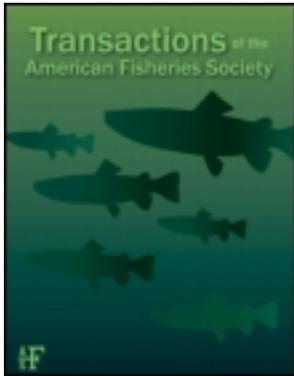


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Interspecific Resource Competition between the Invasive Round Goby and Three Native Species: Logperch, Slimy Sculpin, and Spoonhead Sculpin

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Abstract.—The invasive round goby *Apollonia melanostomus* (formerly *Neogobius melanostomus*) has negatively affected benthic fish communities throughout the Great Lakes. In this study, we compared the sensory physiology and behavior of three native species—slimy sculpin *Cottus cognatus*, spoonhead sculpin *C. ricei*, and logperch *Percina caprodes*—with those of the round goby to determine the mechanisms that allow the round goby to dominate native fish. The reaction and strike distances of the four species were examined during predator–prey trials using natural amphipod prey *Gammarus* spp. under varying light intensities (0–130 lx) to compare input from the mechanosensory lateral line and visual systems. Trials in the dark (0 lx) indicated that the sculpins and the round goby had similar lateral line sensitivity. However, all three native species had a significant advantage in reaction and strike distance over the round goby at higher light intensities. Interspecific resource competition was assessed by pairing a round goby with a native fish in an artificial stream. Round gobies gained significantly more weight than the native fishes during all trials. Slimy sculpins were able to maintain their weight in the presence of the round goby; however, spoonhead sculpins and logperch lost a significant amount of weight during the trials. These experiments indicate that although the round goby does not possess an inherent sensory advantage, it can dominate resources and outcompete native fish. Thus, round gobies may pose risks for a wide variety of native benthic fishes.

The round goby *Apollonia melanostomus*, formerly *Neogobius melanostomus* (Stepien and Tumeo 2006), is a benthic fish native to the Ponto-Caspian region of eastern Europe. It has spread rapidly throughout the Laurentian Great Lakes since its detection in the St. Clair River in 1990 (Jude et al. 1992; Charlebois et al. 2001). The natural history of the round goby places it in direct competition with native benthic species for food and habitat (Janssen and Jude 2001), and it has been implicated in the decline of native species such as the johnny darter *Etheostoma nigrum* (Lauer et al. 2004), mottled sculpin *Cottus bairdii* (Dubs and Corkum 1996; French and Jude 2001), and logperch *Percina caprodes* (Balshine et al. 2005). Recent evidence indicates that the round goby is colonizing offshore to water depths greater than 50 m (Schaeffer et al. 2005; Walsh et al. 2007) and may threaten deeper water sculpin species such as the spoonhead sculpin *C. ricei* and deepwater sculpin *Myoxocephalus thompsonii*.

Jude et al. (1995) hypothesized that the mottled sculpin was particularly vulnerable to the round goby invasion. These early predictions were supported when the mottled sculpin was extirpated, presumably by the round goby, from portions of Lake Michigan (Janssen

and Jude 2001). Colonization of former mottled sculpin habitat strongly suggests that the round goby can outcompete native species; however, the exact mechanism by which this is accomplished remains unknown. A combination of aggressive behavior, high fecundity, and resource competition by the round goby was attributed to mottled sculpin declines (Jude and DeBoe 1996; Charlebois et al. 1997; Janssen and Jude 2001; Jude 2001; Ray and Corkum 2001). Substantial dietary overlap for benthic arthropods between sculpins, darters, and juvenile round gobies (<60 mm) has been documented in various locations throughout the Great Lakes (Thomas 1997; French and Jude 2001; Carman et al. 2006; Lederer et al. 2006). Although larger round gobies (>60 mm) undergo an ontogenetic change in diet to sedentary bivalves (Jude et al. 1995; Ray and Corkum 1997; French and Jude 2001; Janssen and Jude 2001), in the absence of bivalves, larger fish may continue to compete for other benthic invertebrates (Thomas 1997; Janssen and Jude 2001; Skora and Rzeznik 2001; Carman et al. 2006; Lederer et al. 2006).

The underlying role of sensory systems that may provide the round goby with a competitive advantage remains to be determined. A pilot study by Jude et al. (1995) suggested the round goby had enhanced lateral line sensitivity in comparison with mottled sculpins. However, further characterization of the mechanosensory, visual, auditory, and olfactory systems remains to

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be completed to understand their role in mediating competitive interactions.

