side and 2 gill rakers on the upper limb of the second gill arch on the blind side, it is referred to *A. stomias*. The other two anomalous specimens also had 2 gill rakers on the upper limbs of the second gill arch of the blind side and were also recorded as *A. stomias*.

Discussion

From this study, it is evident that the two species of *Atheresthes* can most easily be distinguished by eye position. The number of gill rakers on first and second gill arches can be used to assist and verify identification.

When identifying specimens, eye position should be examined first. If the upper eye interrupts the profile of the head, this specimen is *A. stomias*; if the upper eye does not interrupt the profile of the head, the specimen is *A. evermanni*. If the head is in bad shape (e.g., damaged during the trawl operation) or if the examiner has difficulty using eye position and head profile to identify a specimen, the gill arches must be examined. Two or more gill rakers on the upper limb of the second gill arch indicates that the specimen is *A. stomias*; if there is only 1 gill raker, the specimen is *A. evermanni*.

The number of gill rakers on the first gill arch has generally been used to distinguish the two species of *Atheresthes*. However, this study demonstrated a greater overlap between the two species in number of rakers on the first gill arch than the second gill arch (Tables 1, 2), indicating that the second gill arch is a better character for assigning individuals to the species.

The study also suggests that the number of gill rakers on the upper limb of the first gill arch is species specific. If there are 4 or more gill rakers, the specimen is *A. stomias*; 2 or fewer gill rakers indicate the specimen is *A. evermanni*.

The uncertainty in examining the first gill arch is when there are 3 gill rakers on the upper limb. Approximately 25% of *A. stomias* and 50% of *A. evermanni* samples had 3 gill rakers on the upper limb of the first gill arch. Thus, when 3 gill rakers are present on the upper limb of the first gill, the second gill arch must also be examined to distinguish the two species.

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PREDATION OF KARLUK RIVER SOCKEYE SALMON BY COHO SALMON AND CHAR

The number of sockeye salmon, *Oncorhynchus nerka*, in Alaska's Karluk River (Fig. 1) declined from millions to thousands during the early part of the present century. Rounsefell (1958) discussed alternative explanations for the decline including a general loss of fertility of the system as the number of salmon carcasses declined, competition, overfishing, subtle changes in climate, and predation; he concluded that the combined effect of predation and fishing was the most probable explanation. Later, Van Cleave and Bevan (1973) suggested that the weir constructed in the river each year to facilitate counting the fish as they entered the system was the most probable cause of the decline. It prevented free movement of both adults and juveniles in the river. All of these hypotheses remain as potential explanations for the decline.

Fredin et al. (1974) described a relation that showed two equilibrium regions between the spawning stock and the resultant run for sockeye salmon in the Kodiak area. We developed a stock-recruitment curve (Fig. 2) for sockeye salmon in the Karluk River basin that also showed two equilibrium regions, and suggested that the population had "col-

