

Mechanosensory based orienting behaviors in fluvial and lacustrine populations of mottled sculpin (*Cottus bairdi*)

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(Received 17 November 2005; in final form 16 January 2006)

Abstract

We compared prey-orienting and rheotactic behaviors in a fluvial (Coweeta Creek) and lacustrine (Lake Michigan) population of mottled sculpin. Blinded sculpin from both populations exhibited unconditioned, mechanosensory based rheotaxis to low velocity flows. Whereas Lake Michigan sculpin generally showed increasing levels of positive rheotaxis to increasing velocities, Coweeta Creek sculpin show varying levels of positive rheotaxis at low to intermediate velocities and often reduced positive rheotaxis or even negative rheotaxis at the highest velocities (12 cm s^{-1}). Blinded Lake Michigan, but not Coweeta Creek mottled sculpin exhibited an orienting response to a small (3 mm diameter) artificial prey (50 Hz vibrating sphere). In conclusion, the two populations differed in the strength and polarity of the rheotactic response at higher velocities and in their responsiveness to mechanosensory cues from epibenthic prey sources. These behavioral differences have most likely arisen from different learning experiences in different habitats and from the greater importance of visual cues to the Coweeta Creek mottled sculpin and mechanosensory cues to Lake Michigan mottled sculpin in the sensory guidance of orienting behaviors.

Keywords: *Rheotaxis, prey orientation, lateral line, habitat selection, stream fish, lake fish*

Introduction

The mottled sculpin (*Cottus bairdi*) is an abundant and broadly distributed scorpaeniform freshwater fish. Mottled sculpin are benthic habitat generalists that typically occupy riffles of creeks and small rivers across northern North America (Petty and Grossman 1996, 2004), although they have also invaded the rocky shores of the Great Lakes. Given their high local abundance (Grossman et al. 2006) and wide geographic range, mottled sculpin are particularly good candidates for studying the effects of local selective pressures on the sensory basis of behavior.

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ISSN 1023-6244 print/ISSN 1029-0362 online/06/020113-130 © 2006 Taylor & Francis
DOI: 10.1080/10236240600688748

Two particularly well-studied populations of mottled sculpin inhabit Coweeta Creek, North Carolina, a 5th-order tributary of the Little Tennessee River, and the southwestern shores of Lake Michigan near Chicago, Illinois. Whereas habitat selection, dietary habits, population dynamics, and reproductive biology have been extensively described in both field and laboratory studies on the Coweeta Creek population (e.g. Grossman et al. 1995; Petty and Grossman 1996; Grossman and Ratajczak 1998; Grossman et al. 2002; Grossman et al. 2006), the sensory biology of prey capture behavior has been the primary focus of laboratory studies on the Lake Michigan population (e.g. Hoekstra and Janssen 1986; Coombs and Janssen 1990; Janssen 1990; Coombs and Conley 1997a, b).

Studies of Lake Michigan populations indicate that mottled sculpin display a series of naturally occurring orienting and capture behaviors when presented with either live (e.g. *Daphnia*) or artificial (a small vibrating sphere) prey (Hoekstra and Janssen 1985, 1986). These behaviors consist of an initial, whole-body orienting response toward the vibration source, followed in some cases (depending on source distance) by a step-wise approach toward the source and eventual strike. In addition to whole-body movements along the horizontal plane of the substratum, mottled sculpin orient their heads toward sources that are either above or below the resting level of the fish's head (Hoekstra and Janssen 1985; Abboud and Coombs 2000). Specifically, when prey are buried in the substratum, mottled sculpin move their head downward until their mandible is flush with the substratum. Conversely, when prey are located above the fish's head, mottled sculpin elevate their head and orient towards the prey. These prey-orienting behaviors can be elicited with relative ease from naive, blinded Lake Michigan mottled sculpin in response to mechanosensory cues alone and all but one (head-down behavior) requires the lateral line system (Hoekstra and Janssen 1985; Janssen 1990; Abboud and Coombs 2000; Coombs et al. 2001). Orienting behaviors like these have not been observed in Coweeta Creek sculpin in either the lab or their natural habitat despite hundreds of hours of observation (Grossman et al. 1995; Grossman and Ratajczak 1998; Grossman et al. 1998; Petty and Grossman 2004).

