A FIELD METHOD FOR DETERMINING PREY PREFERENCE OF PREDATORS

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ABSTRACT

A new field method for determining prey preferences of fish that feed on juvenile salmon is described. The basic elements of this method consist of capturing, tagging or marking, and releasing prey with known characteristics, and comparing these characteristics with those of tagged prey subsequently recovered from the stomachs of predators. The feasibility of this approach is illustrated by two experiments conducted in 1985, designed to assess prey size preferences of predators feeding on juvenile pink salmon during the early sea-life period. The results indicate that yearling coho salmon, *Oncorhynchus kisutch*, were size selective when feeding on juvenile pink salmon, *O. gorbuscha*, preferring the smaller prey. A major advantage of this method is that it eliminates the need to determine the abundances of various prey types in the field. It also allows the investigator to control or precisely measure many of the variables that are known to affect the availability of prey to predators.

Predation plays an important role in shaping the ecological structure of many biological systems. One aspect of predation that has attracted considerable interest is the observation that, when offered a choice of prey types, predators typically show a preference for one of them. The result is that more of the preferred prey are consumed than would be expected, based on the relative abundances of the various prey types.

There have been many attempts to quantify the food or prey preferences of predators (e.g., Hess and Swartz 1940; Ivlev 1961; Schneider 1981) using a wide variety of mathematical indices of preference (reviewed by Cock 1978; Pearre 1982). In some situations, however, this approach clearly is not suitable. For example, in many systems the relative abundances and species composition of the prey can vary substantially over the normal feeding range of the predators. This is particularly evident in fisheries, where piscivorous predators and their prey are often very mobile, and can travel considerable distances during even a single feeding period. In such cases, the proportions of the various prey found in the stomachs of predators may result from variations in the relative concentrations or availability of prey over the extensive area searched by the predator, rather than from any prey preference. It is typically very difficult to determine the concentrations and species composition of prey over such large areas, so indices of preference may not provide much insight into the predation process.

The purpose of this paper is to describe a new method for determing the prey preference of predators in the wild. This method consists of a field experiment in which a number of potential prey with known characteristics are released. These prey are tagged prior to release to allow positive identification even if they mix with other prey of the same type after they are released. The prey preference of the predators is assessed directly by comparing the characteristics of the tagged prey found in the stomachs of predators with those of the prey that were released. The major advantage of this approach is that the relative abundances and other characteristics (species ratios, size composition, etc.) of the various prey types are known in advance and additional field measurements are not required. In addition, if only tagged prey are compared, there is much less ambiguity in assessing the preference of predators for each type of prey because the major alternative explanations are eliminated. Although applicable to a wide variety of predator-prey interactions, the details and potential utility of this method are illustrated by two experiments conducted in Masset Inlet and Masset Sound, B.C., Canada. In both cases the goal was to test the hypothesis that natural fish predators were size selective when feeding on juvenile pink salmon, *Oncorhynchus gorbuscha*, during the early sea-life period.

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METHODS

The first experiment was conducted on 26 April and the second experiment during 6 and 7 June 1985. Pink salmon fry were captured in the Yakoun River during 10–18 April using two inclined plane traps with mouth openings of 1.1 m^2. The traps were emptied each morning and the pink salmon transferred by truck to several 1 m^3 net pens attached to the research vessel *Velella*, anchored at Marinelli Point (Fig. 1).

All pink salmon were tagged and marked to allow positive identification after they were released. During 15–18 April 6,000 pink salmon were anesthetized with tricaine-methanesulfonate (MS-222) and tagged with half-length binary-coded wire tags by an experienced tagging crew. Proper placement of each tag was confirmed by passing all fish through