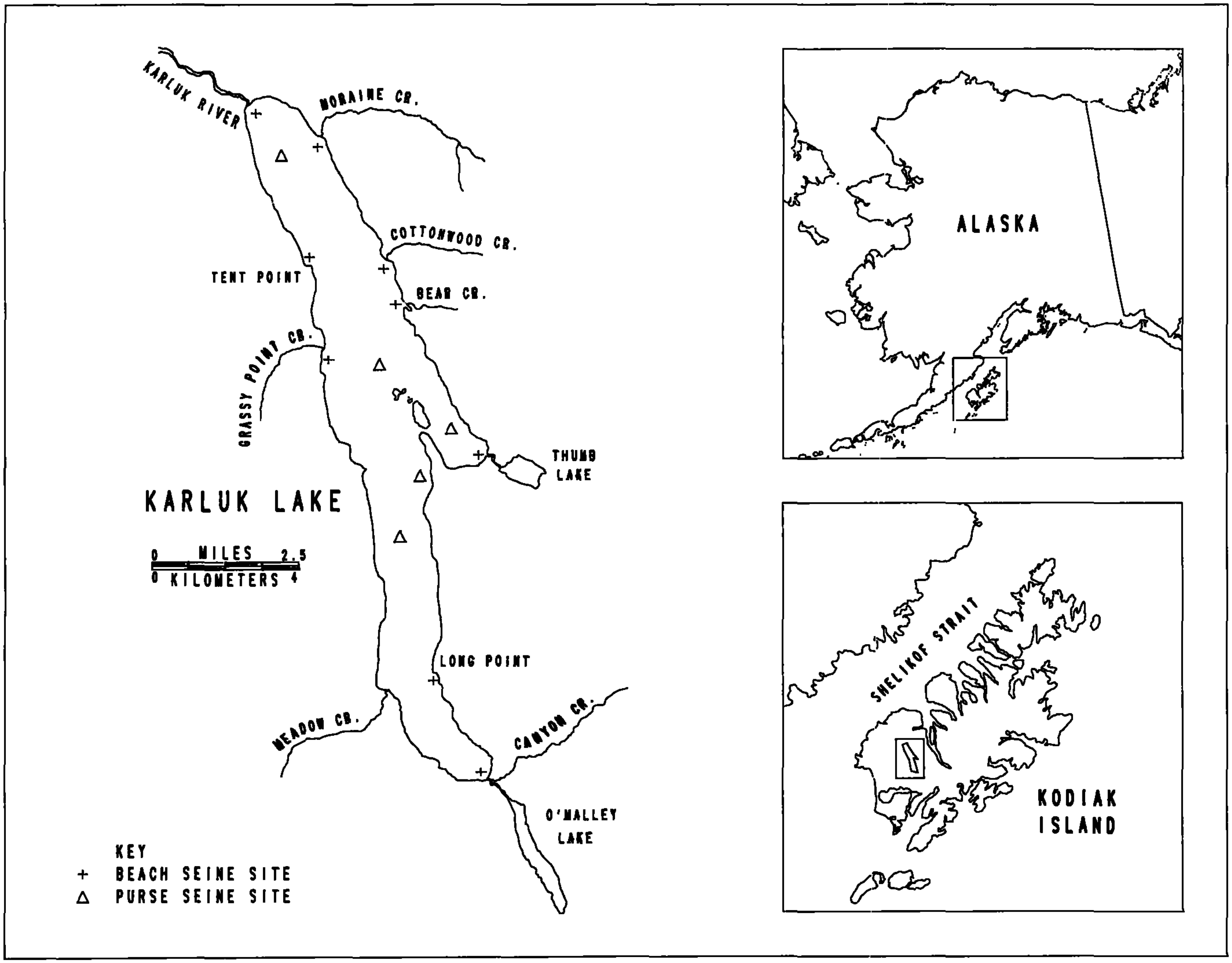

FIGURE 1.—Karluk Lake and associated waters, and sampling sites for a predation study.

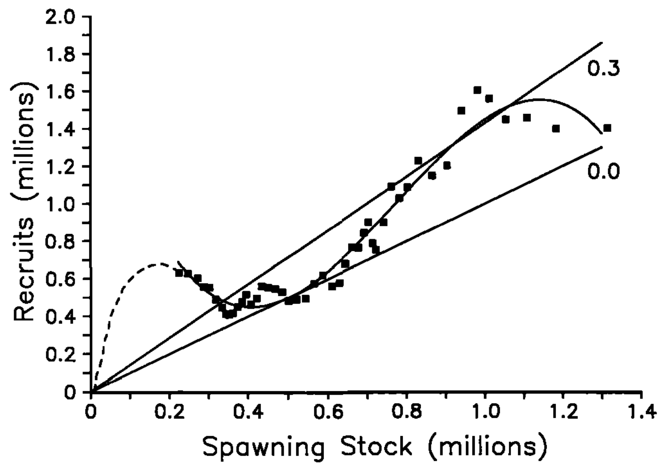

FIGURE 2.—Stock-recuit relation for sockeye salmon in the Karluk River basin. Squares are the running geometric mean (by 9) of stock and recruit estimates for the 1922–77 broods. The curved, solid line was described by $R = 1.83(10^6) + 7.73\,P + 1.29(10^{-5})\,P^2 - 5.58(10^{-12})P^3$; where, R = recruits and P = stock. Ages of fish in the escapement (1922–36 from Barnaby 1944; 1937–69 from the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Auke Bay, AK; 1980–85 from Alaska Department of Fish and Game, Kodiak, AK) were used to estimate the recruits produced by each brood. The diagonal lines show how the replacement line changes as the exploitation rate increases from 0 to 0.3.

lapsed" into the lower of the two. Fishing can cause such a collapse (Peterman 1977) and recovery becomes impossible unless exploitation rates are reduced to levels substantially lower than the rate that caused the collapse.

