

# Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska

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**Abstract:** The interaction between two sculpin species, *Cottus cognatus* and *Cottus aleuticus*, and island beach spawning sockeye salmon (*Oncorhynchus nerka*) was examined in Iliamna Lake, Alaska. We conclude that sculpins actively move to specific spawning beaches and that the initiation of their movements precedes the start of spawning. Sculpin predation on sockeye eggs is positively dependent on sculpin size and on the state of the eggs (fresh versus water hardened), with the largest sculpins able to consume nearly 50 fresh eggs at a single feeding and 130 over a 7-day period. The number of sculpins in sockeye nests is greatest at the beginning of the spawning run, lowest in the middle, and high again at the end, with peak numbers of over 100 sculpins per nest (1 m<sup>2</sup>). We discuss the results in terms of energy flow of marine-derived nutrients into an oligotrophic system and in terms of the coevolution of sockeye spawning behavior and the predatory behavior of sculpins.

**Résumé :** Nous avons étudié les interactions entre les chabots *Cottus cognatus* et *Cottus aleuticus* et le saumon rouge (*Oncorhynchus nerka*) qui fraie près des plages des îles au lac Iliamna, en Alaska. Nous sommes parvenus à la conclusion que les chabots se rendent à certaines plages de fraie, et commencent leur déplacement avant le début de la fraie. Nous avons constaté que l'activité de prédation du chabot, qui se nourrit d'oeufs de saumon rouge, dépend de la taille du chabot et de l'état des oeufs (frais ou durcis), les plus gros chabots pouvant consommer presque 50 oeufs frais en une seule période d'alimentation et 130 oeufs en 7 jours. Les chabots présents dans les nids des saumons sont surtout nombreux au début de la fraie; leur nombre est au plus bas vers le milieu de la période de fraie et redevient élevé vers la fin; en période maximale, on en trouve plus de 100 par nid (1 m<sup>2</sup>). Nous analysons nos résultats sous l'angle du transfert d'énergie survenant à la faveur du passage de nutriments d'origine marine à un système oligotrophe ainsi qu'en examinant l'évolution parallèle du comportement de fraie du saumon rouge et de l'activité prédatrice du chabot.

[Traduit par la Rédaction]

## Introduction

Pacific salmon (genus *Oncorhynchus*) spawning runs are highly predictable in both space and time (e.g., Wood and Foote 1996). These runs result in the transfer of significant amounts of marine-derived nutrients to unproductive freshwater systems (e.g., Bilby et al. 1996). Temporally and spatially predictable resources are important in animal migrations on both local and broad geographic scales, with salmonids representing the positive extreme in predictability as a food resource for other animals (Willson and Halupka 1995). However, few studies have actually examined in detail the ecological relationship between salmonids and those species that exploit them.

Fish predation on salmon eggs has been noted in many

cases, but its effect on salmon production remains questionable. Freshwater sculpins, family Cottidae, have long been suspected as significant predators on salmonid eggs (e.g., Reed 1967; Savino and Henry 1991). However, Moyle (1977) concluded that while sculpins clearly ate salmonid eggs, they tended to eat eggs that were already exposed and at drift, and hence were unlikely to have survived in any case.

Iliamna Lake, Alaska, is the single largest sockeye salmon (*Oncorhynchus nerka*) producing lake in the world, with total runs sometimes in excess of 30 million fish (Eggers and Rogers 1987). Sockeye salmon spawning on island beaches in Iliamna Lake can sometimes account for near 30% of the total escapement to the lake. These beach populations are notable in that the females have a very short spawning duration (e.g., Hendry et al. 1995) and among the largest eggs observed in the species (Quinn et al. 1995).

Iliamna Lake island beaches are typified by large gravel, with large interstitial spaces and few fines (e.g., Leonetti 1997). This high porosity allows wind-generated under-gravel water flow to supply the developing embryos with oxygen, but may also account for the presence of coastrange (*Cottus aleuticus*) and slimy sculpin (*Cottus cognatus*) that have been observed feeding on salmon eggs (Kerns and Donaldson 1968). The greater the substrate size, the greater the ease with which sculpins can move within it, and the more vulnerable salmon eggs are to predation (Phillips and Claire 1966). These sculpins

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derive a significant amount of their nutrients from predation on sockeye eggs and fry (Kline et al. 1993), but questions remain with regard to how sculpin behavior is affected by this resource, how and if sculpins affect this resource, and how and if sockeye salmon behavior is or has (in an evolutionary sense) been affected by the presence of egg predators.

We examine the ecological relationship between the two sculpin species and sockeye salmon spawning on island beaches in Iliamna Lake and compare the distributions of sculpins and spawning sockeye salmon in space and time. We then estimate the magnitude of sculpin predation on the production of sockeye salmon on the beaches through feeding experiments and estimates of numbers of sculpins and sockeye on the beaches. Finally, we address whether "predator satiation", as a means for reducing clutch predation (e.g., Sweeney and Vannote 1982; Furness and Monaghan 1987), may account for the short spawning run and whether sculpin gape limitation may account for the large egg size of island beach sockeye (e.g., Northcote 1954).

## Methods

### Survey of sculpin and sockeye salmon abundance

In 1992, we established a series of 12 fixed sampling locations (hereafter referred to as locations 1–12) along a 180-m section of beach on Woody Island, Iliamna Lake, Bristol Bay, Alaska. The sampling locations covered an area of the beach from an inner bay where sockeye do not spawn (locations 1–5) through the known spawning area (locations 6–10) to the outer point of the bay (locations 11–12) where, again, sockeye spawning does not occur (see fig. 1 of Quinn and Foote 1994). Locations 6–10 were the only ones where sockeye eggs were found buried in the gravel. Hereafter, we refer to the area spanned by these five locations as the "spawning area" and the other seven locations as the "nonspawning area."

Each of the 12 sampling locations had two sampling sites located on a perpendicular path from shore and centred at 0.75 and 1.5 m water depths (the water level rose 0.5 m throughout the month of study). Within sites, we estimated the density of sockeye females and sculpins, with the area surveyed dependent on the species. Sampling sites for sockeye consisted of 5 × 5 m squares that were delineated at the corners by large marked rocks. Sampling sites for sculpins consisted of a 1-m<sup>2</sup> area in the centre of the 5-m<sup>2</sup> area, delineated by a labelled rock (1–12) and a PVC quadrat carried by the surveyor. The centres of the sampling sites (at a given depth) were spaced about 16.3 m apart, with a distance of about 11.3 m between the edges of adjacent 5-m<sup>2</sup> sampling sites. Perpendicular to the shoreline, the distance between sampling sites within a location varied dependent on the slope of the shoreline, from about 15 m in the inner and outer bay where the slope was gentle to only a few metres in central spawning area where the slope was steeper. Sockeye spawned at greater depths than we were able to sample (to about 3.5 m), but our sampling area included most of the area of spawning activity (Quinn and Foote 1994).