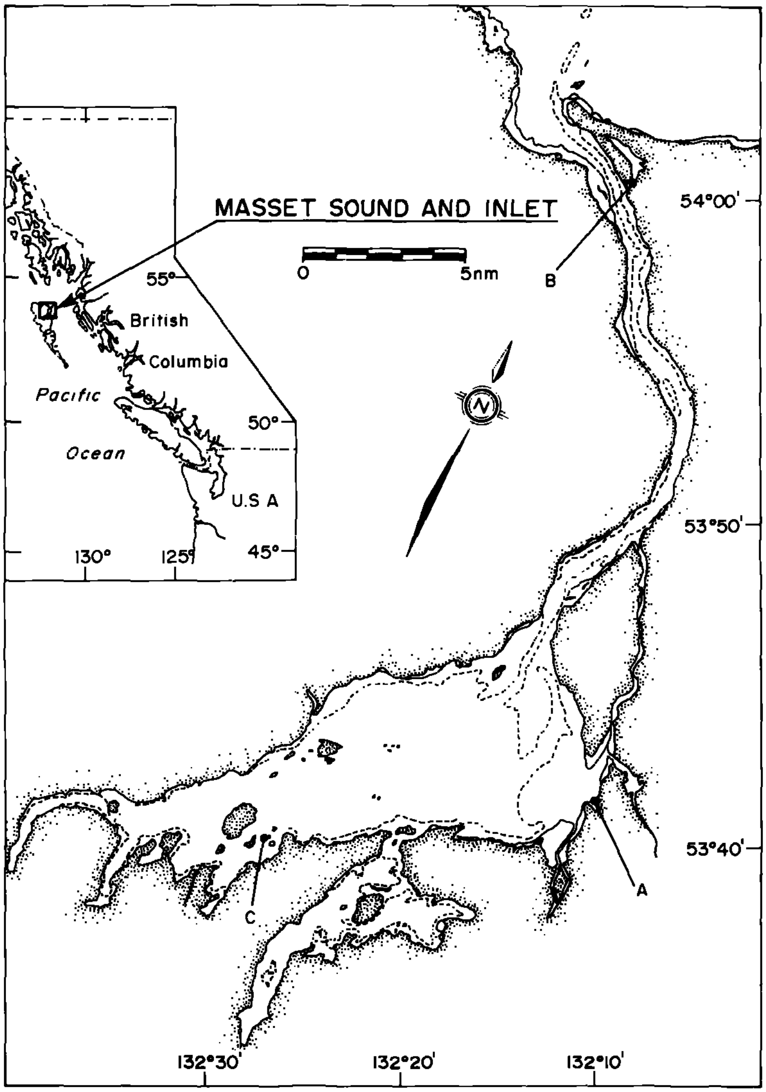

FIGURE 1.—Chart of Masset Inlet showing locations of first (Marinelli Point) (A) and second (B) releases of tagged fish and saltwater enclosure (C) used to hold tagged fish until required for the second experiment.

a 2.54 cm (1 inch) diameter Quality Control Device (QCD), manufactured by Northwest Marine Technology[2] (Shaw Island, WA 98286). Samples of tagged fish were also dissected and examined visually and microscopically to verify tag implantation. Three thousand of these pink salmon were also marked externally by amputating either the left or right pectoral fin. No other fins were amputated. The purpose of the fin clipping was to determine which method (nose tag or fin clip) was more effective for identifying fish recovered from the stomachs of predators.

After tagging and marking, all pink salmon were transferred back into the small, saltwater enclosures. On 20 April the three thousand tagged but unmarked pink salmon were transferred to a larger (51 m^3) enclosure anchored near the southwest end of Masset Inlet, and held until required for the second experiment. This enclosure was shallowed by hand once each week to check the condition of the fish and cleaned with a high-pressure hose every 10–14 days to remove algae growing in the meshes. The food supply of the pink salmon held in this enclosure was not controlled and consisted of whatever came through the meshes. No supplementary food was added. Under this regime the pinks remained very active and appeared healthy.

The first experiment was initiated at 1600 on 26 April, by releasing 3,000 tagged and fin-clipped pink salmon at Marinelli Point. A sample of 99 fish was removed, anesthetized with 2-phenoxyethanol, and the live fork length of each fish measured to determine the size distribution of fish at the time of release. A single beach seine set was made three hours later, in the immediate vicinity of the release site, to collect a sample of potential predators.

The second experiment was initiated by releasing 1,800 tagged pink salmon at 1130 on 6 June, into the boat harbor at Masset (Fig. 1). None of these fish were fin-clipped. A sample of 100 pink salmon was removed prior to the release, and each fish measured to determine the size distribution of fish at the time of release. Two beach seine sets were made to collect potential predators prior to the time of release, the first at 0930 and the second at 1015. A total of sixteen additional sets were made after the release, seven between 1245 and 1826 on 6 June, and nine more between 0900 and 1400 the following day.