Multiple equilibria in an exploited population can be caused by depensatory mortality—the loss of a relatively greater fraction of the population when it is small than when it is large (Neave 1953). Several functional responses (Ricker 1954; Holling 1973) have been used to describe relations between prey density and predation rate—one of which (Type III relation) can produce multiple equilibria in the stock-recruitment curve of a prey population (Peterman 1977). The Type III or S-shaped functional response is characteristic of predators that consume a small fraction of the prey at low prey population density; as prey population density increases, however, the predators rapidly increase the fraction consumed through learning or aggregation. The concave, Type II functional response holds when the fraction consumed is high at low prey density.

The apparent potential for stock collapse, as depicted in the Karluk sockeye stock-recruitment curve, could be the consequence of Type III predation mortality. A preliminary survey of the food habits of fish in the system showed that coho salmon, *O. kisutch*, and two chars—the Dolly Varden, *Salvelinus malma*, and Arctic char, *S. alpinus*—were predators of juvenile sockeye salmon. We set out to determine whether the functional responses for coho salmon and for char were of Type II or Type III. Our approach was to describe the relation between the number of prey eaten per predator and the index of prey abundance provided by the annual counts of adult sockeye salmon that entered the system for spawning. Unfortunately, the study had to be terminated after five years because of a management decision to enhance the productivity of Karluk Lake with commercial fertilizer; we could not eliminate the possibility that the effects of fertilization would confound predation responses. We describe the data that were accumulated during five field seasons and our tentative conclusions concerning the role of predation mortality in the dynamics of these sockeye salmon.

Methods

Sampling sites were established at locations around the littoral zone of Karluk Lake at the outlets of spawning streams and at beach spawning areas (Fig. 1) in 1982. The Karluk River was sampled from the outlet at the lake to about 100 m downstream.

In each of the five subsequent years, a field crew sampled each location at weekly intervals, from late April to October.

Juvenile coho salmon were collected with beach seines and minnow traps, and chars with beach seines, floating gill nets, and hook and line. Only coho salmon larger than 80 mm were found to be predators of sockeye salmon during the April–October sampling period. Since char were captured with hook and line or in gill nets, our samples contained only fish that were large enough to consume sockeye salmon fry. Coho salmon were preserved in formalin for examination later, when the contents of the stomachs were removed and the sockeye salmon fry and fingerlings were counted. The chars were tagged and released after the contents were flushed from their stomachs and preserved in formalin.

Results

Juvenile coho salmon were aggregated around tributary outlets and in the littoral areas of Karluk Lake. The chars were found almost exclusively around the tributary outlets and in the Karluk River. Few coho salmon or chars were captured by seining in the pelagic areas of the lake. We did not distinguish between the two chars.

Predation rates for the chars did not increase as the abundance of sockeye salmon increased (Table 1), but the average number of sockeye salmon fry consumed by each coho salmon did increase and appeared to be depensatory (Fig. 3). A general equation (Real 1979) was used to describe the relation between the predation rate (Y) by coho salmon and the index of prey abundance (X),

$$Y = bX^c/(1 + aX^c). \quad (1)$$

A value of $c = 1$ provides a classic, Type II functional response curve, while values of c exceeding 1.0 provide a sigmoid, depensatory shape. A value of $c = 2$ gives the classic Type III curve.

Best (least squares) fit values for a, b, and c were obtained by transforming Equation (1) into the form

$$\ln(1/Y - a/b) = \ln(b^{-1}) - c\ln(X). \quad (2)$$

Using trial values of a/b, we regressed the left side of Equation (2) on $\ln X$ until we identified the value of a/b giving the lowest residual variance. The

TABLE 1.—Predation on juvenile sockeye salmon by predatory coho salmon (i.e., juvenile coho salmon longer than 80 mm) and chars in Karluk Lake, AK during June and July from 1982 to 1986.

	Coho salmon		Chars		
Year	Number examined	Predation rate	Number examined	Predation rate	Sockeye salmon escapement
1982	252	0.475	—	—	220,000
1983	3,132	0.076	95	0.98	164,000
1984	250	0.661	128	19.45	436,000
1985	956	0.452	485	10.06	420,000
1986	423	0.740	571	4.50	996,000

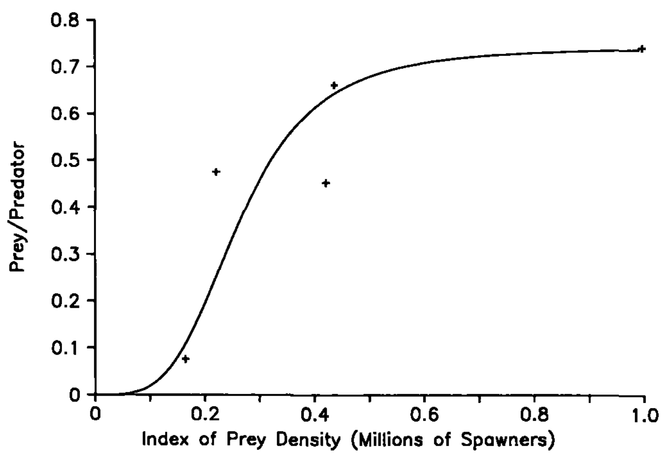

FIGURE 3.—Functional response curve for coho salmon greater than 80 mm (predators) and sockeye salmon (prey) in Karluk Lake. The index of prey abundance was divided by 1,000,000 (e.g. index 0.8 = 800,000 adults in the escapement).