The sites were surveyed by two snorkelers 20 times from 2 August to 7 September (on 2 August, only the 0.75-m sites were surveyed). This period encompassed the total spawning run of sockeye salmon, plus 1 week on either end. All sockeye females holding position within the 5-m<sup>2</sup> grid were counted, including those whose central position was on the imaginary line connecting the corner points. To provide a more specific measure of the temporal nature of egg deposition, each female was identified as to whether she had or had not yet completed spawning (see Quinn and Foote 1994). We refer to these as "spawned out" and "breeding," respectively.

Sculpin numbers were assessed within the same twenty-four 1-m<sup>2</sup>

sites over the course of the season to minimize the total area of disturbance. Sculpin numbers were assessed by surface counts and then by digging among the rocks with the use of a steel pole. The gravel was dug to a depth at which no more sculpins were uncovered (10–20 cm). Counted sculpins were gently guided out of the grid. We did not differentiate sculpins by species, but their length was assigned to one of three predetermined categories (small, >50 to <75 mm; medium, >75 to <100; large, >100 mm total length (TL); the PVC quadrat had eight 0- to 10-cm scales marked on it). Fewer than 5% of all sculpins observed were <50 mm TL.

We found no significant differences in either sockeye or sculpin numbers between sites–depths within sampling locations and strong positive correlations between sockeye and sculpin numbers over time within each site (results not presented). As such, we present only the mean number per sampling location, pooled over the two depths.

### Length and condition of sculpins

We examined the weight–length relationship of slimy and coastrange sculpins captured by dip net before (3–5 August), during (14 August), and after (30 August) the sockeye spawning period in 1993 to determine if sculpins gain weight in association with the spawning of salmon. We did not use condition factor indices (see Cone 1986), rather, within species, we first compared the natural logarithm of the weight–length relationship over time with analysis of covariance (ANCOVA) and then adjusted the weight of each fish to the natural logarithm of mean total length of both species collected (4.238). The adjustment for each individual was made as follows:  $\ln WT'_i = \ln WT_i - (\text{pooled slope}_s \times (\ln TL_i - 4.238))$  where  $\ln WT'_i$  is the adjusted weight of the *i*th fish,  $\ln WT_i$  is the weight of the *i*th fish, and pooled slope<sub>s</sub> is the pooled slope from ANCOVA per each species (2.86 and 3.42 for slimy and coastrange sculpins, respectively). Twelve sculpins with large internal parasites were excluded from the analyses.

### Feeding studies

In experiments run in an enclosed bay, we examined (i) the number of eggs that could be consumed by hungry sculpins of both species and various sizes within a 1-h feeding period and (ii) the potential number of eggs that could be consumed over the course of the major sockeye spawning period (7 days). The former provides an estimate of the number of eggs that could be eaten during a single spawning, and the latter provides an estimate of the overall effect of sculpin egg consumption on sockeye production.

### Egg consumption in a single feeding period

The diameter and hardness of salmon eggs change once they are exposed to water. Over the course of about an hour, they absorb water and harden in a process referred to as "water hardening". We considered that this process might have substantial effects on the number of eggs that might be consumed by a given sculpin and on the minimum size of sculpin that could consume eggs. Hence, for both sculpin species, we examined egg consumption of both "fresh" eggs and those that had been water hardened for at least 1 h in lake water. We measured the weight of 40 eggs together ( $\pm 0.01$  g) and the diameter of 10 eggs in a row ( $\pm 1$  mm) before each trial. The eggs from eight beach-spawning female sockeye were used, with eggs from three females used in both fresh and water-hardened treatments. We examined the relationship between egg consumption and sculpin length in a series of 12 experimental containers. The enclosures, made of fine-mesh stainless steel screen, had 15-cm-high sides mounted on a 40 × 40 cm square bottom. The cages were placed on metal stands, with the water level in each at about 10 cm. The bottom of each cage was covered with fine gravel upon which the eggs were clearly visible. A 15-cm-long, 6-cm-diameter weighted black ABS pipe was provided as shelter for the sculpins.

Sculpins were collected from spawning grounds by snorkelers using dip nets and then held without food for 4 days prior to testing. On the eve of a trial, six sculpins of each species were selected and placed

singly, and randomly, in each of the enclosures. A trial consisted of placing 40 eggs near each sculpin and then collecting and counting all remaining whole eggs at the end of a 1-h period. To get a more accurate estimate of what we observed in the wild, only sculpins that showed a propensity to feed in our chambers were tested. This propensity was tested by placing a few eggs in a 50-cm-long, 1-cm-diameter glass tube, with a squeeze ball on one end and a screen blocking the other end. The eggs were "moved" in front of the sculpin by lightly squeezing the ball. The sculpins were selected for testing if they attempted to feed on the available eggs. Most sculpins responded, but the proportion was not recorded. In addition, 10 sculpins >70 mm that either did not feed or fed only on one egg during testing were considered outliers and excluded from the analysis.

### Egg consumption over a 7-day period

This experiment was conducted in 1993 and 1994. The design was balanced over years in terms of size range and species tested to avoid any confounding effects of time and weather. Water temperature ( $\pm 0.1^\circ\text{C}$ ) was recorded with a hand-held thermometer about six times per 24-h period in 1993 and with a HOBO<sup>TM</sup> temperature logger every 8 min in 1994. In 1993, the average water temperature during the experiment was  $12.69 \pm 0.15^\circ\text{C}$  (SE,  $n = 39$ ) and in 1994 was  $13.31 \pm 0.05^\circ\text{C}$  ( $n = 750$ ).

Experiments were conducted in opaque floating plastic containers with a removable lid, with the lid just above the lake surface. The containers measured  $35 \times 28 \times 15$  cm deep and were divided in half with a fine-mesh vertical stainless steel screen so that two sculpins could be tested simultaneously within each container. Fresh lake water could enter through the containers by  $5 \times 10$  cm rectangular openings covered with fine screen at each end of the container. Each of 12 containers was tethered to separate posts in 1.5 m of water. Weighted black ABS pipes were provided for shelter.

We examined sculpins over 70 mm TL because these were most abundant on the spawning grounds. We tested six sculpins of each species in four size stanzas (70–79, 80–89, 90–99, and >99 mm). In each container, we placed a single sculpin on one side of the divider and a size-matched member of the other species on the other. No interactions between sculpins were observed. For 7 days, we repeated the process when at about noon each day, we gave each sculpin a set number of fresh eggs and then collected all of the remaining eggs the following morning (number eaten = number placed in pen – number of whole eggs remaining). Three slimy sculpins (each >97 mm) died during the experiment (two in 1993 and one in 1994) and were replaced.