[2]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

The beach seine used to capture potential predators was 46 m long and constructed of 6.4 mm stretched nylon mesh. All potential predators were examined immediately after capture. Each measured fish was anesthetized in 2-phenoxyethanol, and the stomach contents obtained by either hydraulic flushing or dissection. All fish remains in the stomach contents were examined visually or microscopically to identify prey to the species level, using Hart (1973) as a general reference and Phillips (1977) to identify juvenile salmon. All juvenile salmon found in the stomachs of predators and any live juvenile salmon captured along with the predators were measured (if possible), examined for missing fins, and passed through the QCD several times to determine if they were tagged.

Yearling coho salmon, *Oncorhynchus kisutch*, captured on the first day of the second experiment were used to obtain an estimate of the total population of coho salmon in the vicinity of the release site. All coho salmon captured on 6 June were retained, anesthetized with 2-phenoxyethanol, and marked using a hot-wire branding device. At 2000 on 6 June, these coho were sorted to remove any that did not appear healthy and fully recovered, and the remaining 170 were released. All coho captured the following day were inspected to determine if they were marked. The numbers of marked and unmarked coho were used to derive a simple (single census) Petersen estimate of the total population of yearling coho salmon in the vicinity of the release site using the following equation (Ricker 1975):

$$N = \frac{(M + 1)(C + 1)}{(R + 1)} \tag{1}$$

where N = total number of coho salmon at time of marking
M = number of coho salmon marked and released on 6 June
C = total number of coho salmon captured on 7 June
R = number of marked coho salmon recaptured on 7 June.

The 95% confidence interval for the population estimate was obtained by substituting into this equation the fiducial limits of the number of recaptured coho salmon, from tables of the Poisson distribution (Ricker 1975). These figures were used to estimate the total number of tagged pink salmon eaten by coho salmon in the second experiment, using the equation

$$T = (P * N)/E \quad (2)$$

where T = total number of pink salmon eaten
P = total number of pink salmon in all stomachs examines
N = estimated total population of coho salmon, from Equation (1)
E = total number of stomachs examined.

RESULTS

The 3,000 tagged and marked pink salmon released at Marinelli Point on 26 April ranged in size from 34 mm to 41 mm, with an average of 38 mm (Table 1). A total of 57 juvenile sockeye salmon (*Oncorhynchus nerka*), 5 pink salmon, 2 chum salmon (*O. keta*), 4 starry flounder (*Platichthys stellatus*), 1 sturgeon poacher (*Agonus acipenserinus*), and 210 yearling coho salmon were captured in the single beach seine set done after the tagged fish were released. All five pink salmon had been fin-clipped and tagged. Three of these pinks had fork lengths of 37 mm and the other two were both 38 mm long. The two chum salmon had fork lengths of 41 mm and 40 mm. The four starry flounders and single sturgeon poacher were all small and were immediately released. All 210 coho salmon were measured and their stomach contents examined for evidence of predation on juvenile pink salmon. A total of 90 coho salmon had remains of fish in their stomachs, including 51 pink salmon, 1 chum salmon, and 14 juvenile salmon that could be identified only as either pink or chum salmon, due to extensive digestion (Table 2). One additional coho salmon had eaten two Pacific sandlance, *Ammodytes hexapterus*, but all other fish remains were too digested to positively identify. Out of the 23 tagged pink salmon found in the stomachs of these coho salmon, only 18 were sufficiently intact to permit measurements of their fork length (Table 2). The average length of these pink salmon was significantly less ($t = 8.02$; $P < 0.001$) than the average length of the pink salmon that were released (Fig. 2). Twelve of the eighteen tagged and measurable pink salmon found in the stomachs of the coho were clearly missing a pectoral fin. The pectoral fins of all the other fish were too digested to be certain whether or not they had been fin-clipped. The average length of the 12

TABLE 1.—Characteristics of tagged juvenile pink salmon released in each experiment and those subsequently recovered by beach seining. Nr = no. released; Ns = no. fish in prerelease sample; Min = minimum fork length; Max = maximum fork length; $\bar{X}$ = mean fork length; C.I. = 95% confidence interval for $\bar{X}$; Nc = no. of tagged salmon recaptured by beach seining; H = no. hours after release of tagged fish.