The mechanosensory lateral line is also now known to play a significant role in rheotaxis (i.e. orientation towards or away from a current) (Montgomery et al. 1997). Rheotaxis is a wide-spread behavioral characteristic of fishes living in environments with currents, including mottled sculpin in Coweeta Creek (Facey and Grossman 1990). Upstream orientation may enhance the ability of mottled sculpin and other fish (e.g. trout) to both locate and intercept prey as they are swept along by the current (Arnold 1974; Montgomery et al. 1997). Alignment with the current should also reduce the energetic costs of holding station in strong currents (Facey and Grossman 1992). At current speeds high enough to displace fish downstream, rheotaxis relies predominantly on visual and to a lesser extent, tactile cues (Arnold 1974). However, at low current speeds ($<10 \text{ cm s}^{-1}$), the superficial neuromasts of the lateral line system play an important role (Montgomery et al. 1997; Baker and Montgomery 1999a, b) in this behavior. Thus, rheotaxis, like other behaviors, relies on a number of different sensory cues.

At present, however, it is uncertain whether rheotaxis or its sensory basis differ among either populations or species inhabiting environments that differ in ambient current and light levels. Recent studies of Arctic grayling (*Thymallus arcticus*) indicate that fluvial populations, even those raised from hatching in lacustrine environments, show innately greater tendencies for positive rheotaxis than lacustrine populations (Kaya 1991; Kaya and Jeanes 1995). Likewise, Brannon (1967) demonstrated genetically based differences in the rheotactic behavior of three different races of sockeye salmon. Consequently, there is

evidence of significant intraspecific variation in the rheotactic behavior of salmonid fishes, which may have a genetic origin (see Arnold 1974 for review). Nonetheless, the relative importance of different sensory systems (e.g. lateral line *versus* vision) to rheotactic behavior is unknown.

In this study, we examined the importance of mechanosensory cues to prey orientation and rheotaxis in mottled sculpin from two geographically, ecologically and perhaps, taxonomically distinct populations (Coweeta Creek and Lake Michigan). We also quantified the effects of current velocity on mechanosensory based rheotaxis and location preference in a flume for both Coweeta Creek and Lake Michigan mottled sculpin. Whereas the mechanosensory lateral line plays a dominant role in the non-visual feeding behavior of nocturnal Lake Michigan mottled sculpin, its importance to the feeding behavior of Coweeta Creek mottled sculpin and to the rheotactic behaviors of both populations is unknown.

We have used the term "population" to describe mottled sculpin from Lake Michigan and Coweeta Creek, because these groups are currently described as the same species. Nonetheless, recent work has shown that mottled sculpin are probably polyphyletic (Kinziger et al. 2005), although both Coweeta and Lake Michigan forms are in the same polyphyletic clade (Uranidae). However, the published phylogeny is based on a single locus, small sample sizes for the two groups ($n \leq 4$), and without consideration of morphological traits. Consequently, it is unclear whether Lake Michigan and Coweeta mottled sculpin are different or closely related species.

Methods

Animal collection and care

We collected mottled sculpin ranging in size from 6.2 to 8.0 cm (standard length, SL) from Lake Michigan (Winnetka, IL) using baited minnow traps placed on the bottom in 1–4 m of water near shore, whereas we obtained mottled sculpin from Coweeta Creek (North Carolina) using direct-current electrofishing (Freeman et al. 1988). For experiments, we used only fish that quickly displayed normal behaviors and showed no evidence of external or internal injury, which represented the vast majority of sculpin collected (see Grossman et al. 1995; Petty and Grossman 2004). Mean and standard deviations of SL for Coweeta Creek fish (7.1 ± 3.6 cm) was similar to those of Lake Michigan mottled sculpin (7.2 ± 3.6 cm). We housed fish at Loyola University in 10 or 20 gallon aquaria at densities of 1–4 fish/tank. We used dechlorinated tap water in both home and flow tanks and the temperature was maintained at $15 \pm 2^\circ\text{C}$. To isolate mechanosensory contributions to the orienting behaviors, visual cues were eliminated by blinding mottled sculpin while under anesthesia (MS-222) using (1) complete enucleation, or (2) lens removal followed by aspiration of the retina (Coombs and Conley 1997a). After surgery, the fish were allowed to recover for at least 1 week or until they fed regularly. We fed the fish with two to three small pieces of squid either 5 days/week (rheotaxis experiments) or 3 days/week (prey-orienting experiments) and kept daily records of fish condition and food acceptance to ensure that the experimental animals were in good health. All mottled sculpin were treated identically in the laboratory to minimize the effects of handling bias. Protocols used in the collection and laboratory handling of mottled sculpin were approved by Institutional Animal Care and Use Committees at the University of Georgia and Loyola University Chicago (see <http://www.research.luc.edu/compliance/iacuc>).