The current study describes a series of experiments conducted to determine the effect of the round goby on other native benthic species. Additionally, predator-prey trials compared the visual and mechanosensory systems of the round gobies and native fish species to determine what advantages, if any, the round goby may possess.

Methods

Collection and husbandry.—Round gobies and logperch were captured with baited (Berkley Power-Bait) minnow traps or a seine (15 × 2 m with 0.6-cm mesh) at three sites in the Duluth-Superior Harbor, Lake Superior: Park Point and Arrowhead Point, Minnesota, and Barker's Island, Wisconsin. Slimy and spoonhead sculpins were caught at depths of 30–120 m in bottom trawls near Stockton Island in the Apostle Islands, Wisconsin. Fish were transported from each location in coolers, and collection and transport mortality remained low (<5%) for each species.

Fish were segregated by species in laboratory aquaria at the University of Minnesota Duluth. All fish were placed into recirculating systems with mechanical, chemical, biological, and ultraviolet (UV) filtration and a 16 h light : 8 h dark cycle. Water temperature was maintained between 15°C and 20°C. Fish were fed no. 3 commercial trout pellets (Silver Cup Fish Feed) to satiation every 48 h. All fish were acclimated to the laboratory conditions for a minimum of 30 d before experimentation. All experiments conformed to the University of Minnesota institutional animal care protocols.

Behavioral interactions.—Artificial streams were constructed using three 2.4-m × 1.2-m × 0.3-m fiberglass tanks. Water depth was maintained at 17 cm, and each stream was lined with pea gravel and subdivided into eight cells (48 × 35 cm) using perforated Plexiglas partitions. Illumination was provided by 60-W incandescent bulbs and light intensity regulated from 100 to 130 lx across the water surface. Each cell was provided with a single 5-cm-diameter × 15-cm-long polyvinyl chloride (PVC) pipe for shelter. The water temperature and light-dark cycle were held constant at 15 ± 1°C and 16 h : 8 h, respectively. Flow rate was 5 L/min and each stream emptied into a communal reservoir. The reservoir water was sequentially treated with mechanical, biological, chemical, and UV filtration before being recirculated. Water quality data (ammonia, nitrate, nitrite, and pH) were collected weekly to ensure uniform conditions in each stream.

The fish were weighed individually at the start of each experiment and weekly thereafter. For weight measurements, fish were netted, placed on a paper

towel, carefully blotted to remove excess water, and then transferred to a Mettler balance and weighed to the nearest 0.1 g. Each trial was conducted for 21 d and the fish in each cell were given a ration of 50 mg of commercial fish pellets (no. 3 Silver Cup Fish Feed) per fish every other day. Intraspecific controls consisted of two fish of a single species placed in a cell, while the interspecific cells contained one native fish and one round goby. Similar-sized fish (7.2 ± 0.1 cm total length [TL] [mean ± SE], 3.76 ± 0.01 g wet weight) were placed in each cell to minimize size-biased dominance. Each fish was assessed during weekly measurements for physical damage (e.g., fin damage, skin lesions). If a fish exhibited any sign of injury or disease, it was removed and the trial for that cell discontinued. Fish that escaped a cell, died, or showed signs of injury or disease were considered "mortalities"; in these cases, the weight data from the remaining fish were not used. Survival percentage was calculated by the total number of fish from each species remaining alive in their original cell at the end of the 3-week trial divided by the number of fish of that species that started the trial. A small number of fish (<15%) were tested twice; however, all were returned to species-specific aquaria for 3 weeks before being used in another trial.

Predator-prey interactions.—Predator-prey interactions were conducted using the methods described in Richmond et al. (2004). Trials were conducted in a 27-cm-diameter aquarium with a water depth of 4 cm. The arena was surrounded by a 1-m × 1-m × 1.8-m opaque enclosure to shield fish from observers and eliminate extraneous light sources. A Sony Handycam digital video recorder (30 frames per second) with infrared capability was positioned 60 cm above the aquarium to record predator-prey interactions. Illumination was indirectly provided by four 100-W incandescent bulbs positioned 35 cm away from the water surface. Light intensity was controlled using a Powerstat variable transformer (Superior Electric, 3PN116C) and measured with a light meter (Sper Scientific Ltd., 840020). Light intensity was adjusted to 0, 5, 25, 50, or 130 lx (±1 lx) across the water surface. Water temperature of the experimental aquaria was maintained at 18°C.

