$

$r^2 = 0.88$, the maximum returns would occur at releases of about 610,000 smolts (Figure 7B).

The survival of chinook and coho salmon from the other hatcheries that release salmon into the Strait of Georgia followed a similar trend. The relationship between the number of chinook salmon smolts released and the number of adults returned by brood year (total catch in all fisheries and any returning to the rivers) for all Strait of Georgia hatcheries (Figure 8A) was described by

$$R = 0.036\ Pe^{(-1.89 \times 10^{-7})P},$$

$r^2 = 0.81$. We again used a Ricker curve because preliminary returns for 1985 and 1986 brood years indicate total returns will be approximately 22,000 and 42,000, respectively; hence the curve appears to be dome shaped. The estimated maximum return was 70,072 at a release of 5,300,000.

The relationship between the total number of coho salmon smolts released into the Strait of Georgia and the total number of returns (Figure 8B) was described by

$$R = 0.139\ Pe^{(-2.07 \times 10^{-7})P},$$

$r^2 = 0.87$. The estimated maximum return of 247,030 occurs at a release of 4,830,000.

Discussion

The observations of spiny dogfish feeding on salmon provide the first evidence that this small shark may be an important predator of salmon in the Strait of Georgia. The number of spiny dogfish with pieces of larger salmon in their stomachs dur-

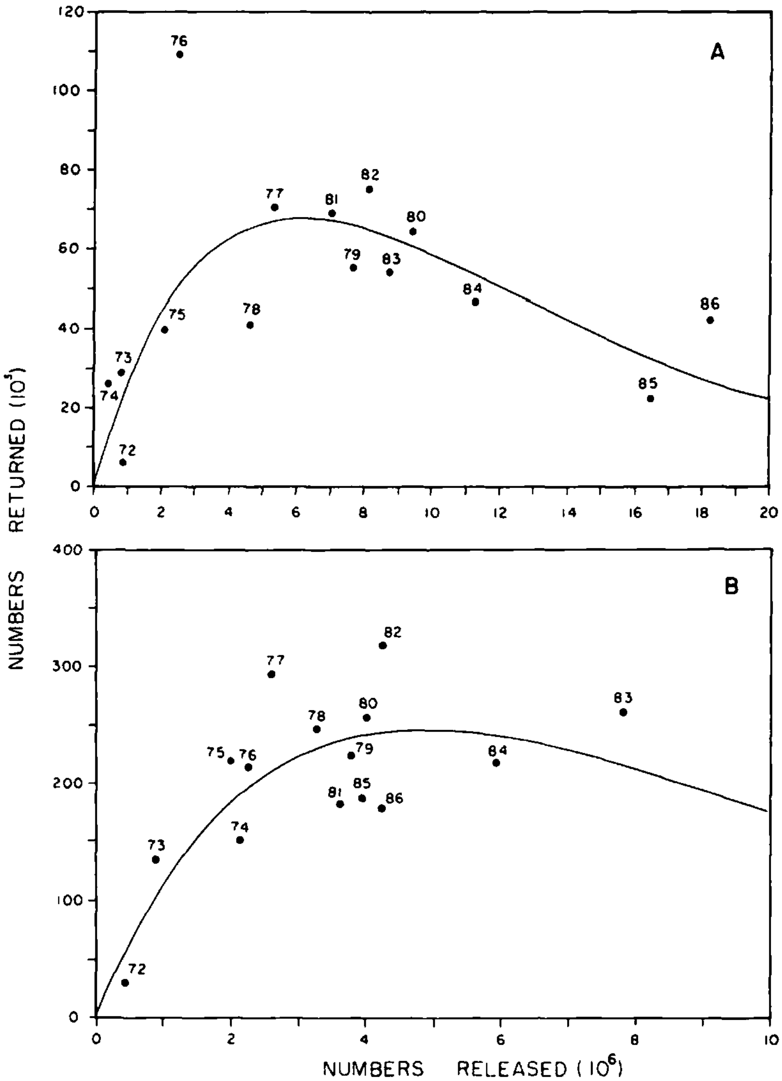

FIGURE 8.—Returns of adults compared to the releases of fry, smolts, or both from hatcheries throughout the Strait of Georgia for each brood year of (A) chinook salmon fry and smolts, brood years 1972–1986, and (B) coho salmon smolts, brood years 1972–1986. Solid lines are fitted Ricker curves.

