The role of chemoreception in salmon-egg predation by coastrange (*Cottus aleuticus*) and slimy (*C. cognatus*) sculpins in Iliamna Lake, Alaska

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Abstract: Egg predation by coastrange sculpins (*Cottus aleuticus*) and slimy sculpins (*C. cognatus*) may be a major factor affecting sockeye salmon (*Oncorhynchus nerka*) production in Iliamna Lake, Alaska. In this study, we examined the potential roles of visual and chemosensory cues in egg predation by sculpins. A field study tested whether sculpins were differentially attracted to minnow traps baited with eggs that were (*i*) visible with no odours present, (*ii*) visible with odours present, or (*iii*) not visible with odours present. Our results indicated that sculpins do not require visual cues for detecting salmon eggs. However, attraction to sockeye eggs did require chemical cues emanating from the eggs. To characterize the chemical attractants that emanate from salmon eggs, we tested whether sculpins were attracted to test odours in a two-choice maze. Test odours were prepared by soaking eggs in lake water. Sculpins preferred egg wash to lake water but demonstrated no attraction to ovarian fluid versus lake water, suggesting that the attractive substances are derived directly from egg material. These results are discussed in relation to the known sensory mechanisms involved in feeding by sculpins as well as to the ecological relationship between spawning sockeye salmon and sculpins.

Résumé : La prédation des oeufs par des Chabots côtiers (*Cottus aleuticus*) et des Chabots visqueux (*C. cognatus*) affecte sans doute considérablement la production de Saumons nerka (*Oncorhynchus nerka*) du lac Iliamna en Alaska. Au cours de cette étude, nous avons examiné le rôle des stimuli visuels et chimiosensoriels qui déclenchent la prédation des oeufs par les chabots. Au cours d'une expérience sur le terrain, nous avons installé des pièges à ménés contenant des oeufs (*i*) visibles sans odeur, (*ii*) visibles avec odeur, (*iii*) non visibles avec odeur, et tenté de déterminer si les chabots réagissent différemment aux différentes conditions. Nos résultats indiquent que les chabots n'ont pas besoin du stimulus visuel pour détecter la présence des oeufs. Les déclencheurs chimiques sont cependant nécessaires pour que les chabots repèrent les oeufs. Pour déterminer quelles substances chimiques émanent des oeufs de saumon, nous avons vérifié si les chabots sont attirés par les odeurs dans un labyrinthe offrant deux choix. Les odeurs expérimentales ont été préparées en trempant des oeufs dans de l'eau du lac. Les chabots préféraient l'eau de trempage des oeufs à l'eau de lac non traitée, mais n'ont manifesté aucune attirance pour le liquide ovarien vs l'eau du lac, ce qui indique que les substances qui attirent les chabots sont directement reliées aux oeufs. Ces résultats sont examinés en fonction des mécanismes sensoriels qui contrôlent l'alimentation des chabots et en fonction de la relation écologique entre les Saumons nerkas et les chabots pendant la fraye des saumons.
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Introduction

Iliamna Lake, in southwestern Alaska, supports the largest run of sockeye salmon (*Oncorhynchus nerka*) in the world. Mil-

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lions of maturing salmon return each summer to spawn at their natal sites either in lake tributaries or at mainland and island beaches. Spawning salmon are thought to provide a significant input of nutrients to freshwater systems and may be a critical food resource for a number of freshwater predators (e.g., bears, eagles, fishes) (Willson and Halupka 1995). In particular, sculpins (*Cottus* spp.) in Iliamna Lake derive a significant proportion of their nutrients from predation on sockeye salmon eggs and fry (Kline et al.1993). Recently, Foote and Brown (1997) demonstrated that the two freshwater sculpin species inhabiting the lake, coastrange sculpins (*C. aleuticus*) and slimy sculpins (*C. cognatus*), are major predators of salmon eggs at spawning sites on island beaches in Iliamna Lake. Coastrange and slimy sculpins are small benthic fish that are able to move within the large gravel of the island beaches to feed on recently spawned eggs in salmon nests (Kerns and Donaldson 1968; Roger 1971; Foote and Brown 1997). Just prior to and during the period of salmon spawning, sculpin densities on spawning beaches rise dramatically, and during years of low salmon density, sculpins may consume as many

as 15% of the eggs spawned on certain island beaches (Foote and Brown 1997). Prior to the arrival of spawning salmon, sculpins appear to be in poor condition, suggesting that the ability to detect and utilize the egg resource may be critical for subsequent growth and survival (Foote and Brown 1997).

While sockeye salmon eggs may be an important energy resource for coastrange and slimy sculpins, this resource may only be available to sculpins for a short period during or soon after sockeye salmon spawning. Typically, island-spawning sockeye salmon spawn only on specific beaches and have an extremely restricted spawning period, the majority of females completing spawning within 7 days (Quinn and Foote 1994; Hendry et al. 1995; Quinn et al. 1996). Sculpins may be able to penetrate salmon redds after spawning to consume eggs, but within an hour after fertilization, the eggs swell and harden, making them less susceptible to predation (Foote and Brown 1997). The extreme spatial and temporal clumping of sockeye spawning suggests that sculpins must be able to quickly and readily locate salmon eggs soon after spawning in order to fully utilize this resource.

