

A comparison of the willingness of four species of Pacific salmon to risk exposure to a predator

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Theory and recent experimental evidence indicate that prey animals should be willing to incur some level of predation risk while foraging. This level of risk will be determined by the costs (i.e., lost foraging opportunities) and benefits (i.e., reduced probability of mortality) associated with predator avoidance. We tested the hypothesis that the optimal trade-off between obtaining additional food and avoiding predators is species specific with four species of Pacific salmon; chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), and pink salmon (*O. gorbuscha*). We also tested the relative vulnerability of the salmon to the predator used in our experiments. Our results demonstrated that chinook salmon were significantly more willing to risk exposure to a predator to obtain additional food than were chum and coho salmon. Pink salmon were intermediate between chinook and the other species. Furthermore, this difference exceeded that which could be explained by variation in length and weight between species. Experiments to test vulnerability to the predator indicated that coho salmon were significantly less vulnerable to the predator than were chinook and chum salmon. If these behavioral differences persist throughout their lives, there should also be differences in the population response of these salmon species to fluctuation in predator density.

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Risk of predation has received considerable attention from behavioural and community ecologists (for recent reviews see Kerfoot and Sih 1987, Lima and Dill 1990). Behavioural ecologists have demonstrated that the threat imposed by predators can alter the areas in which an animal chooses to forage, the types of food it will consume, its tendency to join groups, and a host of other effects. These behavioural modifications can generate community level effects by altering individual growth rates, reversing interspecific competitive abilities (Persson 1991, Werner 1991) and precipitating interspecific interactions which extend beyond adjacent trophic levels (for an example see Mittelbach and Cheson 1987, Mittelbach 1988).

Recent theoretical models and laboratory experi-

ments indicate that the willingness of individuals of a given species to risk exposure to a predator in order to gain additional food will be determined by characteristics of the animals' life history (Werner and Gilliam 1984, Gilliam and Fraser 1988, Abrahams and Dill 1989). Given that life history characteristics are species-specific, the level of risk different species are willing to incur while foraging should also be species-specific.

Few studies have compared interspecific responses to risk of predation. A notable exception is Kotler's (1984) demonstration that different desert rodent species are willing to accept different levels of risk. Kotler concluded that risk of predation was a major force structuring desert rodent communities. Pacific salmon species (*Oncorhynchus* spp.) offer an opportunity to examine

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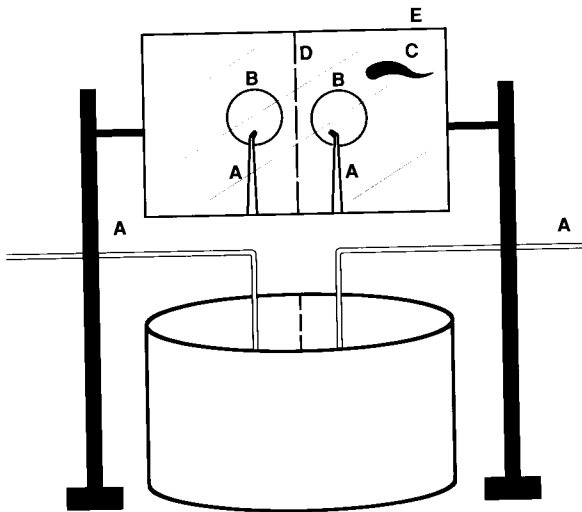


Fig. 1. Apparatus used to measure the relative willingness of different salmon species to risk exposure to the predator. Food is delivered to the apparatus via plastic pipes (A) where it floats within rings of tygon tubing (B). A predator (C) is restricted to one side of the apparatus by a mesh partition (D) rendering one side of the apparatus safe, the other risky. Fish were observed in the apparatus by a mirror (E) mounted over the tank. See text for details.

interspecific responses to risk similar to that offered by the desert rodent species. Five of the species are anadromous and semelparous but within that general pattern have adopted different solutions to their life history problems, especially as juveniles (Healey 1986, Randall et al. 1987). The differences in life history pattern shown by juveniles could lead to differences in the costs and benefits associated with different foraging strategies.

The four species chosen for examination in this study illustrate the range of juvenile life history strategies among the semelparous species. Pink (*O. gorbuscha*) and chum (*O. keta*) migrate to sea immediately after emerging from their gravel spawning nests in the spring whereas coho (*O. kisutch*) typically spend one or two years in freshwater before migrating to sea. Chinook (*O. tshawytscha*) migrate to sea either immediately after emergence, after about 2.5 months of freshwater residence, or after a year or more in freshwater. Patterns of freshwater residence for coho and chinook vary among spawning populations (Healey 1982a, 1986, Randall et al. 1987).