ing the fall and winter was surprisingly high. The aggregation of spiny dogfish in the vicinity of the Big Qualicum River in the fall and early winter of 1988–1989 and 1989–1990, as indicated by an increase in the CPUE, coincided with the aggregation of adult salmon in the estuary prior to their spawning migration into fresh water, suggesting that spiny dogfish may be attracted by the salmon. The larger salmon eaten by spiny dogfish throughout the fall and early winter (seasons when 8.0% of feeding spiny dogfish in 1988–1989 and 15.9% in 1989–1990 contained remains of large salmon) included adult salmon before they entered fresh water and spawned salmon that were washed from the river into the estuary. The prespawning adults eaten may have been alive or the remains of fish killed by other means such as seal predation; however, very few seals were observed. It is difficult to believe that a spiny dogfish could catch a live adult salmon, but the possibility cannot be rejected. The feeding that occurred in the early winter was on dead spawned salmon that were washed into the ocean, because no mature salmon remained in salt water. The impact that predation on prespawning adults has on total returns is difficult to assess until it is determined how the adults were killed. If the spiny dogfish attacked and killed the salmon, the mortality may be high even though spiny dogfish abundance is relatively low at this time of year, because abundance of adult salmon is also relatively low. It is important to know if mortality of aggregating prespawning adults is high, because optimizing hatchery production requires an understanding of all sources of marine mortality.

The recovery of tagged smolts showed that predation occurred on chinook and coho salmon smolts reared in the Big Qualicum Hatchery. About 3% of the hatchery-released salmon were tagged in 1988 and 1989, so we would not expect to find large numbers of tagged salmon in the stomachs of spiny dogfish. We collected 176 freshly digested salmon from spiny dogfish stomachs from mid-May to mid-June in 1988 and 1989. We found 1 tagged salmon in 1988 and 9 in 1989. All 10 tagged salmon, about double the expected number of tag recoveries (3% of 176), were from the Big Qualicum Hatchery. Furthermore, the timing of predation corresponds to the hatchery release schedule, and the sizes of the salmon eaten were similar to the sizes released. Therefore, it is probable that many of the young chinook and coho salmon consumed were released from the Big Qualicum Hatchery.

In 1988, the estimated mortality was about equivalent to the total release of chinook and coho salmon. In 1989, the estimate of mortality was considerably lower; however, each annual mortality estimate probably is related to the behavior of the smolts in the sampling area. Both spiny dogfish and salmon smolts can move offshore and out of the sampling area. Spiny dogfish feed on salmon smolts in the offshore areas, as indicated by the predation that occurred almost as soon as smolts were intentionally released offshore. The sharks also appear to be attracted to salmon smolts, as evidenced by the predation on salmon smolts in the net-pen. Therefore, spiny dogfish may follow aggregations of salmon smolts and mortality outside of the sampling area would not be measured. The calculations of total salmon mortality, therefore, indicate that predation by spiny dogfish is an important source of early marine mortality of salmon produced at the Big Qualicum Hatchery and probably are not relative indices of survival.

The potential impact of predation mortality on smolt survival can be studied by examining the pattern of salmon returns from hatcheries releasing smolts into the Strait of Georgia. The relationship between releases and returns we identified indicates that mortality of smolts released from the Big Qualicum Hatchery increased gradually as more smolts were released each year. The pattern of gradually increasing mortalities with increasing releases was virtually identical for all hatcheries studied (Figure 8). We believe this indicates that predation in general and spiny dogfish predation in particular may be the major source of the early marine mortality of salmon released from the Big Qualicum Hatchery and other hatcheries around the Strait of Georgia.

Our view that predation is the cause of the gradual decline in survival is based on the belief that most marine mortality of salmon occurs shortly after smolts enter salt water. Several studies indicate year-class strength is determined at this time (Parker 1971; Ricker 1976; Hargreaves and LeBrasseur 1985; Fisher and Pearcy 1988). Also, studies of the releases of chinook salmon from the Big Qualicum Hatchery show a constant proportion of the stock returning at each age (Farlinger et al. 1990). This indicates that the number of smolts that will survive to be caught in the fishery or return to the hatchery probably is determined early after the smolts enter salt water. Predation, therefore, is an attractive mechanism to explain the causes of the variation in the size of the brood year.