	Tagged fish released							Tagged fish recaptured						
Date	Species	Nr	Ns	Min	Max	$\bar{X}$	C.I.	Species	Nc	Min	Max	$\bar{X}$	C.I.	H
4/26/85	pink	3,000	99	34	41	38.1	37.9–38.4	pink	5	37	38	37.4	36.7–38.1	1.5
6/6/85	pink	1,800	100	36	51	44.4	43.8–44.9	pink	3	42	46	44.3	39.2–49.5	1–3
								pink	12	40	50	44.7	42.7–46.6	3–5
								pink	4	40	47	42.8	38.0–47.5	5–7
								pink	0	—	—	—	—	21–26

TABLE 2.—Number and size of juvenile salmon found in stomachs of predators in each experiment. Sets = no. beach seine samples; S = no. of stomachs examined; N = total no. juvenile salmon in stomachs; Nc = no. of tagged fish in stomachs; Nm = no. of tagged fish whose fork length could be measured; Min = minimum fork length; Max = maximum fork length; $\bar{X}$ = average fork length; C.I. = 95% confidence interval for $\bar{X}$; JS = juvenile pink or chum salmon.

					Juvenile salmon found in predator stomachs							
					All salmon		Tagged salmon only					
Experiment	Date	No. sets	Predator	S	Species	N	Nc	Nm	Min	Max	$\bar{X}$	C.I.
1	4/26/85	1	coho	210	pink	51	23	18	34	38	35.6	35.0–36.2
					chum	1	0					
					JS	14	0					
2	6/6/85	16	coho	374	pink	17	15	15	36	45	40.7	39.3–42.1
			staghorn	24	pink	0						
			Dolly Varden	15	pink	0						

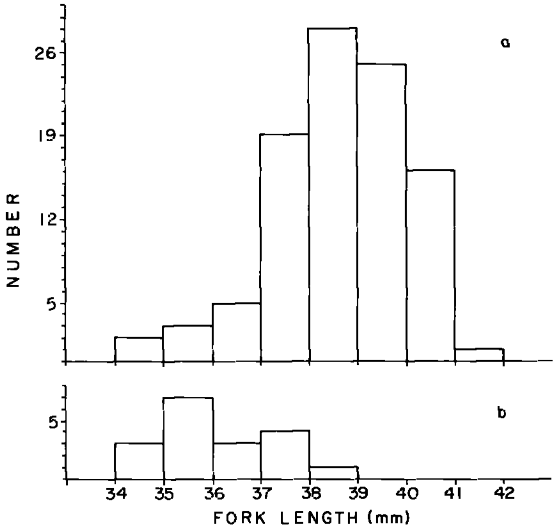

FIGURE 2.—Size-frequency distribution of sample of tagged pink salmon released in the first experiment (A) and all tagged pink salmon subsequently recovered from stomachs of predators (B).

fin-clipped fish was 35.4 mm, which is not significantly different (t = 0.47; $P > 0.50$) from the average length of the 18 tagged and measurable pink salmon.

Pink salmon released in the second experiment ranged in size from 36 to 51 mm fork length, with an average of 44.4 mm (Table 1). A total of 1 juvenile sockeye salmon, 1 juvenile chum salmon, 28 yearling coho salmon, 6 Pacific staghorn sculpin (*Leptocottus armatus*), 10 Pacific herring (*Clupea harengus pallasi*), approximately 500 larval walleye pollack (*Theragra chalcogramma*), 20 Pacific snake prickleback (*Lumpenus sagitta*), 1 red Irish lord (*Hemilepidotus hemilepidotus*), 6 Dolly Varden (*Salvelinus malma*), and 10 starry flounder were captured in the 2 beach seine sets done before the release. Examination of the stomach contents of all the coho salmon, five staghorn sculpins, the red Irish lord, and all the Dolly Varden provided no indication that any of these fish had recently eaten juvenile pink or chum salmon. The seven additional beach seine sets done on 6 June after the release of the tagged pink salmon captured a total of 271 coho salmon, 33 Dolly Varden, 46 staghorn sculpin, 2 coastal cutthroat trout (*Salmo clarki clarki*), 55 pink salmon, and 3 chum salmon. Nineteen pink salmon had been tagged (Table 1). All the untagged pinks were larger.