The species and stocks within species that migrate to sea immediately after emergence from the gravel typically have rapid growth rates as juveniles whereas those that remain in freshwater grow more slowly. For example, pink and chum salmon in the ocean grow to lengths of 110–140 mm by August, whereas chinook and coho in freshwater may be only half these lengths in August (Healey 1980, unpubl.; Crone and Bond 1976; Groot & Margolis 1992). Rapid growth has been interpreted to

be a tactic by which salmon minimize predation mortality by outgrowing the foraging capability of some predators (Parker 1971, Healey 1982b). Since rapid growth also requires a heavy commitment to foraging, one could argue that pink and chum must be willing to accept significant predation risk in order to obtain food (Lima and Dill 1990). The more slowly growing coho and chinook should be less willing to do so. The relationship between growth and risk taking may not be so straightforward, however. All four species have the capacity to grow very rapidly and the slower growth of coho and chinook in fresh water may be a function of food limitation rather than a reflection of risk aversion. An argument that is equally plausible to that sketched above is that coho and chinook, having elected to remain in unproductive fresh water habitats for an extended period, must forage very actively and accept high predation risk to achieve any growth at all.

Rather than pose any a priori hypotheses about risk taking, therefore, our objective was to determine whether the species differed in their risk-taking behaviour and to interpret any differences in the context of what is known about the juvenile life history patterns of these species. In this paper we describe significant differences in the willingness of the species to risk predation to obtain food and significant differences in the vulnerability of the species to capture by the predator.

Methods

Experiment 1: Relative willingness to risk exposure to a predator

Two series of experiments were conducted during 1988 and 1989. Except where noted, both experiments used the same methodology. In 1988, chum, coho, chinook, and pink salmon fry were obtained from eggs hatched at the Pacific Biological Station, Nanaimo, British Columbia. The chum, pink, and coho salmon were from the Nitinat, Puntledge, and Robertson Creek stocks, respectively. The chinook were a hybrid between the Conuma and Quesnell stocks. Approximately 700 individuals of each species were held in outdoor fibreglass pools (one pool per species) with a continuous flow of brackish water (10‰). The fish were fed ad lib quantities of White Crest (TM) salmon pellets three to four times daily. In 1989, experiments were repeated using chum, coho, and chinook salmon fry. The chum and chinook were from the Nitinat stock, the coho were from the Kitimat stock. Approximately 500 juvenile salmon of each species were obtained from the Nitinat (chum), Rosewall (coho), and Seaspring (chinook) hatcheries. All hatcheries were located on Vancouver Island. These species were held separately in outdoor fibreglass pools provided with a continuous flow of freshwater at ambient temperature (between 10° to 15°C) and fed as above.

To compare the different species' willingness to risk exposure to a predator, they were given access to two sources of food; one safe and the other risky. Both food sources provided the same amount of food. However, the amount of food available to each individual fish is a function of both the absolute amount of food and the number of individuals competing for it. If all individuals initially feed in the safe area, then the relative amount of food available in the risky area will increase continuously through time as the food in the safe area is consumed. At some time, the perceived benefits of feeding in the risky area will exceed the perceived cost (energetic and mortality probability) of risking exposure to a predator, and it should now be profitable for the fish to use the risky feeder. Thus, the time at which these fish switch to feeding at the risky feeder should serve as an index of their relative willingness to risk exposure to a predator. The sooner these fish start feeding in the risky area, the lower will be the energetic reward for risking exposure to a predator. If the optimal level of risk is determined by the animal's life history characteristics (Werner and Gilliam 1984), then the point at which animals switch from using the safe feeder to the risky feeder should differ between species.

We created this situation in an outdoor, circular, fibreglass tank (2 m diameter by 1 m). The tank was supplied with a continuous flow of ambient water (between 10° and 15°C), maintained at a depth of 50 cm. Brackish water (10‰) was used in 1988 and fresh water in 1989. A mesh partition divided this tank in half. The stretched mesh size of 2.1 cm allowed the juvenile salmon to easily pass through the partition while restricting a predator to one side. In 1988 the predator was one of three adult coho salmon (600–800 g) and in 1989 one of three adult rainbow trout (*O. mykiss*; 800–1000 g). This created a "safe" and a "risky" side.