Pacific salmon experience low survival in the marine environment. Exact estimates of marine survival are difficult to find, but estimates for wild salmon from the Big Qualicum River before the hatchery was established ranged from 0.2 to 7.4% for chinook salmon and from 5.4 to 15.5% for coho salmon (Fraser et al. 1983). Our study indicates that, in recent years, the average marine survival of hatchery-reared chinook and coho salmon in the Strait of Georgia has been consistently lower than for wild salmon. There is evidence that hatchery rearing produces fish that are less wary of predators (Fenderson et al. 1968; Swain and Riddell 1990) or are more domesticated (Vincent 1960; Doyle and Talbot 1986) than wild fish and thus more susceptible to predation. The behavior of hatchery-reared salmon is altered because of crowding, and only a short period of crowding seems to be enough to cause the change (Keenleyside and Yamamoto 1962). A study of Atlantic salmon *Salmo salar* in Sweden showed a much higher average survival for wild fish than for smolts reared in hatcheries (Österdahl 1969). Volovik and Gritsenko (1970) attributed high predation rates on a hatchery-reared stock of pink salmon *Oncorhynchus gorbuscha* in the former Soviet Union to behavioral changes induced in the hatchery that made released fish more susceptible to predation than wild pink salmon. A conclusion from a North American review of studies of predation on Atlantic salmon was that hatchery-produced smolts appeared to be more vulnerable to predation than wild smolts (Ruggles 1980). Studies have shown that some form of conditioning to predation improved the survival of hatchery-reared salmon after they were released from the hatchery. Experiments in which naive hatchery fish were exposed to predation indicated that the mortality of hatchery fish, which normally was 14–30% higher than that of wild smolts, was lowered by the experience (Kanid'yev et al. 1970).

The predation process is typically described (Holling 1959) as a numerical response (change in predator abundance per unit time) and a functional response (prey eaten per unit time). In this study, there was an on-shore movement of spiny dogfish in the spring that we believe was a response to the movement of salmon smolts into salt water and to an accumulation of other food sources such as juvenile Pacific herring (Hay et al. 1989). Pacific herring were a major food of spiny dogfish, accounting for up to 10–20% of their diets during the study. The small percentage of spiny dogfish that preyed on the hatchery-reared chinook and coho salmon indicates that the numerical response to the salmon smolt accumulation is confined to a small percentage of the spiny dogfish in the area. Also, spiny dogfish that fed on salmon were at the low end of their functional response curve because their stomachs contained only two or three salmon on average but could have held considerably more (one spiny dogfish contained 17 salmon). Thus, both the numerical and functional responses of predatory spiny dogfish could increase substantially.

Increasing freshwater survival of coho and chinook salmon through hatchery rearing was expected to increase total survival, but it was not expected that the marine environment would impose a maximum on the relationship between number of released smolts and survival to adults. The occurrence of a dome-shaped survival curve for hatchery-reared salmon indicates that survival decreases as releases increase beyond an optimum threshold, resulting in fewer adult returns. Coho salmon releases for all Strait of Georgia hatcheries appear to be close to the optimum for maximum survival. However, coho and chinook salmon releases from the Big Qualicum Hatchery and chinook salmon releases from all hatcheries exceed the optimum for marine survival. Because the increase in mortality as releases increase beyond the optimum may be related to crowding in the rearing channels or other hatchery practices, the survival of salmon might improve if hatchery-reared salmon were made more wary of predators. The removal of predators from the sea may not be possible because of large incidental catches of other species. Also, removal of predators would be expensive because many predators would have to be removed even though relatively few spiny dogfish prey on salmon and the predators that remain could increase the number of salmon they eat substantially. Thus, reducing releases and improving the ability of smolts to avoid predation may be the best methods of improving survival.

There are short-term pitfalls to this approach, however. Reductions in hatchery output of only one species may not achieve previous levels of production for that species because spiny dogfish in the area may respond numerically and functionally to the total abundance of hatchery-reared salmon released. There is also a possibility that releases of both chinook and coho salmon at the optimum levels estimated in this study will not achieve previous levels of survival immediately because spiny dogfish (and other predators) have adapted to the large current releases and both their numerical and their functional responses may be stronger now than when the releases of salmon from hatcheries were first increasing.

We believe that adaptive or experimental hatchery practices along the lines we suggest could improve salmon survival. Hatchery practices must be at least as adaptive as the predators that await the hatchery-reared salmon at the river mouth.

Acknowledgments

We are grateful for the experience and capabilities of R. Scarsbrook. We thank G. Ladouceur, C. Neville, and L. Lapi for the use of hatchery survival and catch data and M. Saunders and R. Kronlund for assistance in data analysis. We appreciate the comments of L. Margolis.