Prey orientation studies

To determine whether Coweeta Creek mottled sculpin displayed the initial whole-body orienting response when exposed to the artificial prey (i.e. epibenthic vibrating source), we first brought naive, newly collected individuals of both Coweeta Creek and Lake Michigan populations into the lab and treated them in identical ways. Fish were held and blinded as described above. After a one week recovery period, we tested fish in their home tanks to see if they would successfully feed (i.e. accept at least one, bite-size piece of squid delivered from the ends of a long-nose forceps for a minimum of one piece of squid per day). Specifically, small pieces of squid were dangled near the head of the fish to create both chemo- and mechanosensory cues. Squid was also used as a reinforcer for fish that made orienting responses to artificial prey during subsequent test sessions. Squid, rather than biologically relevant prey items (e.g. macroinvertebrates) was used as a food source because it was inexpensive, easy to deliver, and readily taken by both Coweeta Creek and Lake Michigan populations. Moreover, the frequency with which sculpin accepted this food item could also be used to assess general health and motivation to feed (see following paragraph) in a way that was not confounded by the biological relevance of different prey items to different populations.

Animals were fed on test days only (Monday, Wednesday, and Friday) and deprived of food on non-test days. We chose this food deprivation and reward schedule because the orienting behavior of Lake Michigan sculpin to artificial prey is highly contingent upon hunger motivation and food acquisition. Thus, these procedures are necessary to rule out the possibility that low response frequencies could be due to confounding variables like motivational state (Coombs 1995).

Only sculpin that fed successfully in their home tanks were used in the next experimental phase, which determined if individuals would also feed in the experimental tank. We transferred mottled sculpin that fed in their home tanks to the experimental tank via hand-held nets and acclimated them for 15 min. This tank was identical to that used in previous research on prey-orienting behavior of Lake Michigan mottled sculpin (Coombs and Conley 1997a, b) and was constructed from glass (50 cm long \times 50 cm wide \times 36 cm high), filled with water to a depth of 9 cm and isolated from substratum vibrations by a vibration-isolation table (TMC) (Coombs and Conley 1997a, b). A video camera below the tank recorded the animal's behavior during the test sessions. To ascertain whether mottled sculpin would feed in the experimental aquarium, we hand-fed fish at 5 min intervals during test sessions scheduled during the same time and days of the week as feeding in the home tank. These attempts continued for 2 weeks and no other food, other than that offered in the experimental tank, was given. If a mottled sculpin fed successfully in the experimental tank, it was then used in prey orientation tests.

We began tests by transferring a mottled sculpin with a hand-held net to the experimental aquarium where it acclimated for 15 min. After acclimation, we waited until the fish moved to within detection range of the artificial prey (2–6 cm away), and then turned on the signal (i.e. vibrating artificial prey, see below) for 5 s and observed the mottled sculpin's response. To eliminate the observer bias and to provide an objective criteria for defining the orienting response, we used *post hoc* measurements of the fish's position before and after the trial onset to compute the orienting frequencies from digitized video frames (Snappy, Inc.) using SigmaScan Pro imaging software (SPSS) (Coombs et al. 2001). Time-stamped (17 msec resolution) video frames were also used to compute reaction times (time elapsed between the signal onset and the initiation of the orienting response). The responses were scored as "hits" if the fish moved toward the source (i.e. the fish-to-source distance and/or angle

decreased) and the reaction time of the response was less than the trial duration (5 s). If the daily orienting frequency of an individual fish was 70% or greater (based on 3–6 trials/day) for a minimum of 3 days/week, we classified the animal as having successfully exhibited the whole-body orienting response.

We generated artificial prey vibrations using a small plastic sphere (6 mm in diameter) attached to a minishaker (B&K 4810) by a stainless steel rod (a 16 gauge, 12 cm long blunt-tipped syringe needle) as used in previous experiments with Lake Michigan sculpin (e.g. Coombs and Conley 1997a, b). This apparatus produced a 50 Hz sinusoidal oscillation of the sphere in the horizontal plane. We set the peak-to-peak amplitude of vibration ($\sim 0.1 \text{ m s}^{-1}$ at the source) to fall within a range that typically elicits orientation responses from Lake Michigan mottled sculpin within 9–12 cm (Coombs 2000). Source vibrations were pulsed on (500 ms) and off (500 ms) for a total of 5 s per stimulus trial. A modular hardware system (e.g. digital-to-analog converter, programmable attenuator, etc.) (Tucker Davis Technologies) under computer control regulated the timing of the stimulus presentation, the frequency, and the amplitude of the sphere oscillations (Coombs 2000).