The food used in this experiment was Murex Medium (TM) dried ocean plankton (*Euphausia pacifica*). This food was delivered remotely to the experimental tank through plastic pipes. Five ml of food (0.258 g) was placed in a chamber within these pipes. The end of each pipe was connected to a compressed air line via tygon tubing. At the start of each experiment, compressed air was used to force the food through the pipes and into the experimental tank. The food landed within a circle of floating tubing that, since the food floated, restricted it to the area circumscribed by the tubing (Fig. 1). This ensured that there was no mixing of food between the safe and risky areas.

To determine the relative willingness of the different species to risk exposure to a predator, they were tested in all possible pairs. This experimental design allowed a direct comparison of the relative behaviour of all species. Although daily variation in the behaviour of the predators may affect the *absolute* level of risk in the apparatus, it should have no influence on the *relative* measure of risk-taking, as measured in each experiment.

The order in which species pairs were tested in the apparatus was randomized. Before each experiment, 10 individuals of approximately equal size from each species were removed from the holding tanks. All individuals were anaesthetized with 2-phenoxyethanol and their fork length and wet weight recorded. Individuals of one species also received a freeze-brand on their dorsal surface (approximately 1 cm long, anterior to their dorsal fin). This served to distinguish the two species in the apparatus. The presence of the freeze-brand was considered a second factor in the experimental design. Thus, all possible species pairs, including the presence or absence of the freeze brand were examined, providing 12 possible combinations in 1988 and 6 possible combinations in 1989. Combinations were repeated twice in 1989 so that an equal number of experiments was performed each year.

Species pairs were held together within a flow tank and fed dried ocean plankton. After the fish were readily accepting the food, they were placed in the experimental tank between 08.30 and 09.30. To familiarize the fish with the apparatus, they were fed ocean plankton via the feeding pipes four to five times during the day. Each feeding was separated by at least two h and, after the final feeding, food was loaded into the feeding tubes in preparation for experiments the following day.

The following day, food was added to the tank four times at approximately 0900, 1100, 1300, and 1500 hours. Following the addition of food, fish were observed through a mirror mounted over the tank at a 45° angle and the area in which they were feeding was recorded every 30 s for 25 min. Species identity could be determined by observing the presence or absence of the freeze-brand with binoculars.

Fish were used only once in this experiment. All fish were removed from the tank after the final observation period. The number of surviving individuals for each species was determined, and the weight and fork length of these individuals was recorded.

For each paired comparison, we subtracted the time the unmarked species crossed to the dangerous side from that time for the marked species. This method generated a positive value if the marked species crossed first, and a negative value if it crossed second. Experiments in which neither species exploited the dangerous side were not included in this analysis. Since two species participated in each trial, and the comparison of interest was between species, we employed contrast analysis within the SAS GLM procedure to maintain independence within the data set. To insure independence of data, separate comparisons between species were made when they were the marked and unmarked species. Due to differences in methodology, data from 1988 and 1989 were analyzed separately.