### Head morphology of slimy and coastrange sculpins

We compared head morphology of the two sculpin species in an attempt to account for variation in feeding rates on eggs. The following measurements were made with electronic callipers ( $\pm 0.01$  mm) from a broad size range of sculpins: (i) jaw protrusion (JPRO, distance from the middle of the jaw to the perpendicular intersection of a line joining the posterior extent of the jaw), (ii) jaw width (JW, greatest distance between the margins of the jaw), (iii) head length, (iv) head depth, (v) maximum head width, and (vi) head width at the eyes. We estimated mouth area (MA) by dividing the equation of the area of an ellipse by one half:  $MA = \frac{1}{2}[\pi(JPRO \times \frac{1}{2}JW)]$  where JPRO and  $\frac{1}{2}JW$  represent the two radii of the ellipse. We analyzed the morphological variation by ANCOVA of individual traits relative to body length.

### Susceptibility of eggs to sculpin predation

We measured the susceptibility of salmon eggs to sculpin predation by a direct and indirect method. Indirectly, we monitored the "attractiveness" of fresh eggs contained in minnow traps to sculpins throughout the spawning period on three separate spawning beaches in 1993 (Woody Island, Fuel Dump Island, and Painted Rock on Porcupine Island).

Standard "Gee" minnow traps were baited with 40 g ( $\pm 1$  g) of

fresh eggs, which were encased in a Vibert incubation box (the eggs could be seen and smelled but not eaten). On each spawning beach, and within areas where sockeye were known to spawn, five stations were established 5 m apart along a 1.5-m depth transect marked with numbered white rocks. About every 2 days, at each station, a baited minnow trap was set 2–3 h before dusk and collected 14–18 h later. Each captured fish was identified to species, counted, a subsample measured (TL), and then all released back onto the spawning ground.

Direct estimates of sculpins in 112 sockeye female nests were made on Woody Island beach throughout the spawning period in both 1992 and 1993. Individual territorial sockeye females that had not yet completed spawning were first identified by snorkelers from a distance (i.e., nests were selected without knowledge of sculpin numbers). A 1-m<sup>2</sup> quadrat was placed around the centre of the nest and all sculpins within were counted. The presence or absence of eggs within the nest was also recorded.

## Results

### Temporal and spatial distribution of sculpins and sockeye salmon

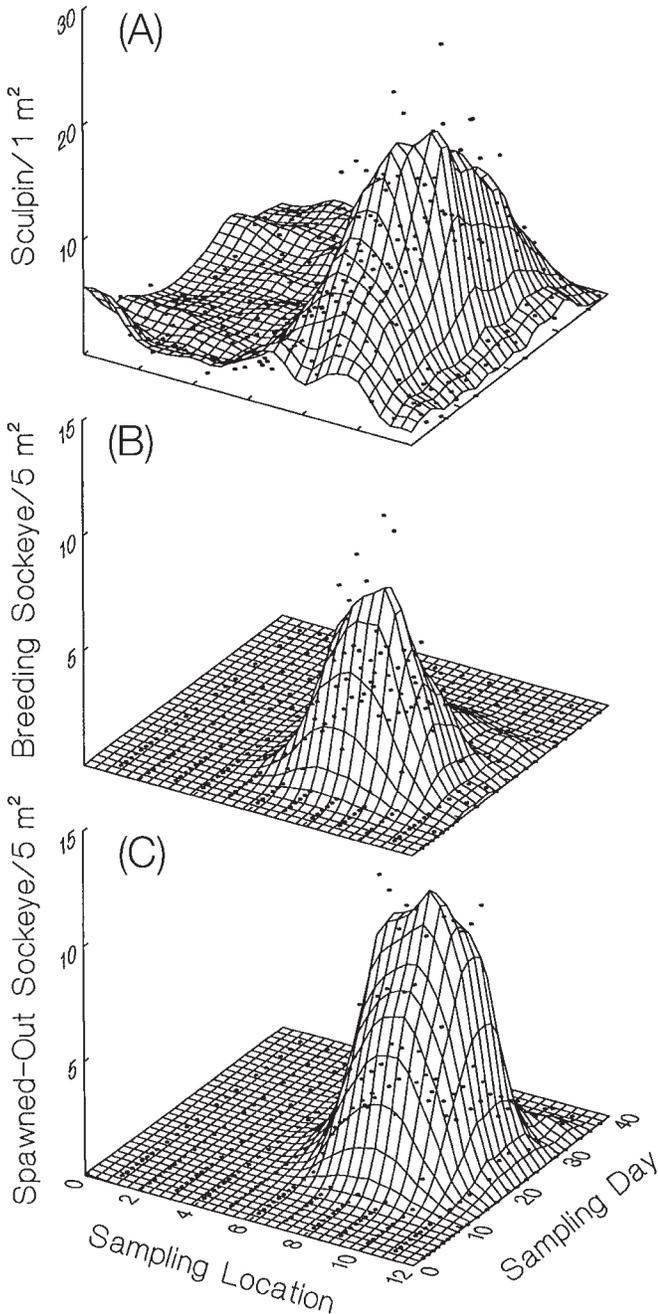
Sockeye spawning activity occurred within a 21-day period. Females first began nest construction on 8 August (12 females within our twenty-four 5-m<sup>2</sup> sampling sites) and the last breeding female on the beach was noted on 29 August. After 8 August, the density of breeding females increased rapidly, with most females completing spawning between 9 and 17 August (Fig. 1B). Peak densities of breeding females of about 13 per 25 m<sup>2</sup> occurred on 11 and 13 August, just 3 and 5 days after the commencement of spawning. After these dates, the number of spawned-out females rose rapidly, with virtually no females remaining alive on the beach by the end of August (Fig. 1C).

Quantitative sampling of sculpins was started on 2 August, 6 days before the first sockeye females established territories. Even then, sculpins were more abundant on the portion of the beach where sockeye spawning activity would eventually occur compared with areas where spawning did not occur (Fig. 1A). Sculpin abundance increased in these areas in the days preceding 8 August, when sockeye females first established nest sites, and continued to increase until about 4 days after the density of breeding females peaked on 13 August. Sculpin abundance declined slightly in the sampling areas where little or no sockeye spawning activity was observed, although there were slight increases at the beginning and end of the sockeye spawning period. On the five sampling days from 13 to 23 August, sculpin abundance in the 10 sampling sites within the spawning area averaged 12.9/m<sup>2</sup> compared with 0.9/m<sup>2</sup> in the 14 sampling sites in the nonspawning areas, a 14.3-fold difference.

As the density of sockeye females began to decline after 23 August, so too did the density of sculpins (Fig. 1A). However, even after all sockeye were gone from the spawning beach, sculpin abundance remained higher in the area formerly used by the spawning sockeye (4.5/m<sup>2</sup> on 7 September) compared with those sites that were not used (1.0/m<sup>2</sup>). At this time, no salmon eggs were visible and there were few salmon carcasses present, thus limiting sculpins' easy access to food.