Rheotaxis experiments

We conducted rheotaxis experiments in a flow tank (artificial stream) used in previous experiments on Lake Michigan sculpin (Kanter and Coombs 2003) and similar in design to that described by Vogel and LaBarbera (1978). The main body of the tank consisted of a rectangular plexiglass channel ($44 \times 18 \times 17 \text{ cm}$) with circular openings at each end. These openings were connected via a circular PVC return tube (10.2 cm diameter). Water depth in the main chamber was 15.5 cm – well above the benthic positions normally held by mottled sculpin in both natural and laboratory streams (Grossman et al. 1995; Grossman and Ratajczak 1998). A motor-driven impeller, placed at the downstream end of the tank, produced flows that varied in velocity according to the number of motor revolutions per minute. A digital display of motor revolutions per minute (RPM) on the motor controller ensured accurate repeatability of different flow velocities. The motor was mounted on a separate bench to prevent vibrations from being transmitted to the flow tank.

The flow tank contained two collimators placed upstream of the experimental section to reduce turbulence and to create a relatively uniform flow. Each collimator consisted of 500 soda straws (each 3 cm long) that were glued together and was used to cover the entire cross section of the tank. The fish were placed in the test arena ($16.5 \times 27.5 \text{ cm}$) with the second collimator as an upstream boundary, and a mesh screen supported by a plastic grid (egg crate) as the downstream boundary. The mesh screen prevented the mottled sculpin from being drawn into the impeller.

Video analysis of multiple, parallel dye streaks in the flow tank revealed that bulk flow in the experimental region of the tank (at the level of the fish) was unidirectional and uniformly distributed at all the flow velocities tested (Kanter and Coombs 2003). Moreover, the dye-streak measures of the flow velocities in the center of the tank at different motor speeds were in excellent agreement with those made by a commercially available flow meter (Marsh-McBirney Model 2000) (Kanter and Coombs 2003); this was also used in previous field measures of current velocities in Coweeta Creek (Grossman and Freeman 1987; Facey and Grossman 1992). Finally, the dye-streak analysis showed a classic parabolic distribution across the width of the tank, with dye streaks in the center traveling at faster rates than dye streaks near the tank walls, due to the boundary layer effects.

We conducted rheotaxis experimental sessions 3 days/week (Monday, Wednesday, Friday). Each experimental session (~50–60 min/day) consisted of four consecutive segments with each segment consisting of a 10–15 min acclimation period followed by a 5 min test period. We tested fish individually and transported them to the experimental tank in water-filled, plastic-lined nets to minimize the potential damage to the superficial neuromasts of the lateral line system. During each session, we recorded the position and the behavior of the test mottled sculpin using a video camera placed below the flow tank.

Prior to the beginning of an experimental session, we randomly generated the order in which different velocities (0, 4, 8, and 12 cm s^{-1}) were presented to the test fish. The impeller was then adjusted to produce the desired velocity, and mottled sculpin acclimated for 10–15 min. We then videotaped the mottled sculpin's behavior for 5 min. At the end of the first 5 min period, we adjusted the motor speed to produce the next randomly chosen velocity. The fish were then allowed an additional 10–15 min to acclimate to the new flow speed before being videotaped for another 5 min period. We followed this procedure until each fish was subjected to all four flow velocities. Different orders of test velocities were then randomly generated for the next several days of experimental sessions, until each fish ($N=6$) had been tested six times at each velocity. If, at the randomly chosen time the fish was not in the horizontal plane along the substratum, as is typical for these benthic fish (Grossman and Ratajczak 1998), the frame was rejected and a new random time was generated. For each position, we used SigmaScan Pro to determine the fish's heading with respect to the oncoming flow, defined as the angle between the fish vector (a line down the midline of the fish from the snout to the position of pectoral fin insertion) and the flow vector (a line parallel to the flow direction and intersecting the fish vector at the point of pectoral fin insertion, Kanter and Coombs 2003).