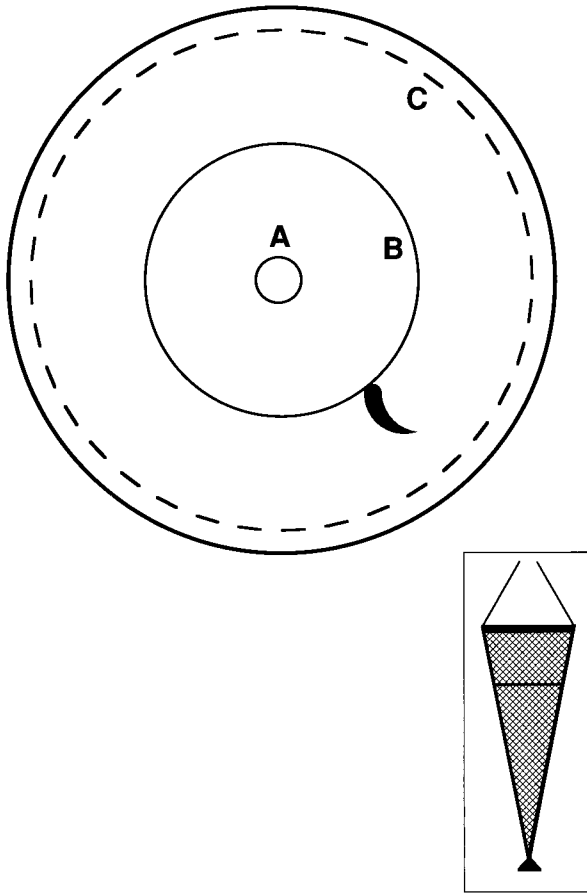


Fig. 2. Overhead view of apparatus used to measure the relative susceptibility of the different salmon species to the predator. Individual fish were released from a central chamber (A, see inset for details) when the predator was 50 cm from the chamber, as indicated by a line drawn around the chamber (B). The fish may escape the predator by swimming through a mesh partition encircling the apparatus (C).

Experiment 2: Susceptibility to predation

To determine whether all species were equally vulnerable to the predator, they were exposed to a standardized encounter. Experiments were conducted in a 2500-l circular tank (Fig. 2), 2 m in diameter, which contained a predator (a 1-kg rainbow trout). A mesh partition (mesh size 2.1 cm) was attached 20 cm from the inner wall of the tank and restricted the predator to the central portion of the tank.

To standardize encounters between predators and prey, the prey were constrained to the centre of a tank by a conical enclosure (see inset, Fig. 2). This enclosure was constructed of fine mesh attached at the top to a plastic coated metal ring (10 cm in diameter) tapering to a point at the bottom which was attached to a suction cup. The suction cup secured the enclosure to the bottom at the centre of the pool. A mesh floor was attached

10 cm from the rim to prevent the fish from becoming trapped in the narrow end of the enclosure and to standardize the depth at which encounters occurred. The enclosure was secured to monofilament fishing line and, via a pulley, led to an observation hut 15 m from the experimental chamber. Releasing the monofilament fishing line caused the metal ring at the top of the chamber to fall to the bottom of the tank. The conical shape of the enclosure prevented the fish from becoming trapped in the netting and the high density of metal ring provided near instantaneous release of the prey fish.

Experiments were performed in a random order and separated by a least three h to prevent the predator from becoming satiated. During each experiment, a group of either chinook, coho, or chum salmon were tested as individuals (no pink salmon were available for this experiment). Each group consisted of ten individuals, all of which were removed from holding tanks and anaesthetized with 2-phenoxyethanol in order to obtain their fork length and weight. The fish were provided at least two d to recover from the anaesthetic before being used in these experiments.

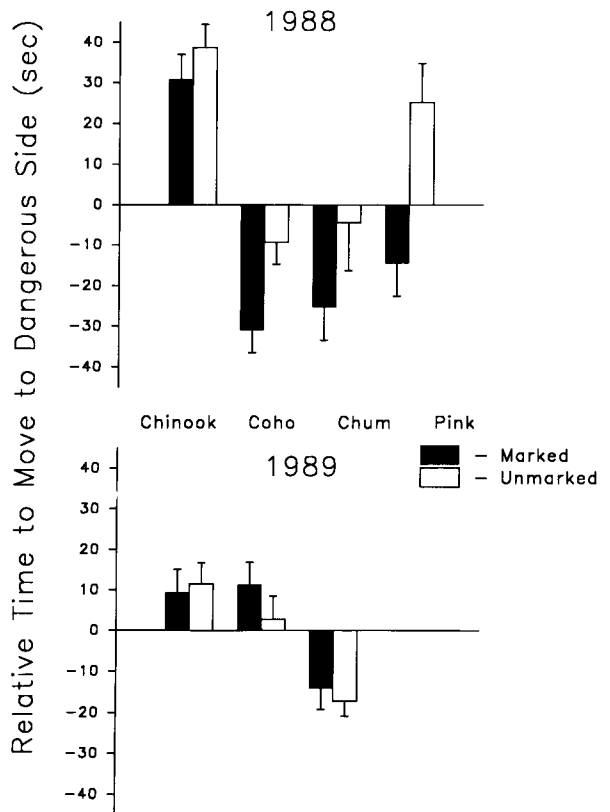


Fig. 3. Summary of the risk-taking behaviour of the different salmon species for 1988 and 1989. Positive values indicate the species moved first to risk exposure to a predator (see text for details). Error bars correspond to one standard error.

Table 1. Summary of contrast analysis comparing the relative willingness of the different salmon species to risk exposure to a predator. Error df was 29 in 1988, 33 in 1989. All numerator df were 1.