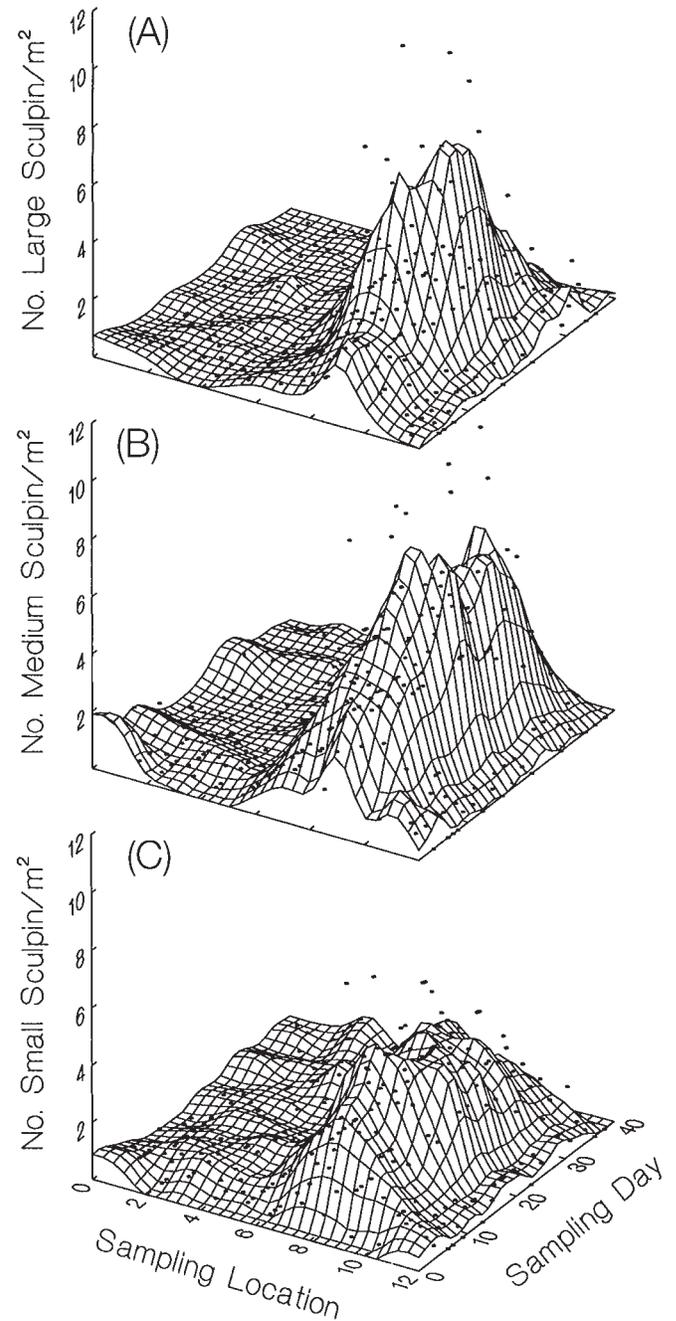
All known sizes of both sculpin species were present in our study area, although the smallest observed (<50 mm TL) comprised less than 5% of the total. The three size-classes of sculpins we enumerated followed the same spatial and

**Fig. 1.** Spatial and temporal distribution of sculpins and sockeye salmon females at Woody Island beach. Each point is the mean number of fish at the two sites (0.75 and 1.5 m depths) sampled at each of the 12 locations evenly spaced along 180 m of beach. Distance-weighted least squares analysis (SYSTAT, Inc.) was used for smoothing. (A) Sculpin density; (B) spawning sockeye female density; (C) density of sockeye females that have completed spawning. Sampling days start on 1 August.



temporal pattern in abundance as described above, although the medium (75–100 mm) and large (>100 mm) sculpins were more numerous on the spawning grounds, showed greater increases and decreases in numbers, and were found relatively less often outside the spawning area than small sculpins (50–75 mm) (Fig. 2).

**Fig. 2.** Spatial and temporal distribution of three size-classes of sculpins on Woody Island spawning beach: (A) large (>100 mm TL), (B) medium (76–100 mm TL), and (C) small (50–75 mm TL).

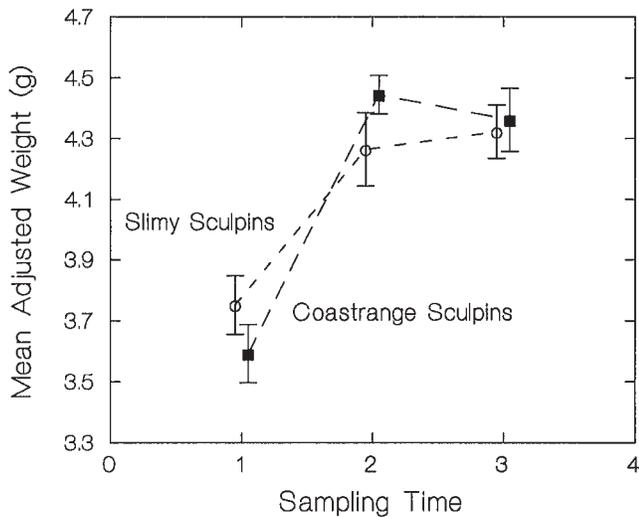


When the spatial and temporal distributions of sculpins and sockeye are viewed together, the near-perfect match in their distributions is clear (Figs. 1 and 2). The highest densities of sculpins occurred with the highest densities of breeding sockeye salmon. Sculpin density declined dramatically at the boundaries of the spawning area and was uniformly low outside it.

**Length and condition of sculpins**

The mean total length of both slimy and coastrange sculpins captured by dipnet in 1993 varied significantly over time

**Fig. 3.** Adjusted weight ( $\pm$  SE) of slimy sculpins (open circles) and coastrange sculpins (solid squares) captured on Woody Island beach before (1: 4–6 August), during (2: 14 August), and after (3: 1 September) the completion of spawning by sockeye salmon in 1993. Stomach contents are included in fish weights. Adjustments and analyses were done on natural logarithms of all measurements (see Methods).



( $F_{2,284} = 7.96$ ,  $P < 0.001$ ). Mean size was smallest before the arrival of the sockeye, largest during the presence of the sockeye, and intermediate afterwards (slimy:  $64.38 \pm 1.97$  (SE) mm,  $n = 40$ ,  $75.77 \pm 1.89$  mm,  $n = 51$ , and  $69.36 \pm 1.50$  SE mm,  $n = 58$  for early, middle, and late samples, respectively; coastrange:  $68.88 \pm 1.69$  mm,  $n = 68$ ;  $73.31 \pm 2.42$  mm,  $n = 49$ ;  $71.67 \pm 2.42$  mm,  $n = 46$ ). There was no significant difference between species in size ( $F_{1,284} = 0.64$ ,  $P > 0.4$ ), nor was there any interaction between time and species ( $F_{2,284} = 1.41$ ,  $P > 0.2$ ).