The mechanisms that guide sculpins to salmon-spawning beaches and, ultimately, enable them to detect recently spawned eggs in redds are not known. Feeding in sculpins is generally thought to require either mechanosensory detection of prey via the lateral-line system (Hoekstra and Janssen 1985) or visual cues (Neverman and Wurtsbaugh 1992; Miller et al. 1992). In freshwater systems lacking spawning salmon and during most of the year in systems containing salmon, sculpins eat motile prey. These may be either swimming prey in the water column or benthic macroinvertebrates (Hoekstra and Janssen 1985; Cuker et al. 1992; Hudson et al. 1995). In fact, Hoekstra and Janssen (1985) found that mottled sculpins (*C. bairdi*) did not consume immobile prey even if they were touching them, and concluded that chemical cues are not necessary and are ignored in the absence of mechanical stimuli. Moyle (1977) suggested that sculpins only eat salmon eggs that are dislodged from their nests and thus floating (i.e., moving) downstream. He hypothesized that "once eggs are buried, they are relatively unavailable to sculpins because sculpins seem to require moving prey." However, in some systems at least, sculpins do eat immobile salmon eggs in the spawning gravel (Reed 1967; Savino and Henry 1991; Hudson et al. 1995; Biga 1996; Foote and Brown 1997), suggesting that they must use other senses, such as touch, chemoreception, or vision, to locate them (Savino and Henry 1991).

In this study we examined the potential roles of visual and chemosensory cues in facilitating egg detection and predation by coastrange and slimy sculpins. Specifically, we hypothesized that Lake Iliamna sculpins can use chemosensory cues exclusively to locate and consume sockeye salmon eggs. To test this, we conducted field experiments on spawning beaches to determine whether sculpins were attracted to sockeye salmon eggs that could be (*i*) both seen and smelled, (*ii*) seen but not smelled, or (*iii*) smelled but not seen. We also attempted to characterize the chemical attractants that might emanate from salmon eggs by examining the responses of sculpins to lake water scented with eggs at different developmental stages and ovarian fluid in a two-choice maze. Our results are discussed in relation to the known sensory mechanisms involved in feeding by sculpins as well as the ecological relationship between spawning sockeye salmon and sculpins in Iliamna Lake.

Materials and methods

Study site
Iliamna Lake is the largest lake in Alaska and contains over 100 identified sockeye salmon spawning areas (Demory et al. 1964). Spawning occurs in inlet streams and at mainland beaches and island beaches located in the eastern portion of the lake. Our study sites were sections of sockeye salmon spawning beaches located on Woody, Fuel Dump, and Porcupine islands (Fig. 1). Sockeye salmon typically spawn at a depth of 0.5–5.0 m from mid to late August at all the sites used in this study (Quinn and Foote 1994; Hendry et al. 1995). The field component of this study was conducted just prior to the sockeye spawning season (August 2–8, 1994) because sculpin densities on the beaches are typically high at this time (Foote and Brown 1997) and we wished to avoid any confounding factors associated with natural spawning of eggs.

Field studies
To test whether sculpins were attracted to sockeye salmon eggs and examine the sensory mechanisms underlying this attraction, standard "Gee" minnow traps were baited with 40.0 ± 1.0 g (mean $\pm$ SE) of sockeye eggs placed in Vibert incubation boxes, which allowed sculpins to see and smell eggs but not consume them. Eggs were collected every 1–2 days from freshly caught preovulatory female sockeye salmon and refrigerated until used. Traps were baited with (*i*) free eggs in incubation boxes (free); (*ii*) eggs enclosed in intact clear Ziploc bags placed in incubation boxes (18.0×16.0 cm) (visible/odours absent); (*iii*) eggs enclosed in clear perforated (eighty 2- to 3-mm holes per side) Ziploc bags placed in incubation boxes (visible/odours present); (*iv*) eggs enclosed in perforated black Ziploc bags placed in incubation boxes (not visible/odours present). Traps baited with free eggs were used to determine whether Ziploc bags would interfere with visual or olfactory detection of eggs (e.g., Ziploc bags might restrict water flow and thus the release of odorants from eggs). In these studies we did not address which chemosensory systems (e.g., taste, olfaction) might be involved in attraction to eggs, but we use "odour" to describe any chemosensory cues emanating from eggs. Each day between August 2 and 7, 1994, 16 traps (4 each in four groups, including one replicate of each of the 4 treatments) were set between 20:00 and 23:00 on one of four spawning beaches located at the west and north ends of Woody Island (see Fig. 1). Within each group the trap location of the 4 treatments was randomized. Traps were set in 1.5–3.0 m of water, with approximately 5 m separating each trap. The two beaches on west Woody Island were sampled twice and the two beaches on north Woody Island were sampled once. Sampling sites were rotated so that no site was sampled on consecutive days. Traps were recovered the following day (13–17 h after setting), the species and number of all fish captured were recorded, and the fish were released. During these experiments, schools of prespawning sockeye salmon would occasionally swim over the spawning beaches but no salmon had settled and begun nest construction on the test sites.