By convention, an angle of 0° (fish headed directly into the flow) represents perfect positive rheotaxis, whereas 180° represents perfect negative rheotaxis. We then plotted and analyzed the distribution of fish-to-flow angles for each mottled sculpin and test velocity. The vector strength of the distribution (Batschelet 1981), which can vary from 0 (fish headings randomly distributed across 360°) to 1 (all fish headings the same), was used as a quantitative measure of the degree to which the mottled sculpin showed orientation preferences. We employed a modified Rayleigh (V) test (Greenwood and Durand 1955) to statistically discriminate between the uniform (random) and the non-uniform distributions centered on an expected mean angle (e.g. 0° for positive rheotaxis, 180° for negative rheotaxis) (see also Zar 1999). The significance of the test statistic, V , can be determined from μ , which is equal to V times the square root of $(2/n)$. For μ values above e.g. 3.274 ($n=100$), the null hypothesis (population is uniformly distributed around the circle) can be rejected at the $p < 0.0005$ level.

We determined whether mottled sculpin displayed preferences for the specific locations within the flow tank by dividing the test arena into four sections: (1) side walls (21.5×3 cm for each wall), (2) upstream end of the tank (16.5×3 cm), (3) downstream end of the tank (16.5×3 cm), and (4) center of the tank (21.5×10.5 cm). We then assigned each mottled sculpin a location based on the position of its head during each of the 25 randomly chosen observation times. We tested for location preferences using a chi-square goodness-of-fit test with expected values based on the area of each tank location (Zar 1999). Although there were too few categories to conduct a partitioned chi-square analysis (Grossman and Freeman 1987; Zar 1999), we identified the tank section with the greatest marginal contribution to the chi-square value.

We also measured sculpin activity during experimental session by counting the number of times that mottled sculpin changed their position during the 5 min test periods.

In nature, mottled sculpin change position by "scooting" along the substratum rather than by continuous swimming (i.e. they are sit-and-wait predators that rest on the bottom, Facey and Grossman 1990; Grossman et al. 1995). We defined a reposition as movement of a mottled sculpin from one holding position to another. Occupation of a new holding position was easily identified by stereotypical braking behavior (flaring of the pectoral fins) and the absence of further movement for an arbitrarily selected period of two full video frames (66 msec) (Coombs and Conley 1997a). We tested for relationships between repositioning frequency and the flow rates using linear regression.

Results

Orientation responses to artificial prey (mechanosensory cues alone)

Both Coweeta Creek and Lake Michigan mottled sculpin successfully completed the initial home-tank feeding test in response to hand-delivered squid (10 of 11 Lake Michigan individuals and seven of nine Coweeta Creek mottled sculpin). By contrast, only one Coweeta Creek individual fed sporadically in the experimental tank (three out of six sessions in two weeks), with the remaining eight not feeding at all for up to eight sessions and over two weeks. All ten Lake Michigan individuals fed in the experimental arena – typically on the first day, but of these, three fed rather sporadically (less than 50% of the time). As a consequence, none of the Coweeta Creek individuals and only seven of the Lake Michigan individuals met our feeding criteria for the final test phase of the experiment involving the artificial prey. Nevertheless, we made several attempts to elicit orienting responses from Coweeta Creek sculpin with the vibrating sphere (mechanosensory cues alone) in a less formal way in both experimental and home tanks without success. Moreover, hand-feeding of blinded Coweeta Creek sculpin in the home tank was successful only when the squid piece was placed in direct contact with the mouth region. In contrast, the blinded Lake Michigan sculpin would respond to the hand-held food with an orienting and strike behavior before the squid came in contact with the mouth and often when squid were vibrated near the side of the head or body. Similarly, all but one of the Lake Michigan individuals meeting our feeding criterion showed orienting responses to the vibrating sphere at or above the criterion rates.

Effects of flow rate on rheotactic behavior

In the absence of flow, the orientation responses of the majority of both Lake Michigan and Coweeta Creek mottled sculpin were randomly distributed (Figure 1). As a consequence, the vector strengths of the angular distributions for the no flow condition were generally <0.3 for all but two Lake Michigan individuals (V9 and M16) (Figure 2a, b). Neither of these individuals showed orientation preferences in the upstream direction, however, and in fact, one fish (V9) showed a distinct preference for the downstream direction (V test for a non-uniform distribution about 180° , $p < 0.0005$). The hypothesis that fish headings were non-uniformly distributed about 0° (i.e. strong upstream orientation) could be rejected for all fish in the no flow condition ($p < 0.0005$ level) (Figure 2c, d).