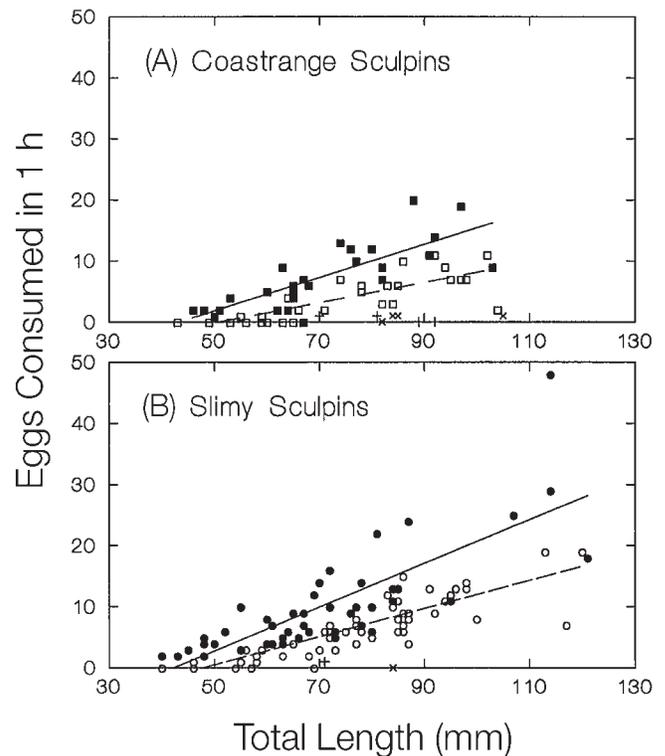
For both sculpin species, the slope of the relationship between  $\ln$ WT and the  $\ln$ TL did not differ over the collection times (slimy:  $F_{2,172} = 1.72$ ,  $P > 0.15$ ; coastrange:  $F_{2,183} = 2.88$ ,  $P = 0.06$ ), but line elevations did (slimy:  $F_{2,174} = 5.72$ ,  $P < 0.005$ ; coastrange:  $F_{2,185} = 27.48$ ,  $P < 0.001$ ). Both species showed a similar ( $F_{1,284} = 0.09$ ,  $P > 0.7$ ) and significant change in adjusted weight over time ( $F_{2,284} = 30.89$ ,  $P < 0.001$ ) (Fig. 3). There was no interaction between species and time of sampling ( $F_{2,284} = 2.23$ ,  $P > 0.1$ ). Fish collected during and after the spawning period were significantly heavier than those collected before spawning commenced (Tukey's test:  $P < 0.01$  between sample 1 and each of 2 and 3;  $P > 0.6$  between 2 and 3).

### Egg consumption over a 1-h period

Both sculpin species readily ate water-hardened and fresh salmon eggs placed in front of them. The water-hardened eggs were heavier ( $0.124 \pm 0.001$  (SE) g,  $n = 91$  versus  $0.100 \pm 0.001$  g,  $n = 69$ ) and had a greater diameter ( $6.17 \pm 0.03$  (SE) mm,  $n = 92$  versus  $5.73 \pm 0.04$  mm,  $n = 71$ ) than fresh eggs. The average percent increase in egg weight and diameter for eggs of the same female was 9.5 and 3.2%, respectively ( $n = 5$  females).

For slimy sculpins, there was a significant difference in the

**Fig. 4.** Regressions of the number of fresh (solid symbols) and water-hardened (open symbols) salmon eggs eaten by (A) coastrange sculpins and (B) slimy sculpins of different lengths in a 1-h period under controlled conditions. Outliers, those fish marked by 'x's and '+'s for sculpins in the fresh and water-hardened egg treatments, respectively, were not included in regression calculations (see Methods). Analyses were done on the natural logarithms of both measurements.

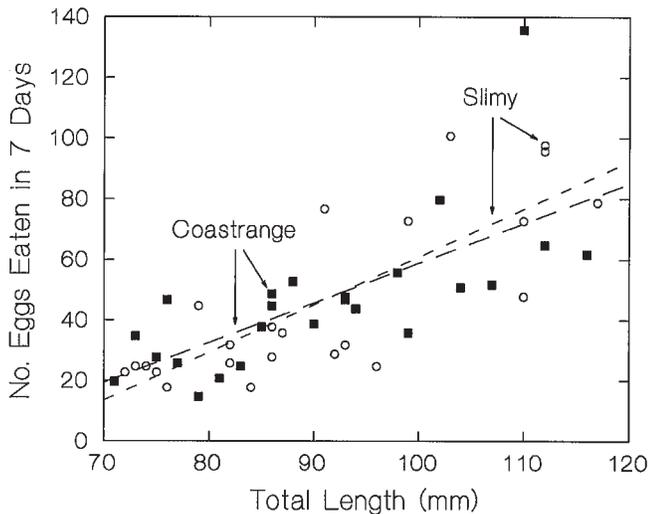


slope of the regression of  $\log_e$  of the number of eggs eaten versus  $\log_e$  of fish length for fresh and water-hardened eggs (ANCOVA:  $F_{1,97} = 4.24$ ,  $P < 0.05$ ,  $R^2 = 0.70$ ) (Fig. 4). Slimy sculpins ate nearly 1.5 times as many fresh eggs as water-hardened eggs on average, with the difference increasing with sculpin size. One of the largest slimy sculpins tested (114 mm) ate 48 fresh eggs within a 15-min period. Similarly, coastrange sculpins also consumed more fresh eggs than water-hardened eggs per fish size ( $F_{1,43} = 24.06$ ,  $P < 0.001$ ), but in this case, there was no significant difference in the slopes ( $F_{1,42} = 0.054$ ,  $P > 0.80$ ).

There were significant differences between the species in the number of both fresh and water-hardened eggs consumed in 1 h. Slimy sculpins ate more fresh and water-hardened eggs than coastrange sculpins ( $F_{1,67} = 9.20$  and  $F_{1,73} = 13.51$ ,  $P < 0.005$ ), with no difference between species in the slope of the relationship with fish length in either case ( $F_{1,66} = 2.63$  and  $F_{1,72} = 0.80$ ,  $P > 0.10$ ).

In both species, there was a lower limit in the size of fish that could consume water-hardened eggs (Fig. 4). These small fish repeatedly attempted to eat eggs, but were unable to get them into their mouths. In slimy sculpins, this lower size limit was about 50 mm TL whereas for coastrange sculpins the lower limit was about 55 mm. In contrast, all five coastrange sculpins tested that were  $< 55$  mm (46–53 mm) and all seven

**Fig. 5.** Regression of the number of fresh salmon eggs eaten over a 7-day period versus fish length for slimy sculpins (open circles) and coastrange sculpins (solid squares).



slimy sculpins tested that were <50 mm (40–48 mm) ate at least one fresh egg. Virtually all of the fresh eggs eaten by small sculpins were broken during ingestion whereas the water-hardened eggs rarely were, even by large sculpins.