On August 7, 1994, we further tested whether visual cues were involved in attraction to eggs by setting a total of eight pairs of empty and visible/odours absent traps at spawning beaches at Woody Island, Fuel Dump Island, and Painted Rock (Fig. 1). Traps were recovered the following day and the species and number of fish captured were recorded.

To determine how long salmon eggs remained attractive to sculpins, we baited traps with eggs as described above and presoaked traps in lake water for 0, 4, 12, and 24 h prior to setting them ($n = 4$ traps/treatment) on spawning beaches on Woody Island (Fig. 1). Traps were recovered the following day and the species and number of fish captured were recorded.

Y-maze studies
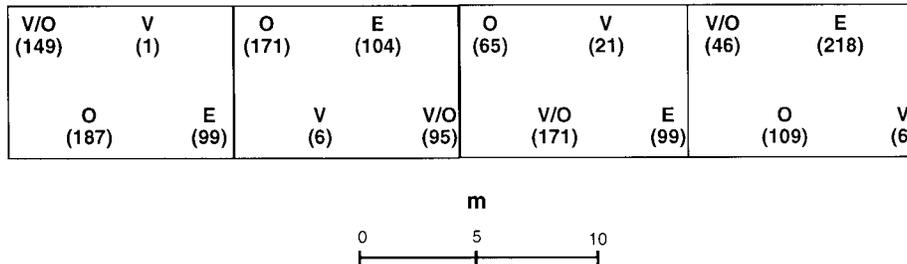To characterize the chemical attractants that emanate from salmon

Fig. 1. Locations of sockeye salmon spawning beaches (·) used for field studies of sculpin attraction to salmon eggs in Iliamna Lake, Alaska.
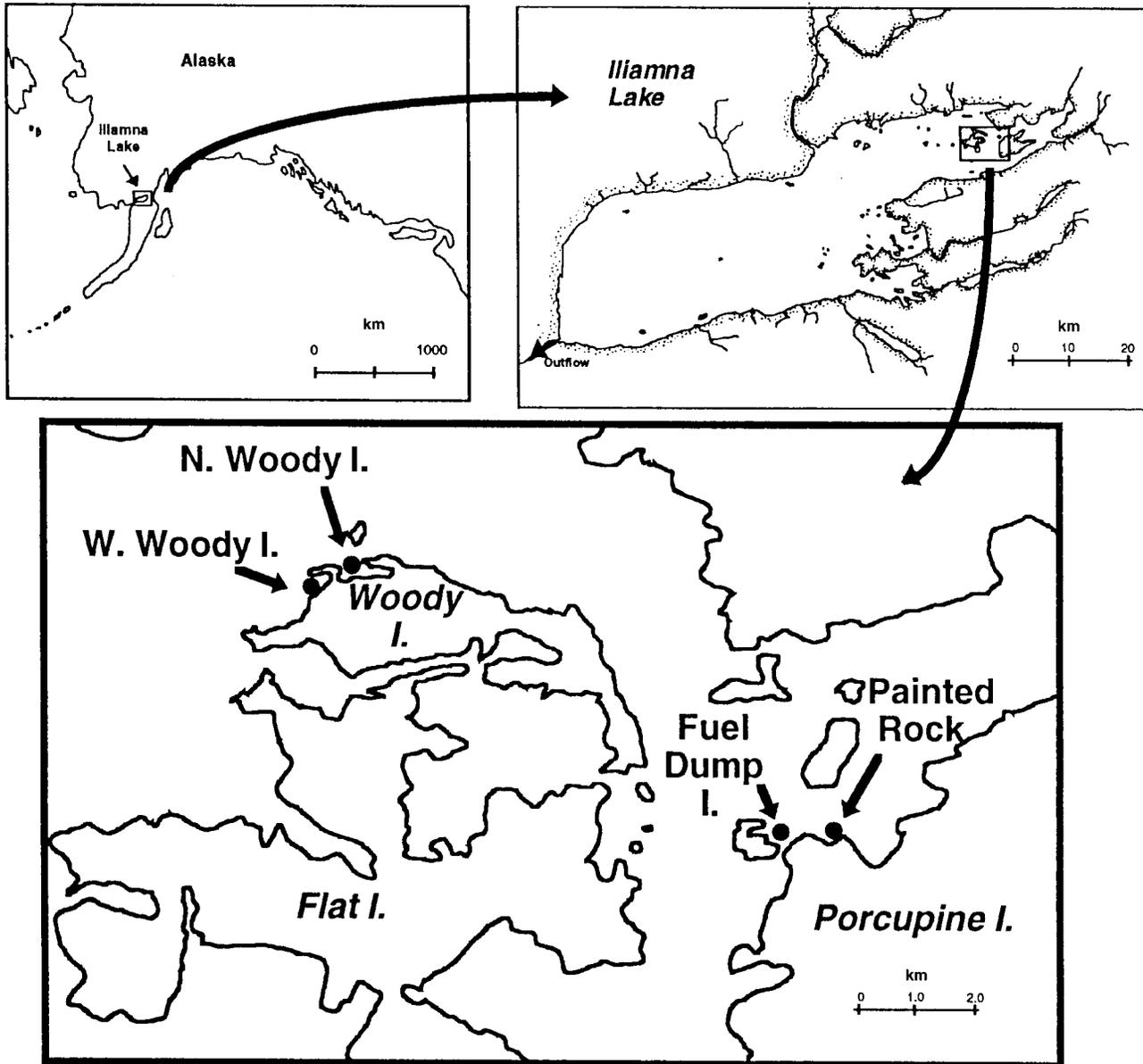
eggs, we tested whether sculpins were attracted to several test odours in three two-choice mazes (90×25 cm) similar to those described by Quinn and Busack (1985). All tests were conducted at the University of Washington's Porcupine Island field camp (see Fig. 1), using coast-range sculpins captured prior to sockeye spawning with egg-baited minnow traps at Fuel Dump Island beaches and maintained in net pens at the field camp. Fifty-four sculpins were tested for each test odorant and each sculpin was tested only once. Sculpins were not fed for at least 4 days prior to testing. Mazes were filled to a depth of 8 cm and received a constant flow of 1.5–2.0 L/min of Iliamna Lake water in each arm. Flow rates varied among mazes and test days, but were within 0.1 L/min of each other in all arms of a particular maze. Test odours were metered into one arm of each maze (1:1500 dilution) via a peristaltic pump. To initiate a trial, one sculpin was placed in the screened downstream section of each maze and allowed to acclimate for 4 min. After acclimation, the screens were lifted and fish were allowed to swim freely in the tank for 5 min. The first arm entered, final position, and time spent in each arm were recorded. Egg odours were prepared by soaking 20 mL of eggs in 100 mL of lake water. We tested both ovulated and unovulated eggs as odour sources to determine if chemical attractants emanating from eggs are present only at specific developmental stages. We also tested ovarian fluid as an attractant to determine if the sculpins' attraction to eggs might be due to odours associated with residual ovarian fluid from the spawning. Ovarian fluid was collected from ovulating sockeye females, diluted 1:20 with lake water, and metered into mazes as described above. After testing, each sculpin was anesthetized (MS 222), its mass and length were determined, and it was placed in an aerated bucket to recover. To ensure that test fish would eat salmon eggs, 6 eggs were dropped into the bucket after the fish recovered from anesthesia, and the number of eggs consumed after 10 min was recorded. Sculpins were released at the end of the trial.