Food was withheld 24 h before a feeding trial. Single fish were placed in the aquarium and allowed to acclimate for a minimum of 30 min. Amphipods *Gammarus* spp. (5.0 ± 0.1 mm TL) were loaded into the tip of a Pasteur pipette and inserted individually 1–2 cm below the water surface and opposite to fish location. If the amphipod was consumed, additional amphipods were added up to a maximum of 20 or until an amphipod remained uneaten for 20 min. If the fish reacted or orientated towards the amphipod during

TABLE 1.—Means \pm SEs for the wet weight (g) gained or lost (–) during the 21-d feeding trials. The number of trials is indicated in parentheses. Significant differences between the initial and end weights for each species and trial are indicated by asterisks (paired *t*-test: $P < 0.05$).

Trial	Slimy sculpin	Spoonhead sculpin	Logperch	Round goby
Intraspecific	0.1 \pm 0.2 (8)	–0.2 \pm 0.2 (8)	0.0 \pm 0.1 (8)	0.3 \pm 0.1* (7)
Interspecific	0.0 \pm 0.08 (28)	–0.4 \pm 0.09* (11)	–0.3 \pm 0.04 * (24)	0.2 \pm 0.08* (28) 0.5 \pm 0.08* (11) 0.4 \pm 0.05* (24)

insertion, the encounter was excluded from analysis. Five to ten fish of each species were tested at each light intensity.

The video recording of the predator–prey interactions was examined frame by frame with Windows Movie Maker (Microsoft) and all distances and angles calculated using ImageJ software (Scion Co.). All distances were measured (in centimeters) from the center of the amphipod to the mid-point of the fish's maxilla. Angles were calculated from the intersection of a line drawn through the longitudinal body axis of the fish and a line drawn from the center of the amphipod to the midpoint of the fish's maxilla. Reaction distance was defined as distance between fish and prey at the moment the fish orientated towards the prey. Strikes were defined as ballistic lunges by the predator that normally mediated prey capture, and strike distance was calculated at the onset of the attack. Strikes were considered successful if the amphipod was captured by the fish.

Statistical analysis.—The initial wet weights of each fish species in a trial were compared using paired *t*-tests to verify that there was no significant difference ($P > 0.05$) in weight between species. Therefore, the net weight gained or lost for fish was calculated at the end of each 21-d trial. The initial and end weights for each species were compared using paired *t*-tests to determine whether the weight changed during the trial.

Strike and reaction distance comparisons from predator–prey trials were performed with nonparametric tests because data often failed the tests for normality or equal variance. The reaction or strike distances for each species at each light intensity were compared using Kruskal–Wallis one-way analysis of variance (ANOVA) on ranks with subsequent Dunn's test for multiple comparisons. At each light intensity, the reaction or strike distance for each native species was compared with that of the round goby by Mann–Whitney rank sum tests.

Results

Behavioral Interactions

The artificial diet proved palatable and of sufficient nutritional value to maintain or increase fish weights

for all species throughout captivity for at least 1 year. During intraspecific trials, slimy sculpins showed a small weight gain, logperch maintained weight, while spoonhead sculpins showed a slight weight loss. However, none of the final weights were significantly different from the initial weights (paired *t*-test: $P > 0.05$; Table 1). In contrast to the native fishes, round gobies gained significant weight ($\sim 10\%$) when paired with a single conspecific (paired *t*-test: $P < 0.05$; Table 1). During interspecific trials, slimy sculpins were able to maintain weight when paired with a round goby (Figure 1). However, both spoonhead sculpins and logperch continued to lose weight at weekly checkpoints and displayed significant weight loss (paired *t*-test: $P < 0.05$; Figure 1; Table 1) by the conclusion of the trial. In contrast, the round goby continued to display significant weight gains independent of the native species in the cell. Skin or fin damage was rarely observed indicating little physical contact between fish pairs within each cell, and survival remained high throughout the trials (Table 2).

Predator–Prey Interactions

All fish readily consumed amphipods indicating the prey was edible and within their gape. In the dark (0 lx), reaction and strike distances of the round goby and both sculpin species were similar (Mann–Whitney test: $P > 0.05$), with median distances ranging from 1.8 to 3.2 cm and from 1.0 to 1.2 cm, respectively (Tables 3, 4). Logperch were inactive in the dark and were not observed to feed. The three nocturnally active species oriented and attacked prey from multiple directions, and reaction and strike angles were not significantly different across species (Mann–Whitney test: $P > 0.05$; Figure 2). While fish reacted to prey directed behind them (at angles of ± 140 – 180°), strikes were rare at these angles. Capture success exceeded 70% in the dark for both sculpins and round gobies (Table 4).