References

Chatwin, B. M., and C. R. Forrester. 1953. Feeding habits of dogfish (*Squalus suckleyi* (Girard)). Fisheries Research Board of Canada, Progress Reports of the Pacific Coast Stations 95:35–38.

Cochran, W. G. 1977. Sampling techniques, 3rd edition. Wiley, New York.

Doyle, R. W., and A. J. Talbot. 1986. Artificial selection on growth and correlated selection on competitive behavior in fish. Canadian Journal of Fisheries and Aquatic Sciences 43:1059–1064.

Fargo J., and A. V. Tyler, editors. 1989. Groundfish stock assessments for the west coast of Canada in 1988 and recommended yield options for 1989. Canadian Technical Report of Fisheries and Aquatic Sciences 1646.

Farlinger, S., N. Bourne, B. Riddell, D. Chalmers, and A. Tyler, editors. 1990. Pacific stock assessment review committee (PSARC) annual report for 1989. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2064.

Fenderson, O. C., W. H. Everhart, and K. M. Muth. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. Journal of Fisheries Research Board of Canada 25: 1–14.

Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, U.S.A., in years of differing coastal upwelling. Canadian Journal of Fisheries and Aquatic Sciences 45:1036–1044.

Fraser, F. J., E. A. Perry, and D. T. Lightly. 1983. Big Qualicum River salmon development project. Volume I: a biological assessment, 1959–1972. Canadian Technical Report of Fisheries and Aquatic Sciences 1189.

Godfrey, H. 1968. Some observations on juvenile marine chum, chinook and coho salmon taken in waters adjacent to Georgia Strait in 1965. Fisheries Research Board of Canada Manuscript Report 955.

Hargreaves, N. B., and R. J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 42:659–668.

Hay, D. E., M. C. Healey, L. J. Richards, and J. B. Marliave. 1989. Distribution, abundance, and habitat of prey fishes in the Strait of Georgia. Pages 37–49 *in* K. Vermeer and R. W. Butler, editors. The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Canadian Wildlife Service, Ottawa.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Jones, B. C., and G. H. Geen. 1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. Journal of the Fisheries Research Board of Canada 34:2067–2078.

Kanid'yev, A. N., G. M. Kostyunin, and S. A. Salmin. 1970. Hatchery propagation of the pink and chum salmons as a means of increasing the salmon stocks of Sakhalin. Journal of Ichthyology 10:249–259.

Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behavior of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour 19:139–169.

Ketchen, K. S. 1986. The spiny dogfish (*Squalus acanthias*) in the northeast Pacific and a history of its utilization. Canadian Special Publication of Fisheries and Aquatic Sciences 88.

Kuhn, B. R., L. Lapi, and J. M. Hamer. 1988. An introduction to the Canadian database on marked Pacific salmonids. Canadian Technical Report of Fisheries and Aquatic Sciences 1649.

Mace, P. M. 1983. Bird predation on juvenile salmonids in the Big Qualicum River, Vancouver Island. Canadian Technical Report of Fisheries and Aquatic Sciences 1176. [Originally published as 1117.]

Österdahl, L. 1969. The smolt run of a small Swedish river. Pages 205–215 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Institute of Fisheries, Vancouver.

Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28:1503–1510.

Ricker, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. Journal of Fisheries Research Board of Canada 33:1483–1524.

Robinson, C. K., L. A. Lapi, and E. W. Carter. 1982. Stomach contents of spiny dogfish (*Squalus acanthias*) caught near the Qualicum and Fraser rivers, April–May, 1980–1981. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1656.

Ruggles, C. P. 1980. A review of the downstream migration of Atlantic salmon. Canadian Technical Report of Fisheries and Aquatic Sciences 952.

Saunders, M. W., G. A. McFarlane, and M. S. Smith. 1984. Abundance, distribution and biology of spiny dogfish (*Squalus acanthias*) in Hecate Strait during Sept 7–Oct 1, 1982. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1754.

Swain, D. P., and B. E. Riddell. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 47:566–571.

Vincent, R. E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Transactions of the American Fisheries Society 89:35–52.

Volovik, S. P., and O. F. Gritsenko. 1970. Effect of predation on the survival of young salmon in the rivers of Sakhalin. Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Instituta Morskogo Rybnogo Khozyaistva i Okeanografii 71:193–209. Translated from Russian: Fisheries Research Board of Canada Translation Series 1716, 1971, Ottawa.

Received August 24, 1990
Accepted January 23, 1992