Fig. 2. Schematic diagram of a representative baited-trap experiment to determine the sensory cues involved in sculpin attraction to salmon eggs. Data are from 16 minnow traps set on one of the west Woody Island beaches on August 3, 1994. Numbers in parentheses are the total numbers of coastrange and slimy sculpins captured in each trap. Treatments were as follows: E, free eggs; V, eggs enclosed in intact clear Ziploc bags (visible/odours absent); V/O, eggs enclosed in clear, perforated Ziploc bags (visible/odours present); O, eggs enclosed in black, perforated Ziploc bags (not visible/odours present).

V/O (149)	V (1)	O (171)	E (104)	O (65)	V (21)	V/O (46)	E (218)
O (187)	E (99)	V (6)	V/O (95)	V/O (171)	E (99)	O (109)	V (6)

m

0   5   10

Data analysis

To control for any possible treatment differences between beaches or days in the field portion of this study, the six trapping sessions were each treated as individual blocks with four replicates of each treatment. Differences between treatment groups were analyzed using Friedman's nonparametric randomized-block analysis of variance (Zar 1984). Multiple comparisons between treatment groups were analyzed by Tukey's procedure for ranked data (Zar 1984). Differences in sculpin numbers captured in empty and visible/odours absent traps were analyzed by the Mann–Whitney U test ($P = 0.05$). Differences in sculpin numbers captured in traps baited with presoaked eggs were analyzed by the Kruskal–Wallis test.

For Y-maze data, the first and last choices of all fish and the arm in which they spent the most time in response to odorant were compared with the 50:50 distribution expected by chance, using the χ^2 test. In all cases, departures from no preference were tested at the significance level $P = 0.05$.

Results

Over the course of the field experiment, coastrange sculpins dominated in numbers in egg-baited traps at all beaches (7375 individuals; 90.9% of fish captured) over slimy sculpins (689 individuals, 8.5% of fish captured). The differences in numbers of slimy and coastrange sculpins captured during this study probably reflect differences in abundance of the two species at Woody Island beaches rather than any bias associated with the sampling protocol (Foote and Brown 1997). Threespine sticklebacks, *Gasterosteus aculeatus* (38 individuals; 0.4% of fish captured), and Arctic char, *Salvelinus alpinus* (15 individuals; 0.2% of fish captured), were also occasionally captured in traps.

