Sculpin Predation on Lake Trout Eggs in Interstices: Skull Compression as a Novel Foraging Mechanism

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Lake Trout (Salvelinus namaycush) spawn in fall and hatch in spring; to protect their eggs over the winter they spawn on rocky reefs, where the eggs settle deeply into interstices. Uptake of water swells the eggs, further protecting them by lodging in crevices. Freshwater sculpin (Cottidae), the primary predator of salmonid eggs, are small, benthic fishes with malleable bodies and large heads. To acquire the lipid-rich resource contained in eggs, sculpin must penetrate deeply into interstices, and have a method to extract lodged eggs. We placed Slimy Sculpin (Cottus cognatus) into a tunnel containing a sequence of funnels with progressively smaller openings to determine the smallest hole they could enter. Forty-three of 138 Slimy Sculpin (31%) moved through openings up to 19.7% smaller than the maximum width of their head, indicating that they compressed their skull to move through the opening. We examined egg acquisition behavior by placing Lake Trout eggs into holes drilled in a Plexiglass plate. Holes varied in diameter from 5.6 to 8.7 mm, and were either shallow (5 mm) or deep (9 mm); after water hardening, eggs were lodged in the smallest holes and loose in the larger holes. Sculpin consumed eggs in the large, shallow holes first, then used suction to extract eggs from small, shallow holes. To extract eggs from small, deep holes, they used a sequence of suction attempts to draw the eggs upward. Sculpin are highly adapted to forage on Lake Trout eggs, including the novel capacity to compress their skulls to access eggs.

SUCCESSFUL acquisition of prey by predators involves a sequence of steps, including prey detection, recognition, approach, capture, handling, and ingestion. For acquiring prey that are hidden in crevices, the processes of detection and capture are particularly challenging; predators may require a non-visual means for detecting the prey, and a specialized method for extracting prey. Some fishes are particularly well equipped for crevice feeding because of their capacity to use suction. Fishes have a range of feeding modalities, including ram, suction, and biting, but the majority of teleosts use suction feeding (Norton, 1991; Gerking, 1994; Westneat, 2005). Suction feeding involves a complex set of movements of bones in the skull, maxillary apparatus, mandible, operculum, and hyoid apparatus that expand the buccal cavity and draw a current of water, with the prey, into the predator’s mouth. This method is highly adaptable, and is used by pelagic predators that chase mobile prey (fish or plankton), by detritivores to pull sediments into the mouth, and by benthic foragers to extract attached or hidden prey (Gerking, 1984; Ferry-Graham et al., 2002). Suction feeding is the primary feeding mode used by benthic predators such as sculpins (Cottidae) for capturing sessile species (Norton, 1991, 1995). Suction or biting are the only strategies possible to acquire prey within interstitial spaces, where movement of the predator is highly limited.

Predation on eggs is a relatively simple problem for a fish predator. Eggs are immobile, usually present in high abundance within a short period after spawning, of fixed configuration (spherical), of approximately fixed size (for one species of fish), easy to process, and offer a high reward in terms of lipid energy. The challenges for the predator are to be in the right place at the right time (i.e., at a spawning site during or after spawning takes place), and have a gape sufficiently large to ingest the egg. The reproductive behavior of fishes must therefore include some strategy for minimizing predator access to their eggs—by scattering them (pelagic and broadcast spawners), guarding them (nest builders or cavity spawners), burying them (redd-builders), or hiding them. Lake Trout hide their eggs using two strategies: (1) spawn in late fall, so that although the egg develops very slowly, predator metabolic rates have also slowed down and their nutritional and energy needs are low (e.g., Fitzsimons et al., 2006); (2) deposit eggs on rocky reefs with open interstices, so that the eggs, which are negatively buoyant, will essentially bury themselves. In a separate study, we found that Lake Trout eggs can penetrate interstices in cobble substrates (mean diameter 12 cm) to at least 1 m. Water hardening adds protection by lodging some eggs into crevices. For predators to obtain eggs ‘concealed’ and entrained into interstitial spaces, they must overcome the challenge of moving into proximity to the eggs through a matrix of rocks.

Few studies have examined strategies for acquiring immobile prey that are deeply hidden in interstitial spaces. Many fish will pick at prey in crevices, dislodging small rocks or shells to access prey underneath them (Shibuno et al., 1994; Jensen, 2005), or burrow into soft sediments or sand to obtain prey detected by vibrations or electromagnetic cues (Kalmijn, 1971; Janssen, 1990), but few non-anguilliform fishes penetrate small, rocky interstices with their entire body. Acquisition of fish eggs in interstitial spaces presents a particular challenge for predators: the eggs are motionless, and therefore not detectable by visual cues or the lateral line (at least until the embryo begins to move within the egg). There is no reaction distance for the prey, and no probability of escape by moving, but for large eggs or small predators, gape may be a limiting factor in acquisition.