The reaction distances increased significantly (Kruskal–Wallis test: $P < 0.05$) in the lighted trials (5–130 lx) with round gobies doubling and the sculpins at least tripling their median range at the highest light intensity (Table 3). Logperch also doubled their median reaction distance at light levels between 5 and 130 lx. Strike

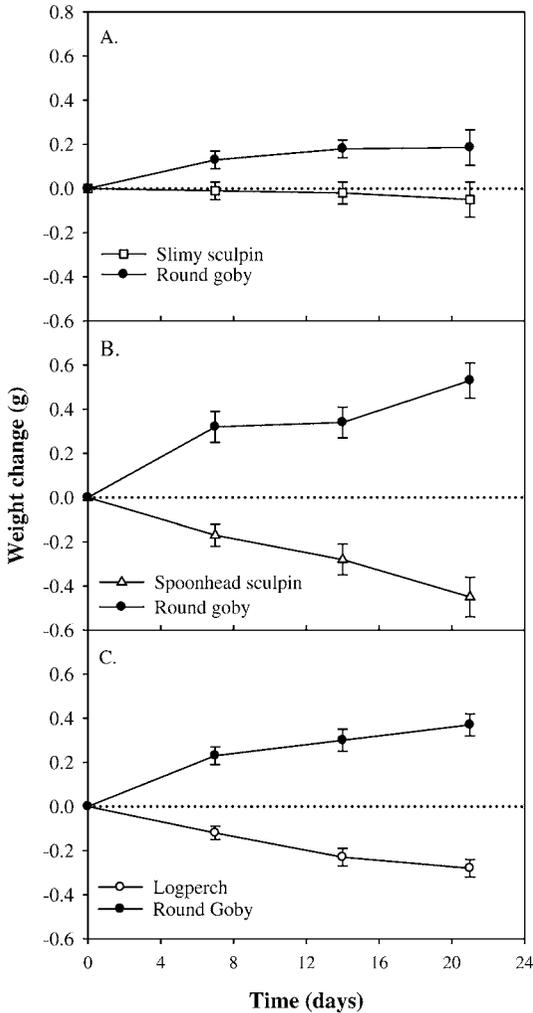


FIGURE 1.—Changes in mean wet weight during three interspecific feeding trials. Panel (A) shows the changes when slimy sculpins were paired with round goby, panel (B) the changes when spoonhead sculpins were paired with round goby, and panel (C) the changes when logperch were paired with round goby. The error bars represent SEs; the dotted line indicates zero weight change.

distance remained relatively constant for slimy sculpins and round gobies with increasing light. Spoonhead sculpins showed a significant gain in strike distance at 5, 50, and 130 lx compared with strikes in the dark (Kruskal–Wallis test: $P < 0.001$; Table 4). Logperch significantly expanded their strike distance at 130 lx compared with 5 lx (Kruskal–Wallis test: $P < 0.001$; Table 4). Both sculpins had significantly greater reaction distance at 5 and 25 lx compared with the round goby (Mann–Whitney test: $P < 0.05$), and all native fishes had significantly greater strike and

TABLE 2.—Percentage of fish that survived each 21-d feeding trial. The number of fish at the beginning of each experiment is indicated in parentheses.

Trial	Slimy sculpin	Spoonhead sculpin	Logperch	Round goby
Intraspecific	100 (8)	100 (8)	100 (8)	87.5 (8)
Interspecific	96.6 (29)	100 (12)	89.7 (29)	95.7 (63)
Total	97.3 (37)	100 (20)	91.8 (37)	94.9 (71)

reaction distances at 50 and 130 lx compared with the round goby (Mann–Whitney test: $P < 0.05$).

The attacks in light were concentrated toward prey located in front of the fish. The majority of slimy and spoonhead sculpins strikes occurred at an angle of $\pm 20^\circ$ from the midline of the fish while logperch strikes showed a slightly broader ($\pm 40^\circ$) distribution. In contrast, round goby strikes showed a bimodal distribution with prey strikes located slightly off center (± 20 – 40° ; Figure 3). Slimy sculpins had the highest capture success (89.2%) in light, followed by round gobies (81.6%), spoonhead sculpins (79.9%), and logperch (74.7%) (Table 4).