The number of sculpins attracted to traps was strongly dependent on treatment ($P < 0.001$). In particular, the total number of sculpins captured in visible/odours absent traps was dramatically lower than in traps with egg odours present (Fig. 2). For coastrange sculpins, eggs enclosed in perforated bags were less attractive than free eggs (95.7 ± 10.7 vs. 152.5 ± 14.9 sculpins/trap (mean $\pm$ SE); $P < 0.05$), indicating that enclosing eggs in bags may impair the release of sensory cues, visual or chemosensory (Fig. 3A). The numbers of coastrange sculpins captured did not differ between visible/odours present and not visible/odours present traps (95.7 ± 10.7 vs. 90.7 ± 11.8 sculpins/trap, $P > 0.5$), suggesting that visual cues are not required for detecting eggs if odours are present. However, attraction to eggs did require chemical cues emanating from

the eggs, as demonstrated by the dramatically lower numbers of sculpins attracted to visible/odours absent vs. visible/odours present traps (5.2 ± 1.1 vs. 90.7 ± 11.8 sculpins/trap, $P < 0.001$; Fig. 3A). The numbers of slimy sculpins captured did not differ between free eggs, visible/odours present, and not visible/odours present traps (8.0 ± 1.0, 9.9 ± 1.3, and 9.2 ± 1.6 sculpins/trap, respectively, $P > 0.5$; Fig. 3B). The number of sculpins attracted to visible/odours absent traps (1.6 ± 0.4) was lower than for all other treatments ($P < 0.001$), again suggesting a requirement for chemical cues emanating from eggs (Fig. 3B). Chemical cues may also have been important in attracting Arctic char to egg-baited traps. Char were captured in free egg (6 fish), not visible/odours present (5 fish), and visible/odours present (4 fish) traps, but never in visible/odours absent traps. There was no apparent effect of treatment on the number of threespine sticklebacks captured in traps, and sticklebacks were frequently caught in unbaited traps.

To further ensure that visual cues were not involved in attracting sculpins to eggs, eight pairs of empty or visible/odours absent traps were set on spawning beaches at Woody Island, Fuel Dump Island, and Painted Rock (see Fig. 1). At all sites there was no difference in the numbers of sculpins captured in empty traps versus traps in which eggs could be seen but not smelled or tasted (slimy sculpins: 1.0 ± 0.4 vs. 1.4 ± 0.5; coastrange sculpins: 0.2 ± 0.2 vs. 0.3 ± 0.3; $P > 0.5$). These results indicate that sculpins respond to traps baited with eggs that can be seen but not smelled as if they were empty traps.

Presoaking the salmon eggs prior to setting traps on spawning beaches ($n = 4$ traps/treatment) resulted in a dramatic decline in their attractiveness to sculpins ($P < 0.005$; Kruskal–Wallis test). Traps baited with eggs presoaked for 12 and 24 h were no longer attractive (6.3 ± 1.6 and 4.5 ± 1.4 sculpins/trap, respectively), and after a 4-h presoak the numbers of sculpins captured was 4-fold lower (22.0 ± 2.3 sculpins/trap) than in traps baited with fresh eggs (95.0 ± 4.3 sculpins/trap).
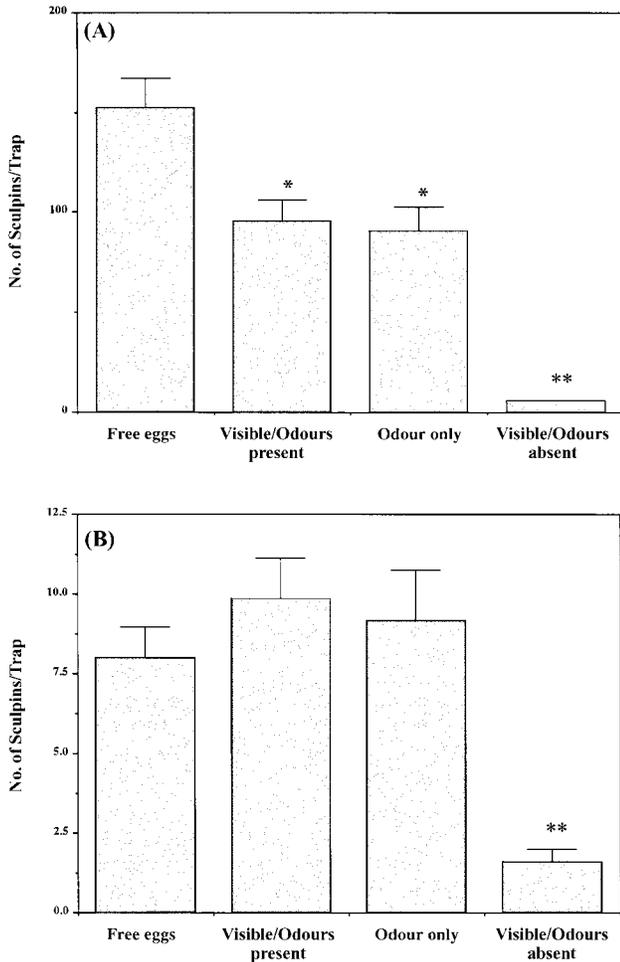
As an initial step in characterizing the chemical attractants that emanate from salmon eggs, we conducted attraction experiments in two-choice mazes, using coastrange sculpins captured on salmon spawning beaches and maintained in the laboratory. We first tested behavioral responses to water containing unovulated sockeye eggs because unovulated eggs were used to bait traps in the field component of the study. As indicated by the first arm entered, sculpins preferred the arm of the maze scented with lake water containing unovulated eggs to lake water alone ($n = 54$; χ^2 test, $P = 0.01$; Fig. 4).