	Chinook	Coho	Chum
Marked species – 1988 data			
Pink	F = 28.48 P = 0.0001	F = 5.27 P = 0.0292	F = 3.05 P = 0.0911
Chum	F = 55.08 P = 0.0001	F = 0.30 P = 0.5889	
Coho	F = 65.55 P = 0.0001		
Unmarked species – 1988 data			
Pink	F = 6.17 P = 0.0190	F = 15.44 P = 0.0005	F = 11.84 P = 0.0018
Chum	F = 37.72 P = 0.0001	F = 0.04 P = 0.8514	
Coho	F = 48.45 P = 0.0001		
Marked species – 1989 data			
Chum	F = 11.63 P = 0.0017	F = 12.95 P = 0.0010	
Coho	F = 0.07 P = 0.7955		
Unmarked species – 1989 data			
Chum	F = 18.13 P = 0.0002	F = 4.87 P = 0.0345	
Coho	F = 4.90 P = 0.0339		

For each experiment, an individual fish was placed in the conical enclosure in the centre of the apparatus. This fish and the predator could then be observed by a mirror mounted over the tank (Fig. 2). When the predator was 50 cm from the chamber (as indicated by a line

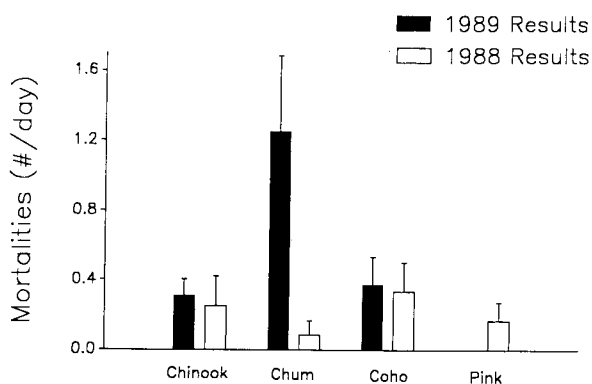


Fig. 4. Mortality rates suffered by the different species in experiment 1 for 1988 and 1989. Error bars correspond to one standard error.

drawn around the central chamber) the test fish was released from the central chamber. If the prey escaped to the outer mesh of the apparatus or survived for 10 s, it was considered to have escaped the encounter. All 10 fish in a group were tested in succession. Those fish that survived were removed after each encounter and their length and weight recorded. The number of survivors from a group provided a single estimate of the probability of escape. As in the previous experiment, fish were used only once.

Results

Experiment 1: Risk of predation

In the absence of food, no fish of any species were observed in the risky side of the tank. Movement to the risky side was only observed after food had been added. The relative willingness of the different species to risk exposure to the predator are summarized in Fig. 3 and Table 1. Analyses were conducted separately to compare species when all were marked or unmarked to maintain independent data (since the measured response was determined by the combined behaviour of the marked and unmarked species pair). However, marking by the freeze-brand had no measurable effect on the relative time to risk exposure to the predator for 1988 ($F_{1,29} = 3.43$, $P = 0.074$) or for 1989 ($F_{1,33} = 0.19$, $P = 0.662$). In 1988, chinook salmon exploited the risky feeder significantly earlier than other species (Table 1). Indeed, all comparisons revealed significant differences except for coho and chum salmon (Table 1), the two species least willing to exploit food in the dangerous area (Fig. 3). No significant difference existed for the chum versus pink comparison when both species were marked. In 1989, differences between the species were not as clear (Table 1), although chum salmon was the species least willing to exploit food on the dangerous side of the tank.

Except for chum salmon, there was little variation in mortality rates (expressed as numbers killed per day) among species both within and between years. Chum mortality differed considerably from the other species, increasing significantly from 1988 to 1989 ($T_{23} = 6.2$, $P < 0.001$, Fig. 4).

Since the fish used were not all the same size (Table 2), it is possible that the interspecific differences in behaviour were merely a reflection of difference in size. We pooled the data for 1988 and 1989 and included the difference in average weight between species pairs in each test (a positive or negative value). This value was used as a covariate in an analysis of covariance which examined the effect of species on the average relative time to move to the dangerous side. As above, data were analyzed separately for marked and unmarked species.

Variation in size had a significant influence on the behaviour of marked fish but not unmarked fish (Table

Table 2. Average size of the different species of fish used in experiment 1 (length in cm, weight in g).