Discussion

Previous investigations have detailed the expansion of the round goby and its influence on native benthic species. While it appears that the round goby can outcompete and displace the mottled sculpin (Janssen and Jude 2001; Balshine et al. 2005), its interaction with other benthic species remained largely unknown. Additionally, the role of the round goby’s vision and lateral line in mediating these behavioral interactions with both prey and other native fish remained to be addressed.

The three native species in the present study were chosen based on their natural history that places them in direct competition with the round goby for abiotic and biotic resources. Both logperch and slimy sculpins inhabit the Duluth–Superior Harbor (L. Evrard, U.S. Geological Survey, Great Lakes Science Center, personal communication) while the spoonhead sculpin is normally found in deeper waters. Logperch inhabit similar shallow habitats that were first colonized by the round goby and populations have declined where round gobies have increased (Jude et al. 1995; Chant 2002; Balshine et al. 2005). The ranges of the slimy and spoonhead sculpins are from near shore to depths of 210 m in Lake Superior and the fish are generally most abundant in waters from 50 to 90 m deep (Selgeby 1988). They are potentially in direct competition with the round gobies during their seasonal inshore migration to shallow spawning sites (Oyadomari and Auer 2004). However, recent evidence indicates that

TABLE 3.—Median reaction distances (cm) at various light intensities. The 25th and 75th percentiles are shown in parentheses and the numbers of fish in the trials in brackets. Different letters indicate significantly different medians for species across light intensities (Kruskal–Wallis test: $P < 0.001$).

Species	Light intensity (lx)				
	0	5	25	50	130
Slimy sculpin	1.8 z (1.0, 4.1) [54]	8.2 yx (5.6, 12.6) [49]	8.5 yxw (3.6, 14.2) [69]	13.0 y (7.0, 18.1) [107]	9.2 yxw (3.8, 13.0) [81]
Spoonhead sculpin	3.2 z (1.9, 4.2) [58]	12.0 y (7.4, 16.1) [61]	9.5 y (1.9, 13.9) [46]	12.1 y (5.0, 16.3) [71]	12.2 y (5.2, 17.5) [68]
Loggerhead	Inactive	4.7 z (1.7, 7.2) [60]	4.2 z (1.9, 7.4) [70]	5.2 z (2.1, 8.0) [82]	9.5 y (4.0, 15.0) [67]
Round goby	2.6 z (1.2, 4.5) [68]	2.9 zy (1.4, 6.4) [48]	4.1 y (1.8, 9.2) [60]	3.1 zy (1.2, 6.9) [77]	5.3 y (2.4, 10.8) [56]

the round goby, after initially colonizing shallow waters, is colonizing offshore to water depths greater than 50 m (Schaeffer et al. 2005; Walsh et al. 2007), which would place them in greater competition with the sculpins.

Behavioral Interactions

The artificial streams provided the opportunity to investigate resource competition in a controlled environment using round goby densities (6–12 fish/m²) that are common in Duluth–Superior Harbor, western Lake Superior (Bergstrom et al. 2008). The artificial diet provided a mechanism to quantify and limit food consumption. All species readily consumed pellets and increased in size throughout several months of captivity. Trial durations were selected to provide sufficient time to record modest weight changes (± 5 –10%) without violating animal care guidelines.

The round gobies were able to significantly increase weight in the presence of each native species and only the slimy sculpin was able to maintain weight in the presence of the round goby. It appears that aggressive behavior of round gobies was sufficient to dominate the limited food supply. However, given the laboratory setting, several other hypotheses cannot be discounted. The continual antagonistic behavior or lack of conspecific social structure may have induced stress or increased metabolism, or both, in the native fishes that contributed to weight declines. Pellets were chosen to enable precise measurement of food given to each cell. However, the four species may not have had the same foraging success for finding or ingesting the pellets. Thus, if one species (i.e., round gobies) foraged more successfully for pellets than the others, it may have influenced the results. Regardless of the underlying cause, native fishes fared worse in the presence of the round goby than with their conspecifics.