Table 1. Behavioural responses of coastrange sculpins to water scented with salmon eggs and ovarian fluid.

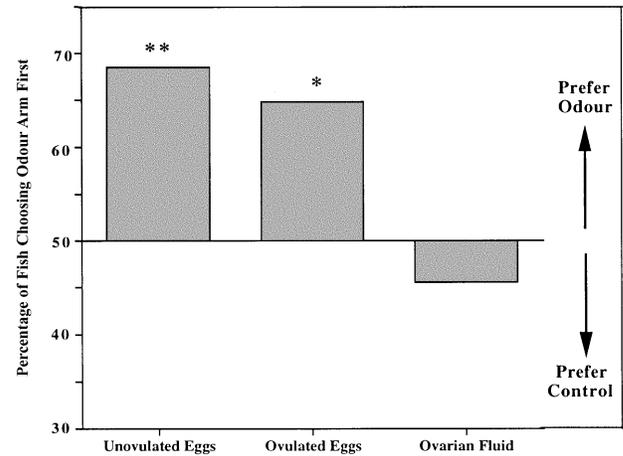| Odour tested	First arm entered		Final position		Time preference	
	Odour	Control	Odour	Control	Odour	Control
Unovulated eggs	37*	17	19	21	25	29
Ovulated eggs	35*	19	21	16	27	17
Ovarian fluid	25	29	21	26	25	29

Note: Data represent the responses of individual fish. "Odour" denotes the arm scented with lake water containing odour and "control" denotes the arm scented with lake water. Only for the first arm entered were there significant departures from the 50% level of no preference (*, $P = 0.05$). Note that the sum of the position numbers is not 54 because some fish were in neither arm at the end of the trial.

Fig. 3. Numbers (mean ± SE) of coastrange (A) and slimy (B) sculpins captured per trap for each treatment. Differences between treatments were analyzed by Tukey's procedure for ranked data ($P = 0.05$); *, significant difference from free eggs; **, significant difference from all other treatments. Note that the y axes have different scales.

Fig. 4. Behavioral responses of coastrange sculpins to water scented with salmon eggs and ovarian fluid. Data are percentages of fish that entered the arm scented with odorant first. Fifty-four sculpins were tested with each odorant. Significant departures from the 50% level of no preference are indicated by one ($P < 0.05$) or two ($P < 0.01$) asterisks.

from egg material (Fig. 4). When presented with salmon eggs after the Y-maze trial, 90.1% of the sculpins ate at least one salmon egg, and the mean number of eggs consumed by all fish was 4.4 ± 0.3 out of 6 eggs offered. These results indicate that any negative results we observed (e.g., no attraction to ovarian fluid) were not due to a lack of motivation to eat salmon eggs. For all odour treatments, final position and time spent in each arm did not differ from a response of 50:50 no preference (Table 1).

Discussion

Previous studies of sculpin feeding behaviour indicated that prey detection is mediated by either visual cues (Neverman and Wurtsbaugh 1992; Miller et al. 1992) or lateral-line detection of prey items (Hoekstra and Janssen 1985). In this study, we demonstrated that coastrange and slimy sculpins use chemosensory cues to locate and feed on sockeye salmon eggs spawned on island beaches in Iliamna Lake. In the absence of odours, sculpins were not attracted to salmon eggs in our minnow traps. When odours were present, sculpins were attracted to immobile eggs in minnow traps, indicating that mechanosensory cues were not required for attraction to prey. These results confirm Savino and Henry's (1991) hypothesis that sculpins must use other senses besides the lateral-line

Using the same measure of attractiveness, lake water scented with ovulated eggs was also attractive to sculpins when tested against lake water alone ($n = 54$; χ^2 test, $P = 0.03$; Fig. 4). Sculpins demonstrated no tendency to enter the arm scented with ovarian fluid versus the lake water control arm ($P = 0.18$), suggesting that the attractive substances are derived directly

system for egg predation (e.g., touch, chemoreception, vision). Our results also indicated that sculpins do not rely on visual cues to locate eggs. Indeed, traps baited with eggs that could be seen but not smelled were no more attractive than empty traps.

Although our study did not specifically address the chemoreceptor system used to detect eggs (i.e., olfaction, taste, solitary chemosensory cells), we hypothesize that this behaviour is olfaction-based (at least for the initial stages of the search). Definitive assignment of egg detection and attraction to the olfactory system will require sensory-ablation studies or physiological testing of the olfactory and other chemoreceptor systems. However, Kleerekoper (1969) suggested that most long-distance chemosensory-directed behaviours of fishes are due to olfaction, and Pavlov and Kasumyan (1990), reviewing the involvement of sensory systems in feeding, concluded that chemosensory attraction to prey items over 1.0 m away generally involved olfaction. Although we did not systematically study the distance from which sculpins could be attracted to eggs, we can estimate this distance on the basis of the average density of sculpins and the mean number of sculpins captured per trap. On August 4, 1994, we captured 196.8 ± 22.5 sculpins in traps baited with free eggs on the north Woody Island spawning beach. While we did not measure sculpin densities in our study, Foote and Brown (1997) reported densities of 4–6 /m^2 on the same beach in early August 1992, and sculpin densities were lower in 1994 (C. Foote, personal observation). If we conservatively assume that all sculpins close enough to detect egg odours were captured in the trap and that odours emanated from eggs purely by diffusion in all directions, we estimate that all sculpins within an area of 39.4 m^2 were captured, which translates into attraction from a distance of at least 3.5 m from the odour source. On one occasion we observed a sculpin swimming directly to a baited trap from at least 10 m away. For a large sculpin, this translates into a distance of over 100 body lengths. Long-distance attraction to eggs was also suggested by Savino and Henry (1991), who found that slimy sculpins found and ate eggs of lake trout, *Salvelinus namaycush*, even though the eggs were present at very low densities.