At intermediate flows (4 and 8 cm s^{-1}), all the mottled sculpin showed clear preferences for upstream orientation with vector strengths of angular distributions ranging from 0.4 to 0.9 (Figure 1). Angular distributions differed significantly from random and were clustered around 0° for all the fish (Figure 2c, d all p 's < 0.0005). However, whereas Lake Michigan mottled sculpin generally showed increasing levels of positive rheotaxis to increasing flow

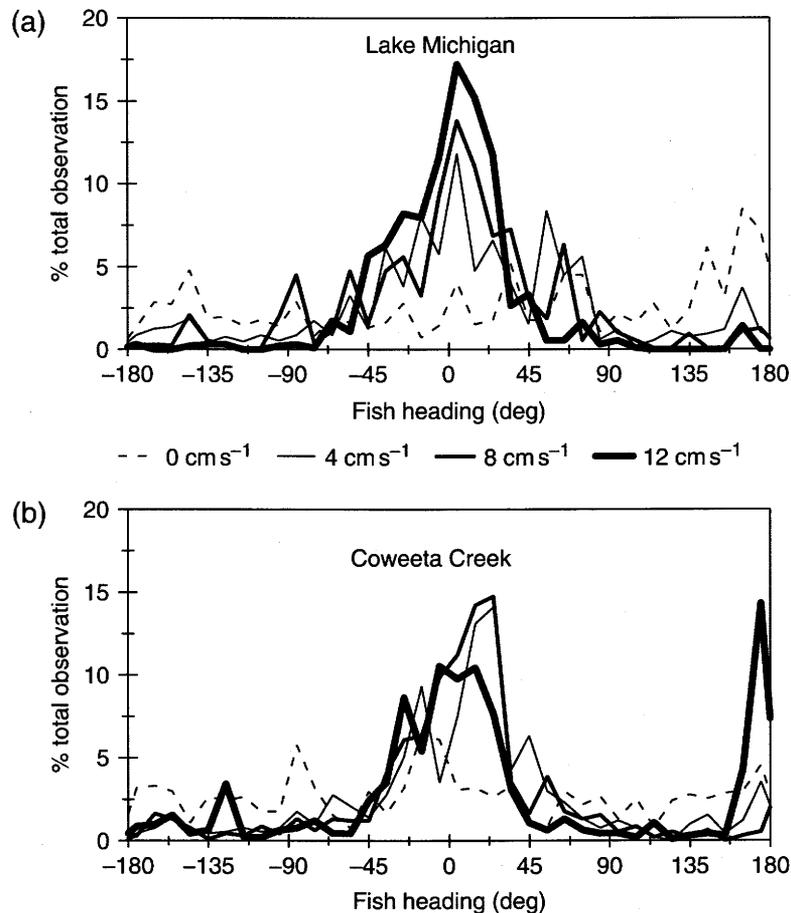


Figure 1. Frequency distributions of fish headings at four different flow rates for Lake Michigan (a) and Coweeta Creek (b) populations. Each line represents the mean of data from six fish.

velocities, with mean vector strength increasing from 0.33 to 0.86, Coweeta Creek mottled sculpin showed varying levels of positive rheotaxis at low to intermediate flow speeds and often reduced levels of positive rheotaxis (two out of six individuals) or even negative rheotaxis (two out of six individuals) at the highest flow speed (12 cm s^{-1}) (Figure 2a, b). In fact, 36 and 46% of the positions occupied by two Coweeta Creek fish (P1 and P3 respectively) were between 170° and 180° ; V tests for non-uniformly distributed headings centered at 180° confirmed the downstream preference at the $p < 0.0005$ level. In contrast, all Lake Michigan mottled sculpin showed a strong, positive rheotaxis at the highest flow rate (vector strengths between 0.67 and 0.96).