	1988				1989			
	Length		Weight		Length		Weight	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Chinook	12.13	1.26	21.02	6.69	10.21	0.67	11.44	2.32
Coho	10.59	0.97	16.46	4.48	9.43	1.11	10.57	3.82
Pink	13.16	0.74	23.58	4.62	—	—	—	—
Chum	13.07	0.84	21.32	3.90	9.67	0.85	8.52	1.91

3 and Fig. 5). However, in both years there was a significant interaction between the effect of species and weight. As illustrated in Fig. 5, the source of this interaction is the different response by the different species to variation in size. The outcome of a paired comparison was strongly influenced by relative size for coho and pink salmon, and less so for chum and chinook. Chinook were relatively more willing to risk exposure to a predator regardless of the sign or magnitude of the weight difference, chum were the reverse. Controlling for this variation, chinook salmon were significantly more willing to risk exposure to a predator than were coho and chum when marked or unmarked (Student-Neuman-Keuls comparisons of means test, $p < 0.05$). No significant difference existed between pink and chinook salmon when both species were unmarked.

Experiment 2: Interspecific differences in vulnerability

Just as the species differed in their willingness to risk exposure to predator, so too did they differ in the probability that they would escape a standardized encounter with the predator (one-way ANOVA of arcsine square-root transformed data, $F_{2,42} = 5.95$, $P = 0.0053$). A Student-Neuman-Keuls comparisons of means test

Table 2. Summary of analysis of covariance to determine effect of species on behaviour (controlling for variation in weight of species pairs) for marked and unmarked species. Error DF = 16.

Comparison of marked species			
Source	DF	F	P
Species	3	5.95	0.0063
Weight	1	21.41	0.0003
Weight × Species interaction	3	8.08	0.0017

Comparison of unmarked species			
Source	DF	F	P
Species	3	5.30	0.0099
Weight	1	3.90	0.0659
Weight × Species interaction	3	4.36	0.0200

($p = 0.05$) indicated that coho had a significantly higher probability of escaping the predator than chinook or chum (Fig. 6).

The fish that escaped the predator were neither larger

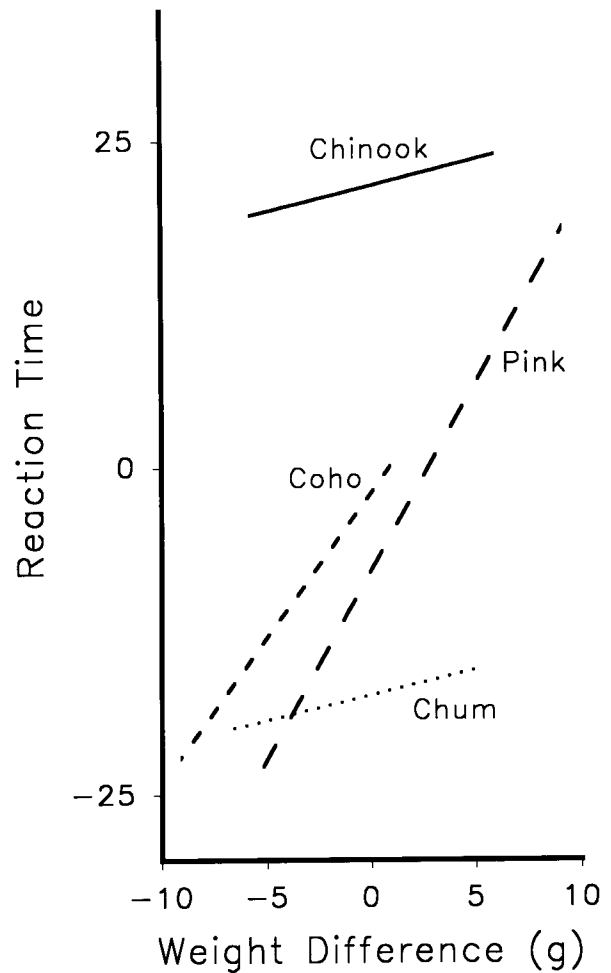


Fig. 5. Movement time as a function of the difference in average wet weight for species pairs. Lines were fitted by least squares and span the range of size differentials employed in these experiments.