The interaction between Lake Trout (Salvelinus namaycush) and their major egg predator, sculpins (Cottus spp.) is interesting in the context of predator–prey dynamics. Lake Trout spawn in fall and eggs incubate over winter, so the eggs are vulnerable to predation, and defenseless, for almost six months. Their large eggs provide a lipid-rich, highly digestible, passive prey throughout the forage-limited winter months. To protect their eggs, Lake Trout spawn on cobble...

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© 2014 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CE-14-016 Published online:

Copeia 2014, No. 4, 000–000
reefs with deep interstitial spaces; the eggs are negatively buoyant, and settle rapidly into interstitial spaces. There, they are protected from water turbulence and from predation by all but the smallest species (Fitzsimons et al., 2007). Sculpins can penetrate interstitial spaces due to their small body size and flexibility (Martin and Olver, 1980; Claramunt et al., 2005; Fitzsimons et al., 2006). Sculpins theoretically have a window of body sizes that is optimal for foraging onLake Trout eggs; an individual must have a gape large enough to engulf an egg, but a head small enough to access eggs in interstices. For example, Biga et al. (1998) found fewer sculpins, and fewer eggs in sculpin stomachs, in smaller substrates. Freshwater sculpins have large, flattened heads and tapering bodies, so their largest dimension is head width.

When eggs are extruded from a female Lake Trout they are soft and fairly malleable; they immediately begin to adsorb water until the chorion limits further uptake, at which point the egg is turgid and is termed 'water hardened.' Eggs are fully water hardened in 20–120 min, depending on ambient water hardness; if this process occurs after the egg has fallen into a crevice between hard surfaces, the eggs become firmly lodged. To acquire these eggs, sculpin must be able to detect an egg, work its body through the maze of connected interstitial spaces to approach the egg, and then extract it from the crevice in which it is lodged. Vision and the lateral line are of no use in detecting a motionless, non-breathing prey, but smell may be useful; sculpin appear to use chemical cues to locate salmon eggs in shoreline habitats (Dittman et al., 1998; Foote and Brown, 1998). A highly flexible and malleable body morphology facilitates access to eggs through penetration of interstices. Acquiring the egg is the final challenge; eggs are spherical and smooth, making them difficult to grasp and pull—they must be engulfed by getting the mandible and maxillary past the widest part of the circumference. If the egg is lodged, suction may be the only method available to a fish in order to extract the egg. Chotkowski and Marsden (1999) determined in laboratory experiments that 42 mm standard length (53 mm total length) was the minimum size of Mottled Sculpin (Cottus cognatus) that has a gape sufficiently large to engulf an egg; however, Fitzsimons et al. (2002) found eggs in sculpin as small as 43 mm total length in the field, but did not specify whether the species was Mottled Sculpin or Slimy Sculpin (C. catus). Slightly smaller sculpin will vigorously ‘attack’ and engulf an egg, but because they lack the force to crush the egg, the egg is eventually spit out, and the process of acquisition is repeated several times (Marsden, pers. obs.).

The goal of this study was to understand the interaction between the Lake Trout reproductive strategy of ‘hiding’ their eggs, and the prey capture abilities of their major predator, sculpins. The study was stimulated in part by observation of Mottled Sculpins captured in Lake Trout emergent fry traps (unpubl. obs.). The capture bottle on emergent fry traps contains a funnel with an opening 12.5 mm in diameter; the funnels are sometimes equipped with a wire or plastic chord across the center of the opening to exclude predators (Marsden et al., 1988). We have found sculpin up to 74 mm total length (TL) in these traps, with head diameters up to 13.5 mm, clearly larger than the trap opening. Apparently, the sculpins must be distorting their heads in order to squeeze into the narrow opening. We used laboratory behavioral trials to determine the relationship between sculpin head size and the smallest opening into which an individual can squeeze, and to describe egg acquisition behavior by sculpins.

METHODS AND MATERIALS

Slimy Sculpin were collected from Browns River, VT, using a backpack electroshocker. Sculpin were housed in a 150 L aquarium with constant aeration and filtration; water temperature was maintained at 8.2°C with a chiller. Eggs were obtained from Lake Trout collected in Lake Champlain during late fall in trap nets; eggs were expressed from ripe females, kept dry to prevent water hardening, and stored prior to use at 5°C. All trials were conducted within seven days of egg collection. Fish were collected under a Vermont Department of Fish and Wildlife collection permit; laboratory work was conducted under UVM IACUC protocol 12-014.