#### Egg consumption over a 7-day period

The number of fresh eggs consumed by both sculpin species over 7 days was similar and positively dependent on body size (slimy sculpin:  $y = 1.58TL - 96.79$ ,  $R^2 = 0.63$ ,  $n = 23$ ; coastrange sculpin:  $y = 1.31TL - 72.42$ ,  $R^2 = 0.49$ ,  $n = 24$ ) (Fig. 5). There were no significant differences in slope (ANCOVA:  $F_{1,43} = 0.460$ ,  $P > 0.5$ ) or line elevation ( $F_{1,44} = 0.006$ ,  $P > 0.9$ ). For each species, independent of body size ( $P > 0.1$ ,  $R^2 < 0.15$ ), nearly half of all eggs consumed were eaten during the first feeding opportunity (slimy sculpin:  $49.8 \pm 2.5\%$  (SE),  $n = 23$ ; coastrange sculpin:  $43.0 \pm 2.7\%$ ,  $n = 24$ ;  $t = 1.85$ ,  $df = 45$ ,  $P = 0.072$ ).

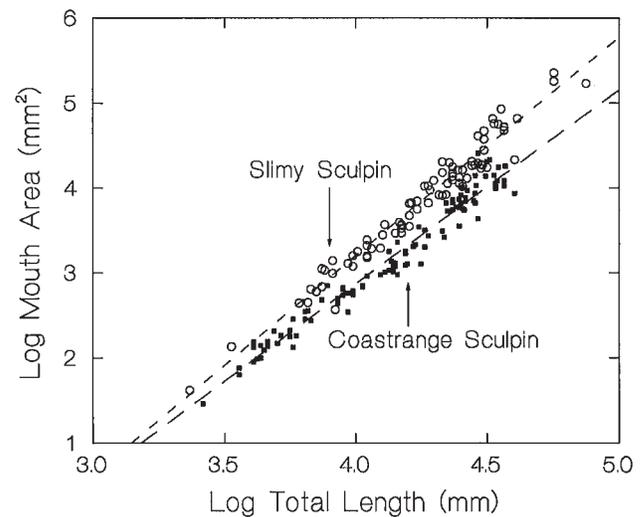
#### Head morphology of slimy and coastrange sculpins

Slimy sculpins have wider jaws (and heads) than do coastrange sculpins at all sizes ( $F_{1,180} = 42.8$ ,  $P < 0.001$ ). Similarly, the jaws of slimy sculpins protrude further than those of coastrange sculpins over all sizes measured, with the difference increasing with increasing fish length ( $F_{1,179} = 48.4$ ,  $P < 0.001$ ). Taken together, slimy sculpins have greater jaw area than coastrange sculpins over all sizes, with the difference increasing with increasing size ( $F_{1,179} = 19.9$ ,  $P < 0.001$ ) (Fig. 6). This difference is consistent with the ability of slimy sculpins to consume water-hardened eggs at a smaller size than coastrange sculpins (Fig. 4).

#### Susceptibility of eggs to sculpin predation

In the days preceding the commencement of sockeye spawning on three separate island spawning beaches in 1993, we caught an average of  $146.4 \pm 27.6$  (SE) ( $n = 10$ ),  $44.1 \pm 8.9$  ( $n = 15$ ), and  $142.6 \pm 35.1$  ( $n = 5$ ) sculpins per egg-baited trap (Fig. 7). After sockeye spawning started on 8 August, the number of sculpins caught in traps dropped abruptly, reaching zero for

**Fig. 6.** Plot of mouth area versus total length of slimy sculpins (open circles) and coastrange sculpins (solid squares) captured on the island spawning beaches. See Methods for formula for calculating mouth area.

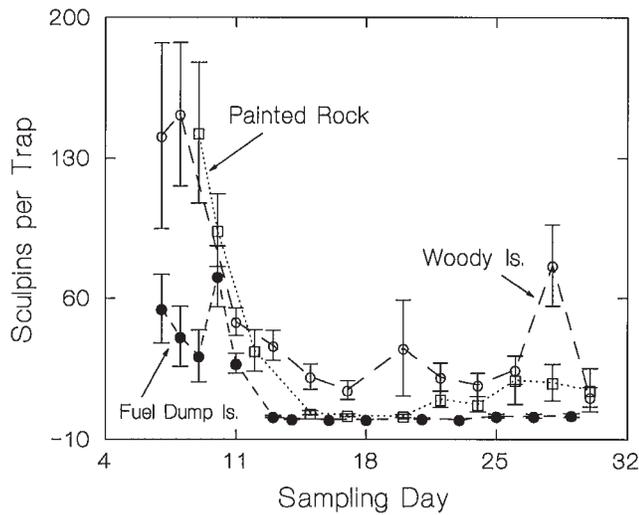


consecutive sampling periods during peak sockeye spawning on two beaches. On all but Fuel Dump Island beach, the numbers of sculpins captured with egg-baited traps increased at the end of the sockeye spawning period. The pattern of capture in baited traps was similar and significant for both species of sculpin (Kruskal–Wallis test:  $P < 0.001$ ). Coastrange comprised 61.5% of the sculpins captured. The average length of captured fish was  $84.0 \pm 0.4$  (SE) mm ( $n = 1133$ ) and  $85.5 \pm 0.3$  mm ( $n = 1518$ ) for slimy and coastrange sculpins, respectively.

The pattern in the number of sculpins found in individual sockeye female nests over the spawning season was similar to that observed in the minnow traps. There were distinctly more sculpins in the nests of the earliest and latest females to spawn than there were in the nests of those spawning during the main part of the spawning period (Fig. 8). In 1992, rough weather prevented quantification of the sculpins per nest of the earliest breeding females. However, we observed one of the first females to spawn on 9 August and noted that her nest contained more than 100 sculpins. After this date, the number of sculpins per nest dropped, but at the end of the run, we quantified a large number ( $71.3 \pm 16.1$  (SE),  $n = 4$ ) of sculpins per nest. In 1993, we purposely concentrated our sampling on the early part of the spawning run to quantify what we had missed in 1992. The number of sculpins per nest with eggs was  $66.1 \pm 7.0$  ( $n = 6$ ) over the first 3 days of spawning and then dropped significantly.

In both 1992 and 1993, there was a significant effect of sampling date and whether or not eggs were present in the nest on the number of sculpins present, with no interaction between the two factors (1992: egg,  $F_{1,75} = 5.37$ ,  $P < 0.05$ ; day,  $F_{1,75} = 17.44$ ;  $R^2 = 0.31$ ; 1993: egg,  $F_{1,31} = 16.66$ ,  $P < 0.001$ ; day,  $F_{1,31} = 12.30$ ;  $R^2 = 0.46$ ,  $P = 0.001$ ). In both years, there were over twice as many sculpins in the nests containing eggs (nests without eggs:  $8.93 \pm 1.26$  (SE),  $n = 29$  and  $17.67 \pm 2.51$ ,  $n = 12$  for 1992 and 1993, respectively; nests with eggs:  $23.00 \pm 2.92$ ,  $n = 49$  and  $38.82 \pm 4.54$ ,  $n = 22$ ).