The stomach contents of 246 coho salmon, 14 Dolly Varden, and 16 sculpins were examined. There was no evidence that any of the Dolly Varden or sculpins had eaten any juvenile pink or chum salmon, although one sculpin had eaten a juvenile coho salmon. However, 13 of the coho salmon had eaten a total of 17 juvenile pink salmon, of which 15 had been tagged. The head was missing from one of the two untagged pink salmon so it could not be measured, but the fork length of the other was 51 mm. The tagged pink salmon found in the stomachs of the coho salmon were typically the smaller ones (Fig. 3), with an average length significantly less (t = 5.06; $P < 0.001$) than the average length of all pink salmon that were released in this experiment (Table 2).

No juvenile salmon were found in the stomachs of predators captured on 7 June. A total of 1 juvenile pink salmon, 141 yearling coho salmon, 1 Dolly Varden, and 115 staghorn sculpins were captured in 9 beach seine sets. The pink salmon was not tagged and none of these predators had recently eaten any juvenile pink or chum salmon. Five of the coho salmon had been branded, so the estimated total population of coho salmon in the vicinity of the release site was 4,047, with a 95% confidence inter-

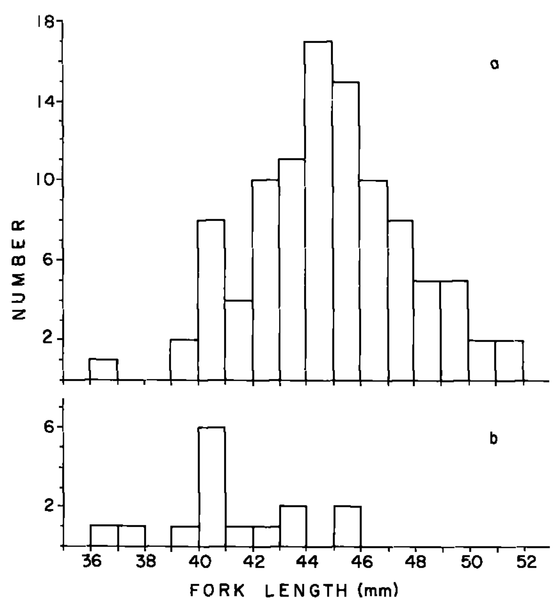

FIGURE 3.—Size-frequency distribution of sample of tagged pink salmon released in the second experiment (A) and all tagged pink salmon subsequently recovered from stomachs of predators (B).

val of 1,912 to 9,339. Based on these figures, it is estimated that coho salmon consumed a total of 162 (9%) of the tagged pink salmon released on 6 June, with a 95% confidence interval ranging from 76 (4%) to 375 (21%).

DISCUSSION

Determining the prey preference of predators in the wild is an important but difficult problem. The two experiments reported here illustrate a new approach to determining the selectivity of predators in the wild. Aside from logistic problems, the success of this method depends on the validity of four main assumptions: 1) predators that are captured and examined, and their stomach contents, are truly representative of the total predator population of interest; 2) tagging or marking the prey does not result in abnormal behavior of either the prey or predators; 3) ingestion and partial digestion of the prey by the predators does not significantly alter the characteristics of the prey that are of primary interest; 4) all of the tagged prey remain equally "available" to the predators for the duration of the experiment.

The first assumption should be valid if the sampling program is appropriately designed, considering the statistical tests that will be used to analyze the data. This is a complex topic and an in-depth discussion is beyond the scope of this paper. However, many extensive references are available (e.g., Anderson and McLean 1974; Cochran 1977; Montgomery 1976).