To determine the smallest space into which a Slimy Sculpin can maneuver, a cylindrical ‘tunnel trap’ was constructed with a series of eight compartments, each 15 cm long, separated by funnels of decreasing diameter (25.4 mm, 22.2 mm, 19.1 mm, 15.9 mm, 12.7 mm, 9.5 mm, 6.4 mm, and 3.2 mm. A 150 L aquarium was partitioned, with the tunnel mounted in the partition, allowing entrance to the tunnel on the end with the largest funnel. The tunnel was then covered with rocks to provide a semi-darkened environment and visually isolate the sculpins from outside disturbance. Slimy Sculpin were placed on the side of the aquarium with access to the tunnel opening. After initial one-day trials with and without bait, we found that sculpin explored the tunnel ‘maze’ without the stimulus of bait; similar to their behavior in the holding tank, they tended to cluster in groups of five or more individuals, usually in close physical proximity to each other and/or in crevices. For the trials, Slimy Sculpin were left for three days in the aquarium. A maximum of 34 Slimy Sculpin were given access to the tunnel at one time; we tested a total of 138 Slimy Sculpin in the tunnel trap, with an average total length of 66.3 mm ± 11.9 SD (range 36.8–90 mm TL) and average head width of 11.6 mm ± 2.3 SD (range 6.3–17.1 mm). After the three-day period, Slimy Sculpin were removed from each section of the tunnel and the compartment in which each individual was found was recorded. All Slimy Sculpin were alive and showed no visible signs of stress (e.g., lethargy, low response to handling, skin infections) when retrieved from the funnel. Slimy Sculpin were lightly anaesthetized with clove oil in order to measure total length and maximum horizontal and vertical width of the head. Head width was measured by gently closing a caliper over the widest part of the head until it was in contact with the closed operculae (Fig. 1); we did not attempt to squeeze the head. To evaluate accuracy of our morphometric measurements, we measured total length and maximum head width of 12 anaesthetized Slimy Sculpin five times, with each Slimy Sculpin measured once in sequence to minimize potential for repetitive measure bias. Regression was used to determine how closely head width was related to total length. Sculpin foraging behavior to acquire eggs was observed using eggs in artificial ‘crevices.’ Sixteen holes were drilled in a grid pattern into a 15 × 15 cm square plate of 1.3 cm thick Plexiglas. The holes were 5.6 mm, 6.4 mm, 8 mm, and 8.7 mm in diameter, and either 5 mm or 9 mm deep; each diameter:depth combination was used twice. A single ‘dry’ egg was added to each hole, and allowed to water harden. Although Lake Trout eggs are nominally 4.6 to 5.7 mm in
diameter (Piper et al., 1982), we discovered that eggs would not fit in the smallest holes. After hardening, eggs were fully lodged into the 6.4 mm holes, but were loose within the larger holes. A single plate containing eggs was placed in the bottom of a 19 L aquarium, and four Slimy Sculpin were added. Each Slimy Sculpin had previously been starved for 48 hr. Missing eggs were recorded at intervals of 5 min; initial observations indicated that Slimy Sculpin fed vigorously for 1 hr, then took eggs infrequently thereafter, so observations were discontinued after 1 hr. Each sculpin was measured (total length and maximum head width) as before, after each trial; a total of eight trials was completed using a total of eight Slimy Sculpin, with each Slimy Sculpin used four times. During each trial, Slimy Sculpin foraging behavior was observed to determine how eggs were acquired.

RESULTS

Forty-three (31%) Slimy Sculpin moved through funnels smaller than the maximum width of their head, indicating that they compressed their skull to move through the opening (Fig. 2). The maximum difference between the hole diameter and head diameter was 19.7%. Maximum error (i.e., difference between smallest and largest measurements) of repetitive measures of Slimy Sculpin was 1.0 mm (average 0.5 mm) for total length and 1.9 mm (average 0.7 mm, or 5.7% of head width) for maximum head width. Total length was closely correlated with head width ($R^2 = 0.89$).