**Fig. 7.** Mean number ( $\pm$  SE) of sculpins captured in sets of five minnow traps baited with 40 g of fresh salmon eggs set on three separate sockeye salmon island beach spawning locations in Iliamna Lake, Alaska, over the month of August 1993.



## Discussion

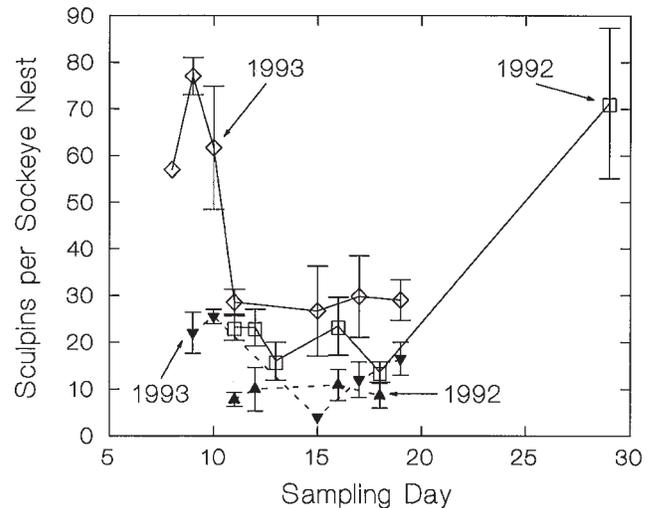
### Relationship between sockeye spawning and sculpin density

The spawning of sockeye salmon on island beaches in Iliamna Lake is predictable in space and time. Commencement date of spawning usually varies by only a few days over years (e.g., Quinn and Foote 1994; this study). Spawning site locations are also highly predictable over a broad scale (kilometres, Blair et al. 1993) and a very fine scale (metres, Hendry et al. 1995). Our results indicate that slimy and coastrange sculpins make significant use of this highly predictable resource by feeding extensively on salmon eggs.

Salmonid eggs are likely a valuable resource for sculpins. They are abundant, easy to catch, and require little handling (see Biga 1996) and are energy rich (about 6200 cal/g dry egg (1 cal = 4.1868 J), Wetzel 1993). Further, their availability in late summer before the long Alaskan winter probably increases their importance in the ecology of the sculpins. The amount of fall energy stores in freshwater fishes can have a direct effect on overwinter survival (Gardiner and Geddes 1980; Smith and Griffith 1994) and on reproduction the following year (Meffe and Snelson 1993). When sculpins arrived on the beach in early August, their condition appeared low, even though the majority of the summer and the associated feeding opportunities were past, and then increased substantially with the spawning of the salmon (Fig. 3). Hershey and McDonald (1985) noted that larger slimy sculpins appeared to be food limited in Toolik Lake, Alaska, and linked this to the exponential increase in rate of mortality of larger sculpins once they reached maturity. If older Iliamna Lake sculpins are also food limited, and unable to recoup the energy losses associated with their late spring and early summer spawning period (Craig and Wells 1976), then an abundant egg resource will likely have significant effects on overwinter survival and future reproduction.

Sculpin numbers increased dramatically over the course of the salmon spawning run on Woody Island and decreased in a

**Fig. 8.** Mean number of sculpins ( $\pm$  SE) observed in the nests of breeding sockeye females (1 m<sup>2</sup>) over the course of the spawning season in 1992 and 1993. Nests in which eggs were found are shown by open symbols; nests without eggs are shown by solid symbols.



less dramatic fashion after spawning completion (Fig. 1A). The increase was noted days before the commencement of sockeye spawning and was apparent only on the spawning beach itself and not on directly adjacent habitats. This spawning site specific increase suggests that sculpins may predict the arrival of the egg resource, and do not simply react to its presence. We know from in situ experiments on Woody Island that sculpins are highly attracted to the odor of fresh sockeye eggs (Dittman et al. 1998) and to the digging actions of females during nest construction (C.J. Foote and G.S. Brown, personal observation; see also Janssen 1990). However, neither event occurred during the first 6 days of our observations, yet sculpin numbers still increased. Salmon increasingly gathered and schooled around the spawning area before settling, but their movements were broad and carried them all around the inner bay, including nonspawning areas. The fact that sculpin numbers increased only in the eventual sockeye spawning area suggests that visual cues of the positions of the schooling sockeye were also not the cues for directed movement by the sculpins. However, it is possible that sculpins were detecting residual cues of previous spawning in the area, as has been shown in lake trout (*Salvelinus namaycush*) (Foster 1985), or had simply learned where the spawning area was from previous experience. Sculpins live up to 8 years in Iliamna Lake (Roger 1971), and hence have repeated opportunities to learn the temporal and spatial distribution of egg resources.

McDonald et al. (1982) reported densities of slimy sculpins in the range of 0.44–2.58/m<sup>2</sup> in rocky littoral areas in Toolik Lake, Alaska. These densities are similar to those that we found in the rocky littoral areas not occupied by salmon, but far below those on the adjacent spawning grounds during peak spawning (Fig. 1A). Given the high peak sculpin densities observed on the spawning beach, it seems likely that sculpins must be arriving from relatively large distances. Significant sculpin migrations (kilometres) have been noted previously in relation to the activities of salmon (Reed 1967; McLarney 1967). However, such movements likely increase their risk of

predation (Brown 1991). In Iliamna Lake, four major sculpin predators, lake trout, Arctic char (*Salvelinus alpinus*), burbot (*Lota lota*), and rainbow trout (*Oncorhynchus mykiss*), are present. On the beaches, sculpins are also accessible to the common merganser (*Mergus merganser*) (Sjöberg 1988).

Sculpins may start their movement to sockeye spawning beaches before the commencement of spawning to maximize their access to the egg resource. The spawning period of island beach spawning sockeye is short (Fig. 1B), with individual females completing spawning in 1–2 days (Quinn and Foote 1994) and most females having completed spawning within a week. If sculpins relied solely on cues of actual spawnings to move to the spawning sites, they could miss feeding opportunities during the time it takes to move to that location.

Sculpins can also increase their access to sockeye eggs by being in nests during spawning events, as this is when the eggs are most available. At spawning, the eggs (about 500–1000 per spawning) are exposed and the easiest to capture. We have shown that sculpins can eat a large number of eggs within minutes of their discovery, particularly if they are freshly spawned (Fig. 4). However, shortly after spawning, the number of eggs that can be consumed drops for two reasons. First, a spawning act lasts only seconds, and over about the next 10 min the female covers the eggs with gravel. Although the eggs within the nest may remain accessible to the sculpins buried with them, they may not be easily localized or accessible to other sculpins. Second, the eggs immediately start to swell and harden, with the process largely complete within an hour of spawning. Consequently, the size range of sculpins that can consume these eggs decreases due to gape limitations (Fig. 6), and those still able can consume fewer of them (Fig. 4). The digestion rate of these water-hardened eggs is also slower than that of freshly spawned eggs (McLarney 1967), further limiting the number of eggs that can be consumed. Gape limitation may account for the relatively low proportion of small sculpins on the spawning grounds (Fig. 2) and act to select for the large egg size of beach spawning sockeye.