results are $a/b = 1.35$, $c = 3.74$ (standard error = 0.79), $R^2 = 0.88$, $\ln(b^{-1}) = 46.98$.

Hence Equation (1) becomes

$$Y = bX^{3.74}/(1 + 1.35bX^{3.74}) : b = e^{-46.98}.$$

Inasmuch as Y ranges between zero and b/a, it seems unlikely that Y, or a corresponding statistical error term for Equation (1) would be approximated by a normal distribution. On the other hand, so long as Y does not rise above b/a (to which Equation (1) constrains it), the left side of Equation (2) lies between $-\infty$ and $+\infty$, and the error term is more likely approximated by a normal distribution. Consequently, we cautiously used the standard error associated with c, to test whether $c > 1.0$; that is, whether the functional response curve is sigmoid (Type III). In fact, c lies more than 3.5 standard errors above 1 (Type II response) and more than 2.2 standard errors above 2 (Type III response). Although the power of a test involving only 5 data points is weak, we feel that a tentative conclusion of depensatory predation by juvenile coho salmon is justified.

Discussion

Many adult salmon as they attempt to get to the spawning grounds, and as they spawn, are killed by Kodiak brown bears. Gard (1971) reviewed the available literature concerning predation of salmon by bears at Karluk and, in years when fish were not abundant, noted that bears had been observed to leave the salmon spawning areas to feed on berries in the local area, indicating that their predation also may be depensatory. We used data from Gard's summary to approximate the relation between the number of adult sockeye salmon in a run (X) and the number of unspawned adults (Y) estimated to have been killed by bears (Fig. 4). Although R^2 was only 0.424, a depensatory relation was indicated as $Y = X^{2.106}/(3102.85 + 0.00435X^{2.106})$; c, from Equation (1), was 2.106, with a standard error of 1.098. Because predation of sockeye salmon by bears, as well as predation by coho salmon, appeared to be depensatory, it is unlikely that predation by coho salmon alone was the sole cause of the complex stock-recruitment curve for sockeye salmon.

Prudent management of these salmon, and of salmon in systems similar to Karluk, may require regulation of harvest to prevent collapse of populations into relatively low equilibrium regions. Harvest levels that would have prevented collapse of the Karluk population can be estimated from the stock-recruitment curve (Fig. 2). An exploitation rate between 30 and 35% of the recruits should have maintained stock sizes associated with the upper equilibrium region. Exploitation at a constant rate of 0.40 increases the slope of the replacement line to the point that collapse of the population into the lower equilibrium region becomes inevitable (see Peterman 1977 for a description of the relation between the size of stability regions and exploitation rate). When depensatory mortality is potentially high for economically important populations, it may be necessary to limit exploitation to less than 35% of the recruits to prevent collapse.

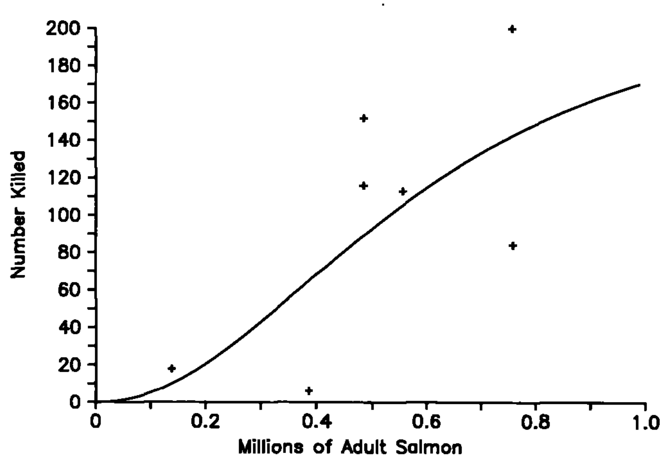

FIGURE 4.—Functional response curve for predation of sockeye salmon by bears. Number killed is thousands of unspawned salmon.

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