In foraging trials, the eight Slimy Sculpin averaged 79.8 mm TL (range 71–90 mm). Sculpin foraging on plate arrays consumed an average of 8.9 of the 12 eggs available in the first hour (range = 4–12). Sculpin explored each plate prior to and during foraging; they did not tend to consume the egg nearest to the last egg consumed (i.e., there was no bias toward adjacent eggs). Eggs from the shallow holes of all diameters were consumed first; there was sufficient space between the egg and the sides of the large holes so that Slimy Sculpin were able to grasp the eggs, whereas they appeared to use suction to remove eggs from the smallest (6.4 mm) holes. Once all eggs from the shallow holes were consumed, Slimy Sculpin began to remove eggs from the deep 6.4 mm holes, then from the larger holes at random (Fig. 3). To acquire the deep eggs, Slimy Sculpins used a series of two to four suction attempts; in the smallest diameter holes, the egg was pulled upward by each suction, then lodged at the new depth, so that the egg eventually reached the surface of the plate and was consumed. Eggs from the larger diameter holes needed to be raised by suction, followed by a ‘grab’ as the egg came within reach and before it fell back into the hole; multiple attempts were usually needed before the egg was seized.

DISCUSSION

The present study shows that Slimy Sculpin have the remarkable ability to facilitate their movement into interstices by compressing their heads up to 19.7%, allowing for entrance into openings smaller than the maximum width of their head. Benthic cottid species mostly have highly flexible bodies which allow maneuverability in tight spaces,
but their large heads would, without compression, limit access to prey located in deep interstices. We have observed Slimy Sculpin penetrate cobblestones stacked to 1 m deep, ‘following’ Lake Trout eggs. Fish skull functional morphology and feeding kinetics have been thoroughly studied (e.g., reviews by Ferry-Graham et al., 2002; Westneat, 2005). However, to our knowledge the ability to contort the skull morphology to allow skull compression has not previously been observed. Skull compression is clearly facilitated by the same complexity of fish skull morphology and mobility of bones that also allows suction feeding, in which multiple bones are moved to expand portions of the head (Westneat, 2005). The ability of sculpin to obtain eggs in crevices is highly advantageous, as it gives them access to interstitial invertebrate prey and to a spatially concentrated, energy-rich egg supply throughout the winter months when other food resources are scarce.

Slimy Sculpin in our trials appeared to minimize the effort to acquire eggs. All food items were of roughly equal energetic value. The easiest eggs to acquire, those that were loosely contained in large, shallow holes, were taken first, followed by eggs lodged in small, shallow holes (Fig. 3). Eggs in deep holes were more challenging for sculpins to acquire in our experimental trials. The holes were all too small to allow the sculpin to insert their heads to grasp the eggs. Acquisition of lodged eggs was facilitated by suction feeding; Slimy Sculpin were able to draw eggs out of deep ‘crevices’ using repeated suction attempts. Eggs in large, deep holes could drop back into the hole, so the eggs in small, deep holes that could be drawn upward in stages appeared to be easier to acquire, and were mostly taken before eggs in large, deep holes. Minimizing handling time is a component of optimal foraging, in which predators optimize the trade-off between energy spent acquiring prey and energy obtained from prey (Werner, 1974; Werner and Hall, 1974). Because suction feeding entails expansion of the buccal cavity, presumably Slimy Sculpin can only access eggs in interstices in which the Slimy Sculpin has space for head expansion, unlike in our foraging arenas.

The question of how Slimy Sculpin detect eggs that are hidden in crevices remains unanswered. Egg deposition by Lake Trout occurs over a fairly short time period (weeks; Martin and Olver, 1980), and is focused in relatively small areas (spawning reefs may be as small as a few hundred square meters; e.g., Marsden et al., 2005). The high density of eggs, milt, ovarian fluid, and even spawning fish generate substantial chemical cues. Sculpins are attracted to chemical cues from concentrated groups of salmonid eggs, as found in redds of stream-spawning species (Mitra and Chivers, 2002; Quinn et al., 2012). Lake Trout eggs, however, are scattered widely across spawning reefs and settle more deeply within substrate, resulting in lower densities of eggs; the ability of Slimy Sculpin to detect single eggs has not been examined.

Sculpin are clearly highly adapted to benthic foraging on large eggs. Their slender, malleable body is well suited for exploring the maze of interconnected interstitial spaces in rocky reefs, and behaviorally they are highly thigmotactic; they are generally found in small spaces. However, consumption of large salmonid eggs requires a large gape. Sculpin have ‘solved’ the problem of acquiring large prey in small spaces by evolving a large head that is also malleable, so that they can access eggs. In spaces where there is room to expand the head but an egg is lodged in a deep crevice, repeated suction attempts allow Slimy Sculpin to draw eggs out.

ACKNOWLEDGMENTS

We thank B. Ladago for assisting with collection of Slimy Sculpin and Lake Trout eggs, and with laboratory trials.

LITERATURE CITED