The two experiments reported here were designed only to demonstrate the utility of this approach and do not clearly show how generally applicable the results are. Only a small number of tagged fish were released and samples of predators were collected with a beach seine, which undoubtedly is biased to some degree in terms of the species and sizes of fish that were captured. In addition, the samples were collected at only one location in the first experiment and over a relatively small area in the second experiment. However, extensive sampling and examination of the stomach contents of fish predators over a 3-yr period indicates that yearling coho salmon are the major predators of juvenile pink salmon throughout Masset Inlet and Masset Sound (Hargreaves in press). The results of these two experiments are also consistent with those obtained from enclosure experiments, which indicate that yearling coho salmon are size selective when feeding on juvenile pink or chum salmon (Parker 1971; Hargreaves and LeBrasseur 1986). Thus, although quite limited in scope, these two experiments provided results that are consistent with those obtained by two other independent, but considerably more expensive and laborious, methods.

The assumption that tagging and marking the prey does not affect the behavior of predators or prey can be assessed either by direct observation or by conducting additional experiments. In some cases it may be possible to design the experiment to allow observation of both the predators and prey throughout the experiment and directly observe any unusual behavior. However, in many cases, additional experiments will probably be required. For the two experiments reported here, the pink salmon used in the first experiment were tagged and fin-clipped; the fish released in the second experiment were tagged but were not fin-clipped. The results of the first experiment indicate that tagging was more effective than fin-clipping for recognizing fish recovered from the stomachs of predators. In terms of behavioral changes, previous work indicated that the mortality of tagged and untagged juvenile salmon was not significantly different when exposed to predators and that tagging juvenile salmon had no noticeable affect on the behavior of either the predators or prey (Hargreaves and LeBrasseur 1986). However, the tagged fish used in these enclosure experiments were not fin-clipped.

Earlier studies have indicated that amputation of fins from juvenile salmon typically results in lower survival rates (Ricker 1949). Marked pink salmon fry also suffer higher mortality than unmarked fry, possibly due to a bias on the part of predators for marked prey (Parker et al. 1963). This is not a major concern in the two experiments reported here because the intent was to determine the size selectivity of predators, rather than any selectivity for marked or unmarked prey. In addition, fin-clipped pink salmon were used only in the first experiment but predators consumed significantly more of the smaller prey in both experiments. This supports the assertion that fin-clipping the pink salmon did not substantially affect the prey size selectivity of the predators. In general, the possibility that the results of these types of experiments may not apply to untagged or unmarked prey can be eliminated by using only tags or marks that are known to have negligible effects on the behavior of both the prey and predators.

The third assumption, that ingestion and partial digestion of the prey by the predators does not significantly alter the important characteristics of the prey, can often be directly verified. For the two experiments reported here, prey size (fork length) was the characteristic that was most important. The observed difference between the average length of the tagged prey that were released and the tagged prey subsequently recovered from the stomachs of predators was 2.5 mm (6.6%) in the first experiment, and 3.7 mm (8.3%) in the second experiment. These are small differences, and the possibility that they might be due to experimental error rather than predator selectivity must be considered. All length measurements were made to the nearest millimeter and numerous remeasurements indicated that measurement errors were negligible at this level of accuracy. To eliminate the possibility that the length of the tagged fish might decrease if they were preserved (Parker 1963), live fish were used to determine the length-frequency distribution of the prey prior to release and all prey recovered from the stomachs of predators were immediately measured. Burgner (1962) reported that the length of sockeye salmon smolts decreased by 2–3% because of *rigor mortis* alone. However, experiments conducted in Masset Inlet in 1984 indicated much smaller changes occur after death in juvenile pink salmon. At temperatures of 9°–10°C, the average length of 26 juvenile pink salmon of known length, fed to and subsequently recovered from the stomachs of 19 yearling coho salmon, decreased less than 1% for periods of up to four hours after ingestion (Hargreaves unpubl. data). In the two experiments reported here, numerous beach seine sets were made to capture potential predators, but all of the tagged pink salmon found in their stomachs were recovered within four hours of the releases of tagged prey. Shrinkage of the prey after ingestion therefore can account for only a small portion of the observed differences in size between the prey that were released and those that were found in the stomachs of predators.

The fourth assumption, that all tagged or marked prey remain equally "available" to predators throughout the experiment, will usually prove to be the most difficult to assess and verify. The availability of prey to predators frequently depends on characteristics of the predators (hunger level, visual acuity, mobility, body or gape size, individual or group behavior, etc.), the prey (abundance, coloration, size, speed, endurance, behavior, etc.), and the environment (habitat complexity, light conditions, etc.). These parameters can interact in a complex manner, so that it is typically only in the simplest situations that all factors that affect the availability of prey to a predator can be thoroughly investigated and understood (Curio 1976; Zaret 1980).