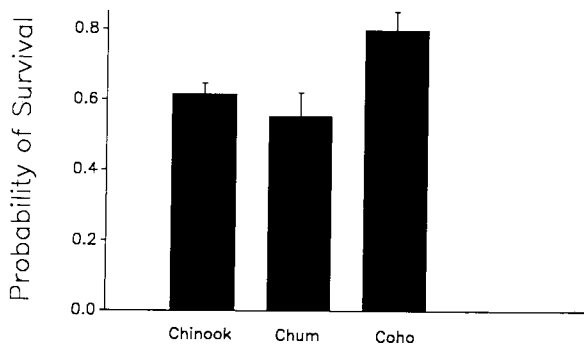


Fig. 6. The probability of surviving a standardized encounter with a predator. Error bars correspond to one standard error.

nor smaller than the average size of fish used in these encounters (Table 4). Therefore, in contrast to the willingness of the fish to risk predation, size had no influence on the ability of these fish to escape the predator.

Discussion

Our results demonstrate that chinook salmon were relatively more willing to risk exposure to a predator to obtain food than were coho and chum salmon. Simple morphological differences between these species (i.e., variation in length and weight) were not sufficient to explain the differences in behaviour between species. Furthermore, variation in their behaviour cannot be accounted for by differences in their relative susceptibility to predation. Indeed, one of the species which was least willing to risk exposure to the predator (coho) was more adept than chinook salmon at avoiding the predator. This difference in vulnerability to the predator suggests that the difference in *actual* risk-taking (i.e., the probability of mortality) between species is greater than indicated by the first experiment.

Magnhagen (1988) has previously compared the response of pink and chum salmon to predator intimidation. Counter to our observations, she demonstrated that pink salmon were more sensitive to the presence of a predator than were chum. However, in her experiment the pink salmon were smaller than the chum, making it difficult to determine whether differences in size or species generated the observed result. Also, the salmon experienced only visual, not actual, encounters with a predator. In our experiments, in which the juvenile salmon faced the real possibility of being eaten, we observed no significant difference or the reverse result (see Figs 3 and 5).

The relative willingness of the four species to risk predation to obtain food was not consistent with either of the general arguments for differences among these species suggested in the introduction. Chinook were relatively more risk-prone than the other species and

coho were significantly less susceptible to the predator. Thus, the species did not segregate in relation to juvenile growth or nursery habitat.

Werner and Gilliam (1984) predicted that, in an environment that is patchy with respect to foraging opportunities and predation risk, juvenile fish should forage in areas that minimize the ratio of mortality rate to growth rate. Experiment 2 demonstrated that chinook salmon were no less susceptible to predation than the other species of salmon. According to Werner and Gilliam's model, chinook must derive the greatest benefit from additional food, potentially due to differences in the efficiency with which they convert food to somatic tissue. We have not been able to find any firm evidence for difference among these species, although different strains of fishes apparently do differ in growth potential (Gjorde 1986). Alternatively, despite their general ecological similarity, the species may be selected for different growth strategies as juveniles due to differences in local predators, time constraints for smoltification, etc.

Brown et al. (1989) have previously compared the effect of predation risk on habitat use by different species of desert rodents. Their results indicate that some species of rodents are less affected by predator intimidation due to morphological differences that provide a superior ability to detect and avoid predators. These data demonstrate that chinook salmon are more willing to risk exposure to a predator, but do not seem to possess any superior ability to avoid predators. This result has potential implications for population dynamics. Species that take greater risks should suffer mortality rates that are closely related to variation in the population density of their predators. This is because species more willing to risk exposure to predators will have high encounter rates with predators and, therefore, predation mortality will be strongly correlated with predator density. On the other hand, such species should exhibit low variation in feeding and growth rates. Thus, the population sizes of these species (but not their growth rates) will be closely linked to the population sizes of their predators.

Species that are less willing to risk exposure to a predator will have growth rates that vary in relation to predator density. Species less willing to risk exposure to a predator will forego opportunities to feed rather than

Table 4. Summary of t-tests comparing the mean weight of each group before and after exposure to predation. Two groups of chum salmon had no survivors, resulting in decreased degrees of freedom for this comparison.

Species	Weight		
	DF	t	P
Chum	12	0.06	0.26
Chinook	14	0.04	0.79
Coho	14	0.19	0.80

risk exposure to a predator and, therefore, the growth rate of these species should be negatively correlated with predator density. Thus, the body size of these fish will vary inversely with the population density of their predators. Holtby and Healey (1990) proposed an analogous explanation for variation in size and survival between sexes in coho salmon. It seems reasonable that a similar model would account for differences between species.

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