#### Potential effects of egg predation on sockeye salmon

The potential impact of sculpin predation on sockeye production was shown clearly in the feeding experiments. Both species of sculpin readily consumed eggs, with the number consumed being directly related to fish size and the state (fresh versus water hardened) of the eggs. Indeed, they appeared to gorge on eggs at the first opportunity. For example, large sculpins could easily consume over 20 fresh eggs, and up to 48, within minutes of their discovery.

The potential number of eggs consumed over the spawning season was also directly related to sculpin size. The largest sculpins of both species could consume over 80 fresh eggs, and up to 135, over a 7-day period. While we do not know how many eggs individual sculpins are consuming over the course of the spawning run, we suspect for a number of reasons that they are feeding to near satiation. First, we often noted that sculpins were bloated with eggs during our surveys. Second, their high motivation to feed on eggs was apparent in our feeding studies, where they readily fed on eggs in unnatural conditions and in broad daylight. Sculpins are typically thought to be nocturnal (e.g., Selgeby 1988), but we observed that they were active on the beaches throughout the day. Third, the

marked decline in the number of sculpins captured in egg-baited traps coincident with the marked increase in the condition of sculpins after spawning commenced (Figs. 3 and 7) suggests that sculpins are finding plenty of eggs to consume outside the traps.

With the data from the beach surveys, our feeding experiments, and from our size estimates of the sculpins on Woody Island beach, we can derive an estimate of the number of sockeye eggs consumed by sculpins. There were about 1000 females on the beach in 1992. We estimated the presence of 844 females in 1990 (Quinn and Foote 1994), and the overall density and numbers appeared similar. Woody Island sockeye females have an average of about 3800 eggs (Blair et al. 1993), indicating that the total number of eggs deposited would be about 3 800 000. Using the average density of sculpins observed on the spawning grounds during their peak abundance (13.5/m<sup>2</sup>; data from August 13, 15, and 17) and an estimate of overall spawning area of about 1200 m<sup>2</sup> (80 m along the shoreline by 15 m out), we estimate that there were about 16 200 sculpins on the beach. To estimate fresh egg consumption, we use an average sculpin size of 85 mm derived from our trap data in 1993, which is consistent with survey data of 1992 (Fig. 2), although larger than those captured by dip net in 1993. Sculpins of this size can consume about 38 fresh eggs over 1 week (Fig. 5), a period that encompasses the majority of sockeye spawning. Taken together, we estimate that about 617 220 or about 16% of the eggs laid may have been consumed by sculpins. The estimate would be higher if total consumption by sculpins were extrapolated over 14 days (25%, based on a consumption of 58.3 eggs per sculpin, C.J. Foote and G.S. Brown, unpublished data), but it would be lower if sculpin predation were not assumed to be on fresh eggs. However, the presence of significant numbers of sculpins in the nests at the time of spawning indicates that the majority of the predation probably occurs within minutes of spawning.

McLarney (1967) estimated that sculpins could take 7% of the eggs available in pink salmon (*Oncorhynchus gorbuscha*) spawning runs, even when the density of sculpins was much lower than we noted and the gravel much less penetrable. The majority of eggs were taken in the stream drift, dislodged during nest superimposition by females, and unlikely to have survived in any case. In contrast, on the island beaches, egg predation by sculpins seems to be principally on viable salmon eggs. Nest superimposition appears uncommon given the brief spawning period, the relatively long mean life span of breeding females (7.4 days), and the rarity of female displacement (Quinn and Foote 1994).

#### Selective nature of sculpin predation on sockeye eggs

The intensity of sculpin predation on sockeye eggs varied substantially over the course of the spawning run. Females that spawned early and, to a lesser degree, late in the run were subject to far greater numbers of sculpins in their nests than those in the middle of the run (Fig. 8), and hence undoubtedly suffered the greatest egg predation. This conclusion is supported by the similar temporal pattern of capture of sculpins in egg-baited minnow traps (Fig. 7). A set number of eggs early and late in the spawning run attracted more sculpins, and hence seemed more vulnerable to predation, than those in the middle of the spawning period. Further, the difference in the intensity of predation is probably greater than that indicated by

differences in the number of sculpins per nest alone. Sculpins captured before spawning started had a significantly lower condition factor than those collected during the run. Given that egg digestion takes many days (McLarney 1967) and that sculpins readily gorge on a large portion (>40%) of the eggs that they will consume at their first opportunity, then individual sculpins that are in sockeye nests early in the spawning run are likely to be hungrier and to eat more eggs than those observed in the nests later on.

The temporal nature of sculpin predation on eggs in the nests of individual females may account for the relatively short spawning season of sockeye salmon on island beach spawning locations in Iliamna Lake (Hendry et al. 1995; Fig. 1B). In 1992, peak spawning was observed within 6 days of the first female spawning, and the majority of females appeared to spawn over a 6- to 10-day period. This is in contrast with stream spawners in sockeye salmon where runs are typically much more extended, including those in Alaska and other parts of Iliamna Lake, lasting 3–6 weeks and sometimes longer (e.g., Demory et al. 1964; Wood and Foote 1996). Sweeney and Vannote (1982) argued that the “predator satiation” hypothesis accounted for the marked synchrony in adult emergence patterns in mayflies, and the same argument appears to apply here. They showed that the percentage of adults succumbing to predators on a given day was inversely related to the total number of adults available as prey each day, which agrees with what we found relative to sculpin predation in sockeye nests. The interesting conclusion from our study is that the abundance of predators over time alone does not reveal the temporal nature of egg predation. In that case, peak sculpin and sockeye numbers coincide. Rather, it is the independent temporal measures of the sculpins per nest and the attraction of sculpins to egg-baited traps that indicate this pattern of selective predation.

The question remains as to how sculpins could potentially have such significant predatory and demographic effects on sockeye salmon spawning on the island beaches when their effects are usually not considered significant in stream habitats (e.g., Moyle 1977). We believe the answer lies in the large substrate on the island beaches. Leonetti (1997) reported geometric mean particle sizes between 35 and 79 mm on Woody Island and Fuel Dump Island spawning beaches, with particles of <13 mm virtually absent (0.6%). Given that sculpins can penetrate cobble and gravel with significant interstices (Phillips and Claire 1966; McLarney 1967; Biga 1996), this porous substrate makes the developing eggs susceptible to sculpin predation while at the same time providing refuge for sculpins from their own predators.

The predictable, temporally and spatially clumped resource of salmon eggs available on the spawning beaches of Iliamna Lake is an important factor shaping the ecology of the two resident sculpin species. They, in turn, appear to have shaped the spawning behavior of the sockeye salmon, specifically their compressed spawning season. Through sculpins, an important exogenous energy source in the form of sockeye eggs is incorporated into the piscivore populations.

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