Predators consumed significantly more of the smaller prey in both experiments reported here, despite substantial differences in the physical characteristics of the two release sites, time of year, and various characteristics of the predators (abundance, species composition, size, feeding history, etc.). This suggests that the availability of prey to the predators was not substantially affected by variations in the characteristics of either the predators or the environment. It also appears reasonable to assume that prey of all sizes remained equally available to predators during both experiments. All of the tagged prey were one species and received identical treatment prior to release. There is no reason to think there were any substantial differences in the physical characteristics among the prey at the time of release, aside from the desired variation in size.

It is conceivable, however, that differences in prey behavior or size might have indirectly influenced the availability of prey to the predators. For example, extensive sampling of juvenile salmon in Masset Inlet has indicated a tendency for larger pink salmon to be concentrated further offshore than smaller pink salmon during the early sea-life period (Hargreaves et al. 1987a, b). Swimming speeds of salmon are also known to increase rapidly with increasing body size (Brett 1965). Thus, if there was any tendency for tagged salmon to rapidly swim away from the release sites, larger fish may have left quicker than smaller fish. The result could be a decrease in the average size of tagged salmon found in the immediate vicinity of the release site and the incorrect conclusion that predators were selectively feeding on the smaller prey.

In fact, however, this possibility appears unlikely. In both experiments the size of the live, tagged fish recovered along with the predators was not significantly different than the size of the fish that had been released as much as nine hours earlier (Table 1). There is also no indication that the mean size of these fish changed in a consistent manner over the course of the second experiment. These results suggest that, if there was any segregation of tagged prey after release, it was probably minor and did not appreciably affect the availability of prey to the predators.

In general, complications arising from variations in the availability of prey to the predators may be reduced or eliminated by limiting the duration of the experiment. If all of the prey are released at one time and location, it is reasonable, and in most cases probably valid, to assume that all prey are equally available to any predators captured in the immediate vicinity a short time later. The amount of time during which the prey subsequently remain equally available to predators will likely vary from one situation to the next. If the prey are very mobile, probably some will eventually become less or more accessible to predators than others. This possibility can be eliminated or at least minimized by keeping the experiment short enough to ensure that the prey do not have sufficient time to segregate or move away from the release site. The magnitude of this problem and thus the appropriate duration for each experiment may be assessed by recapturing some of the tagged prey after the release. The experiment should be terminated when the characteristics of the recaptured prey begin to diverge significantly from those of the original prey population.

Determining the prey preference of predators in the wild is a concern to many biologists. All methods of determining the prey selectivity of predators in the wild are, and will likely continue to be, hampered by the complexity of the related problem of determining the relative "availability" of prey to predators. The advantage of the method proposed here is that it allows the investigator to control some of the major variables that are known to affect the availability of prey. The most important characteristics of the prey (species ratios, abundance, size ranges, etc.) can be determined before any predation occurs and in many cases can also be precisely controlled. The predators remain free to feed on all types of prey in the study area, but for the purposes of the investigator, the choice of prey can effectively be reduced to those with known characteristics and origin. This is a major advantage when compared with the more traditional approach of calculating selectivity indices, as it eliminates the need to determine the relative abundances of prey in the field. It also substantially reduces the ambiguity associated with interpreting selectivity indices for highly mobile predators, where typically there is little or no information available concerning the area traveled by the predator during the feeding period and thus what prey were actually available to the predator.

The specific goal of the two experiments reported here was to determine if predators were size selective when preying on juvenile pink salmon during the early sea-life period. The results indicate that yearling coho salmon were the dominant predator of juvenile pink salmon at two locations, one in Masset Inlet and the other in Masset Sound, and that the average size of juvenile pink salmon consumed by these predators was significantly less than the average size of pink salmon that were released. These results are consistent with those obtained from two other independent approaches and suggest this method may be a viable and cost-effective alternative for determining the prey preferences of predators in the wild. It may be particularly useful for assessing prey preferences of predators feeding on juvenile salmon near hatchery facilities in Canada and the United States, where millions of juvenile salmon are currently tagged and released each year.

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