Whether the weight loss observed in the trials corresponds to a biologically significant decline in fitness is unclear. The 10–15% weight loss exhibited by two of the native species did not affect survival either during the trial or when fish were returned to

home aquaria and provided higher food rations (at least 100 mg · fish⁻¹ · d⁻¹). Considering the concurrent 10–15% weight gain for the round gobies, one would predict that extension of the trial would have resulted in continual weight reduction and observable (i.e., emaciation, reduced movement) conditions in the native fishes. However, our animal care protocols dictated trial length as fish were restricted from losing more than 20% of body weight. Under field conditions, one would predict that round goby behavior would be sufficient to drive the native fish away from the immediate area. As they share similar habitat, the three native species could eventually be displaced to suboptimal habitat and suffer substantial population loss.

Predator–Prey Interactions

The behavioral interactions observed among the fishes indicated round gobies could outcompete native fishes for food. While aggressive behavior appeared to be the main factor in the laboratory that allowed round gobies to dominate the limited artificial diet provided, it is unclear whether round gobies also possess enhanced sensory systems that would facilitate superior detection and capture of natural prey. A previous study reported that round gobies had a greater reaction distance in the dark than did mottled sculpins, suggesting one reason for round goby dominance (Jude et al. 1995).

The three main senses that most teleosts use to locate prey are olfaction, mechanosensory detection, and vision. The predator–prey trials were designed to assess the relative contributions of the mechanosensory lateral line and visual systems. Although olfactory cues were available, mixing of the water column by both predator and prey movements and continued addition of prey throughout the arena would disrupt odor plumes and prevent use of olfaction for point-source location. At 0 lx (dark), all strikes would be presumably mediated by the lateral line and allow its maximum range to be established. Although strikes in the light may be influenced by both lateral line and the visual systems,