Location of prey items by fishes involves a stereotypical sequence of behaviours. Wunder (1927) defined three stages of feeding behaviour: (1) an initial period of arousal when the prey is detected; (2) a search phase to locate the prey item; and (3) uptake and ingestion of the prey. Each of these phases of predation may be mediated by either distinct sensory systems or combinations of sensory systems. Our results indicated that chemosensory cues are sufficient for arousal and location of eggs but do not preclude the involvement of other sensory systems at any stage of feeding behaviour. Initial detection of and attraction to eggs may involve the olfactory system, but other senses (e.g., taste, touch, vision) may be more important as sculpins near their prey. For example, sculpins in Lake Iliamna are attracted to the digging actions of female salmon during redd construction (Foote and Brown 1997). Sculpins are able to locate the source of vibrations transmitted through the substrate with both the ear and the lateral-line system (Janssen 1990; Whang and Janssen 1994), and the sounds associated with nest excavation may facilitate egg predation by attracting sculpins to salmon nests. Furthermore, our study did not address the final stage of feeding because sculpins were not allowed to feed on eggs inside baited traps. Chemosensory cues may be required for locating salmon eggs over long distances, but actual feeding may require visual cues also. During the feeding trials in this study, sculpins often turned their eyes to "look" at eggs before consuming them, and Foote and Brown (1997) reported that sculpins attempted to feed on eggs presented to them in a glass tube.

The involvement of other sensory cues during some phases of egg predation may also explain the results of our Y-maze experiments, which showed no consistent pattern in final position or time spent in each arm. Sculpins are sedentary, and generally poor swimmers (Greenberg and Holtzman 1987; Morgan and Ringler 1992). Typically, when the screens were lifted in the Y-maze trials, sculpins would immediately and actively enter one arm of the maze. In most cases, after exploring one arm of the maze they would retreat and explore the second arm and so on. After a period of exploration, many of the sculpins would cease swimming for the duration of the trial. After the initial odour detection and search, sculpins may ultimately cease their food search in the absnce of additional stimuli to complete the feeding process.

Chemoreceptive detection of eggs may be a specialized form of feeding by some sculpins. Hoekstra and Janssen (1985) found that mottled sculpins did not consume immobile invertebrate prey and that chemical cues were ignored in the absence of mechanical stimuli. Our results also suggest that the ability of sculpins to detect and locate salmon eggs may be species-dependent. Enclosing eggs in perforated Ziploc bags apparently interfered with the ability of coastrange sculpins to locate eggs, but the number of slimy sculpins attracted to traps was not affected by enclosing eggs in perforated bags. These results suggest that slimy sculpins may be more effective than coastrange sculpins at using chemosensory cues to locate eggs.

Sculpins are usually nocturnal feeders (Van Vliet 1964; Broadway and Moyle 1978; Hoekstra and Janssen 1985) that prey primarily on motile benthic invertebrates and free-swimming zooplankton (McDonald et al. 1982; Hershey and McDonald 1985; Hoekstra and Janssen 1985; Hudson et al. 1995). Throughout much of the year, the lateral-line system may be an appropriate sensory system for detecting moving prey in the dark. However, mechanosensory or visual cues may not be adequate for detecting salmon eggs. Typically, spawning sockeye salmon on Iliamna island beaches deposit their eggs at a depth of 10–20 cm in the gravel (Leonetti 1996). In many cases, sculpins are located within the nest at the time of spawning, so eggs may be visually detected as they are released into the gravel (Foote and Brown 1997). After spawning, however, the eggs do not move and are likely invisible once they are buried in the spawning gravel.

Prior to the arrival of spawning salmon, sculpins appear to be in poor condition, suggesting that the ability to detect and utilize the egg resource may be important for subsequent growth and survival, particularly in Alaskan lakes, where the main growing season is relatively short (Foote and Brown 1997). However, this resource may only be available for a short period of time. Sockeye salmon spawning on island beaches have an extremely restricted spawning period, the majority of females completing spawning within 7 days (Quinn and Foote 1994; Hendry et al. 1995; Quinn et al. 1996). This resource is spatially limited as well, with salmon only spawning on certain beaches with appropriate egg-rearing habitat

(Leonetti 1996). Furthermore, females rapidly bury their eggs after spawning, and within hours after exposure to water, eggs water-harden, making them less susceptible to sculpin predation (Foote and Brown 1997).