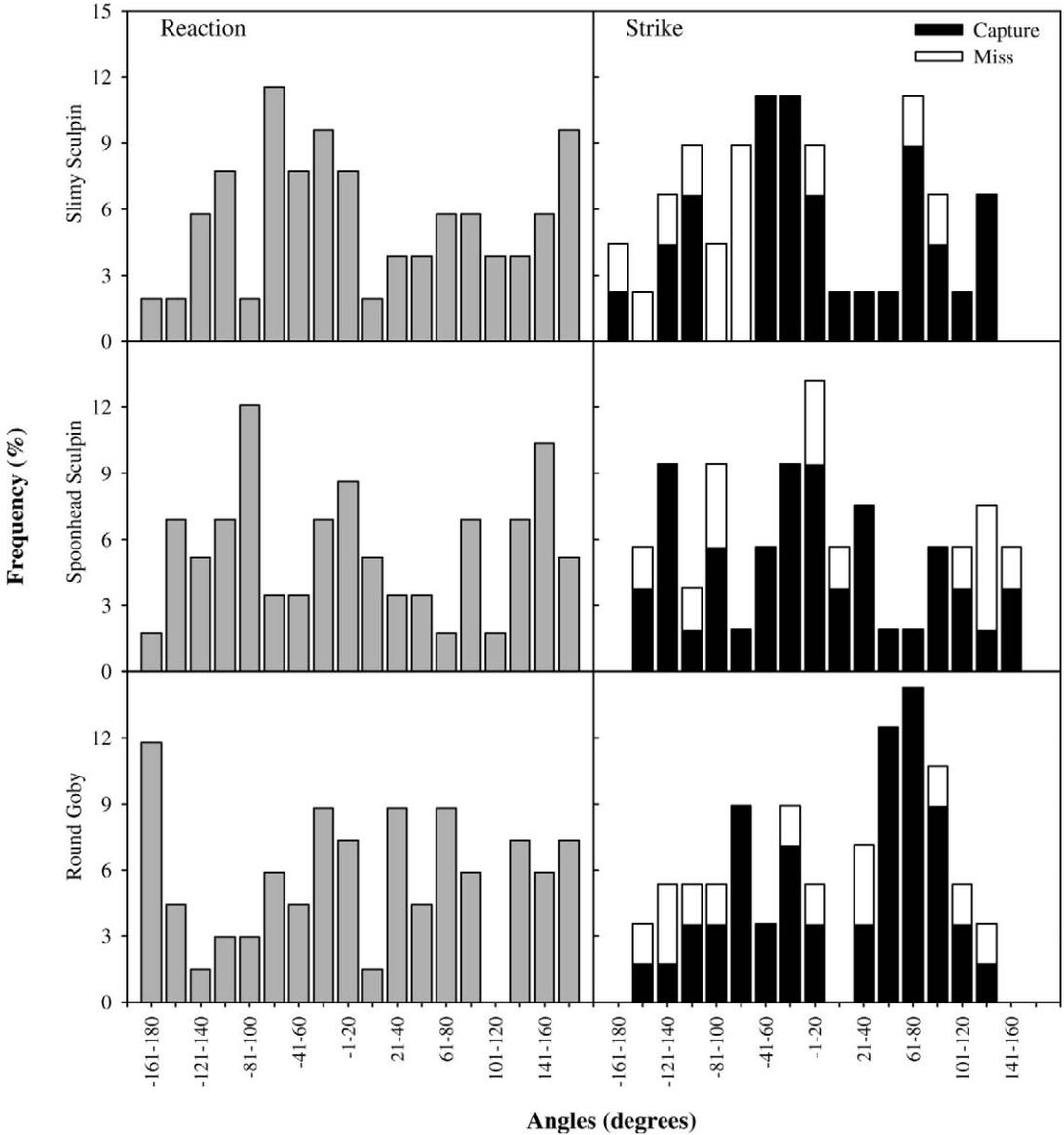


FIGURE 2.—Frequency distributions for the reaction and strike angles in 20° increments for the slimy and spoonhead sculpins and the round goby during predator–prey interactions in the dark (0 lx). Positive angles and negative angles indicate strikes to the right and left side of the fish, respectively. The bars for strike angles are subdivided into unsuccessful (open) and successful strikes (solid).

TABLE 4.—Median strike distances (cm) at various light intensities and percentages of successful strikes. The 25th and 75th percentiles are shown in parentheses on the next line, along with the numbers of fish in the trials in brackets. Different letters indicate significantly different medians across light intensities (Kruskal–Wallis test: $P < 0.02$).

Species	Light intensity (lx)		
	0	5	25
Slimy sculpin	1.2 (71.1%) z (0.8, 1.8) [45]	1.4 (89.5%) zy (1.0, 2.1) [57]	1.5 (89.0%) zy (0.9, 1.7) [82]
Spoonhead sculpin	1.2 (77.4%) z (0.7, 1.7) [53]	2.0 (73.0%) y (1.3, 3.0) [74]	1.4 (75.9%) z (0.9, 1.9) [54]
Logperch	Inactive	1.4 (91.5%) z (1.0, 2.3) [59]	1.2 (80.0%) z (0.8, 2.1) [70]
Round goby	1.0 (78.6%) z (0.7, 1.7) [56]	1.2 (83.0%) zy (0.8, 2.1) [53]	1.4 (85.7%) z (1.1, 1.7) [56]

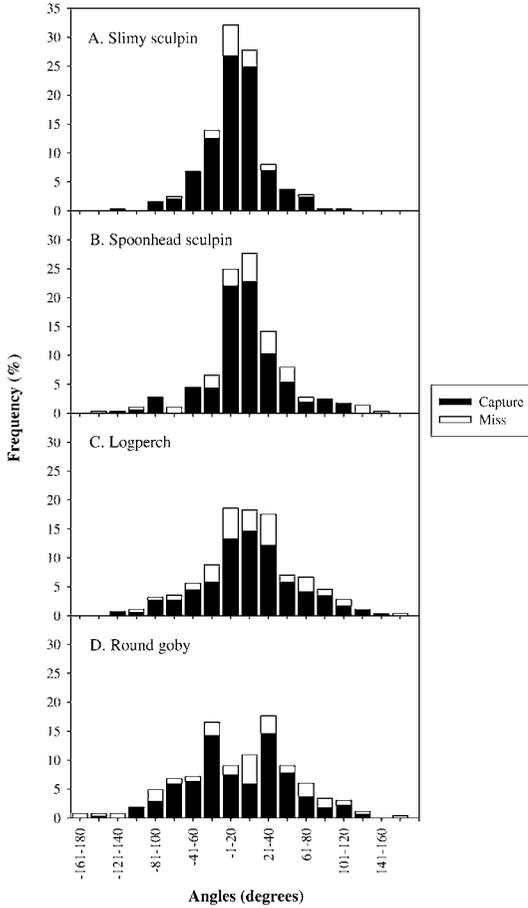


FIGURE 3.—Frequency distributions for strike angles in 20° increments for combined strikes by (A) slimy sculpins, (B) spoonhead sculpins, (C) logperch, and (D) round goby in the light (5–130 lx). Positive angles and negative angles indicate strikes to the right and left side of the fish, respectively. The bars are subdivided into unsuccessful (open) and successful strikes (solid).

strikes outside the maximum range of the lateral line were most probably triggered by visual cues (Richmond et al. 2004; Callahan and Mensinger 2007).

The mechanosensory lateral line detects displace-

ments in the local water field. The wide distribution of the strikes in the dark inferred that each of the three nocturnally active species was receiving input from both its anterior and posterior lateral line to mediate prey capture. Both sculpin species and the round goby showed similar reaction and strike distances in the dark. The reaction distances were one-half of a body length or less, which is consistent with the lateral line ranges reported for other benthic species feeding on naturally occurring prey (Price and Mensinger 1999; Palmer et al. 2005). Strikes were relatively accurate (71% to 78%), indicating that lateral line sensitivity was sufficient to mediate predator–prey interactions. In contrast to mottled sculpins, round gobies do not appear to have an advantage in nocturnal foraging over slimy and spoonhead sculpins. Inactivity of logperch in the dark, however, places it at a disadvantage when confronted with nocturnally active competitors.

Light intensities were chosen to mimic conditions in the Duluth–Superior Harbor and the St. Louis River estuary at approximately 1 m in depth where round gobies are in high abundance (Bergstrom et al. 2008). The estuary is characterized by high concentrations of tannin and suspended sediment (extinction coefficient $[k] = 4.21$; WOW 2004), which absorb and scatter light. The light intensities selected represented night (0 lx), dawn or dusk ± 30 min (5–50 lx), and midday (130 lx). Even small increases in light intensity were sufficient to expand reaction distances with two- to four-fold gains at the highest intensity. Native fishes had significant advantages in reaction and strike distance over the round goby at the two highest light intensities.

The experiments indicate that round gobies do not possess enhanced visual or lateral line systems compared with the three native species. At higher light intensities, the natives maintain advantages in both reaction and strike distances. Thus, with high light intensities or clear water conditions, the native fishes have a visual edge over the round goby. Whether this is enough to offset the round gobies' aggressive behavior remains to be determined as the small cells and artificial diet of the behavioral interaction experiments

TABLE 4.—Extended.

Species	Light intensity (lx)	
	50	130
Slimy sculpin	1.7 (90.2%) y (1.1, 2.4) [112]	1.4 (87.7%) zy (1.0, 1.9) [73]
Spoonhead sculpin	1.8 (89.9%) y (1.3, 3.1) [79]	1.7 (79.3%) y (1.2, 3.0) [82]
Logperch	1.7 (72.6%) zy (1.0, 3.5) [88]	3.3 (67.6%) y (1.2, 10.2) [68]
Round goby	1.1 (69.2%) zy (0.8, 1.6) [78]	1.1 (91.4%) y (0.7, 1.4) [58]

were not designed to address this question. The expansion of the round goby in the Duluth–Superior Harbor has centered in areas of industrial debris with high concentrations of suspended sediment, which would negate the native fishes' visual advantages. In the oligotrophic water of Lake Superior, the euphotic zone extends to 46–60 m where light intensities during the summer months can range from 5 to 25 lx (based on surface intensity of 10,000 lx; Mason and Patrick 1993). Thus, there may be sufficient light in portions of the sculpins' range to confer a sensory advantage and it will be interesting to observe whether the round gobies are successful in competing with native fishes in the clearer waters of Lake Superior.

Consistent with the sculpins' proclivity for deeper depths, one avenue for future research would be to conduct the behavioral feeding experiments at lower temperatures. The native species were chosen based on their similar life history with the round gobies and current and future overlap in Lake Superior. While 15°C is well within the summer temperatures reached in the Duluth–Superior Harbor and the St. Louis River, where the logperch, slimy sculpin, and round goby overlap, the temperatures are below this level for the majority of the year. Additionally, common spoonhead sculpin habitat (50–90 m depth, Selgeby 1988) would have average temperatures that are lower than in the harbor and river. If the native species are more successful at foraging at these lower temperatures, it would give them an advantage over the round goby.

This study provided insights on resource competition between the exotic round goby with three native fish species. The lateral line capabilities are equivalent between the round goby and both sculpins and with the addition of light and visual input, the round goby did not detect or capture prey as effectively as did native fishes. However, the aggressive behavior of the round goby may supersede the native fishes' sensory advantages, allowing the round goby to successfully dominate resources. The capacity to monopolize food throughout the night and day may contribute to native population declines in areas invaded by round gobies.

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