In addition to the physical constraints that water-hardening confers on predation, we hypothesize that it may also limit the time during which chemosensory cues are available for locating salmon eggs. Most of the external components of salmon eggs are insoluble in water, and after water-hardening, eggs are thought to be relatively impervious to most compounds. In many cases, fishes seem unable to detect the odour of water-hardened eggs until just prior to the time of hatching (Myrberg 1966, 1975; Clary 1972). It is interesting to compare our results with those of Clary (1972) and Biga (1996), who seeded artificial salmon redds with fertilized water-hardened eggs but observed no attraction to these redds by slimy sculpins. In our study, traps baited with fresh eggs that were not yet water-hardened when placed in the water were attractive to sculpins. Traps baited with eggs presoaked for 12 or 24 h were no longer attractive, and after a 4-h presoak, the number of sculpins captured was 4-fold lower than in traps baited with fresh eggs. These result suggest that sculpins have only a limited time window for locating salmon eggs before they are no longer attractive.

To ensure that they are able to fully utilize the sockeye egg resource, sculpins apparently "predict" the arrival of spawning salmon in Iliamna Lake. Sculpin numbers rise dramatically on the spawning beaches days before the first spawning salmon settle on the beaches (Foote and Brown 1997). The mechanisms by which sculpins orient to spawning beaches at the appropriate time are not known. It is interesting to speculate that detection of spawning beaches by sculpins may be chemosensory-based as well. For example, lake trout may locate spawning reefs by using odours emanating from egg membranes and feces from the previous year's larval trout (Foster 1985). Once on or near the spawning beaches, sculpins may require further chemical cues emanating from eggs to facilitate the rapid detection of this temporally and spatially restricted resource.

The ability to rely exclusively on chemosensory cues to locate salmon eggs was demonstrated in our experiment, where substantial numbers of free unmanipulated sculpins in sockeye spawning areas entered minnow traps baited with eggs that could be smelled but not seen. This was also suggested by other field data which showed that more than twice as many sculpins were found in sockeye nests with eggs than in those without, and that sculpins were often found in the egg pockets of buried nests (Foote and Brown 1997). To our knowledge this is the first demonstration of a fish predator utilizing chemosensory cues to locate eggs. Indeed, chemoreceptor detection of eggs by fish has only been reported for a few species (Fitzgerald and van Havre 1987; Smith and Whorisky 1988; Reeb and Colgan 1992). Salmon eggs seem particularly unlikely as an odour source because most of their external components are insoluble in water, and water-hardened eggs are thought to be impermeable to most compounds (Heming and Buddington 1988) and presumably release few identifying odorants. However, chemoattraction to salmonid eggs has been reported for zoospores of the fungus *Saprolegnia diclina*, a fish egg pathogen, suggesting that live eggs do release recognizable chemical compounds (Rand and

Munden 1993). A number of arthropod-egg predators (e.g., parasitic wasps) are known to "eavesdrop" on pheromonal signals emitted by mating males and females to locate recently laid eggs (Stowe et al. 1995). We had hypothesized that residual ovarian fluid, a source of salmon pheromones (Emanuel and Dodson 1979) and a strong olfactory stimulant for a number of fish species (Hunter and Hasler 1965; Emanuel and Dodson 1979; Resink et al. 1989), associated with recently spawned eggs might allow sculpins to detect eggs by eavesdropping. However, our results suggest that the egg chemoattractant is derived directly from egg material, because ovarian fluid was not attractive to sculpins.

The chemical nature of the egg chemoattractants remains unclear. In general, feeding stimulants for fish are usually of low molecular weight, nonvolatile, nitrogenous, and amphoteric (Jones 1992). In their study of *S. diclina* zoospores, Rand and Munden (1993) found that the zoospores were attracted to the amino acids arginine and alanine, and hypothesized that these compounds were released from salmon eggs. Amino acids have been shown to stimulate feeding in a number of fish species (Jones 1992). Interestingly, the amino acids alanine and serine are potent odorants and feeding stimulants for Arctic char (Jones and Hara 1985), and these fish also seemed to be attracted to egg-baited traps on the salmon-spawning beaches. To facilitate fertilization, a number of species produce eggs which release specific peptides that are chemoattractants for sperm (Brokaw 1990; Yoshida et al. 1993). Eavesdropping by sculpins on sperm chemoattractants could play a role in salmon egg location.

Chemosensory-mediated detection of eggs has been described in nest-building fish species that provide some form of parental care. During cannibalistic attacks, female threespine sticklebacks use olfactory cues to discriminate between their own eggs and those of other females (Fitzgerald and van Havre 1987; Smith and Whorisky 1988). Similarly, odours emanating from eggs elicit fanning behavior in nesting convict cichlids (*Cichlasoma nigrofasciatum*) (Reeb and Colgan 1992). It is interesting to note that slimy sculpins are also polygynous nest builders and males fan and protect eggs in the nest (Van Vliet 1964). Furthermore, freshwater sculpins are thought to be egg cannibals, feeding on their own eggs or those of other males (Goto 1993). Therefore, chemosensory egg detection and predation on salmonid eggs may have evolved from adaptations associated with reproduction and parental care.

Acknowledgments

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