Location preferences and movement frequency

Mottled sculpin from both populations were not randomly distributed in the flow tank, and 46 of 48 chi-square tests (12 mottled sculpin at four velocities) were significant at the 0.01 level or below. The finding of two non-significant tests out of 48 is expected by chance alone at the 0.05 level. Although inter-individual variation was present, two trends emerged from the data. First, flow rate did not affect location preferences for either Lake Michigan or Coweeta Creek populations in a consistent manner. Second, mottled sculpin were never over-represented in the central portion of the tank regardless of flow rate. These trends were

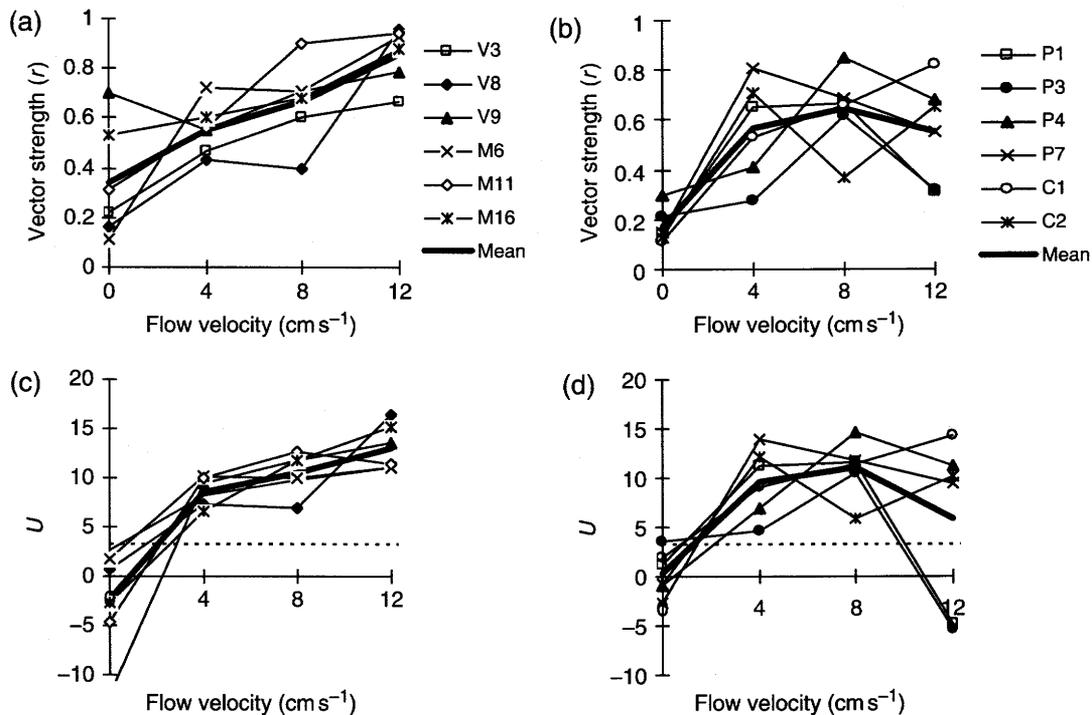


Figure 2. Vector strength of fish heading distributions (see Figure 1) as a function of flow velocity (a, b) and μ values for the V test of circular uniformity (c, d) (see text) for Lake Michigan (a, c) and Coweeta Creek (b, d) mottled sculpin. Thin lines with symbols represent individual functions from six fish, whereas the solid heavy lines represent the mean of six individuals. Dashed lines in bottom panels represent the minimum μ values for rejection of the null hypothesis that headings are uniformly distributed about 0° at the $p < 0.0005$ level (see Zar 1996).

even more apparent from the pooled data for each population (Figure 3), which also revealed some minor inter-population differences. At the three lowest velocities, Lake Michigan mottled sculpin were significantly under-represented in the center of the tank, whereas Coweeta Creek sculpin were significantly over-represented in the downstream section at 0 cm s^{-1} and significantly over-represented in the upstream section at 4 and 8 cm s^{-1} . At the highest test velocity, mottled sculpin from both populations exhibited significant preferences for the sides of the tank.

Mean repositioning frequencies ranged from 2.5 to 64 positions every 5 min and varied widely across individuals and flow rates for both Lake Michigan (Figure 4a) and Coweeta Creek (Figure 4b) sculpin. There was a tendency for repositioning activity to decline with increasing flow rate as the majority of regression line slopes were negative, ranging from -3.25 to 0.95 (Table I). Regression line slopes were significantly different from zero ($0.0006 < p < 0.05$) for four out of six Coweeta Creek individuals (P1, P3, P4, and C2), but only two out of six Lake Michigan individuals (V3 and M6) (Table I).

Discussion

Rheotactic experiments

Our results show that both fluvial and lacustrine populations of mottled sculpin exhibit a mechanosensory based rheotaxis to low velocity flows, as has been reported for several

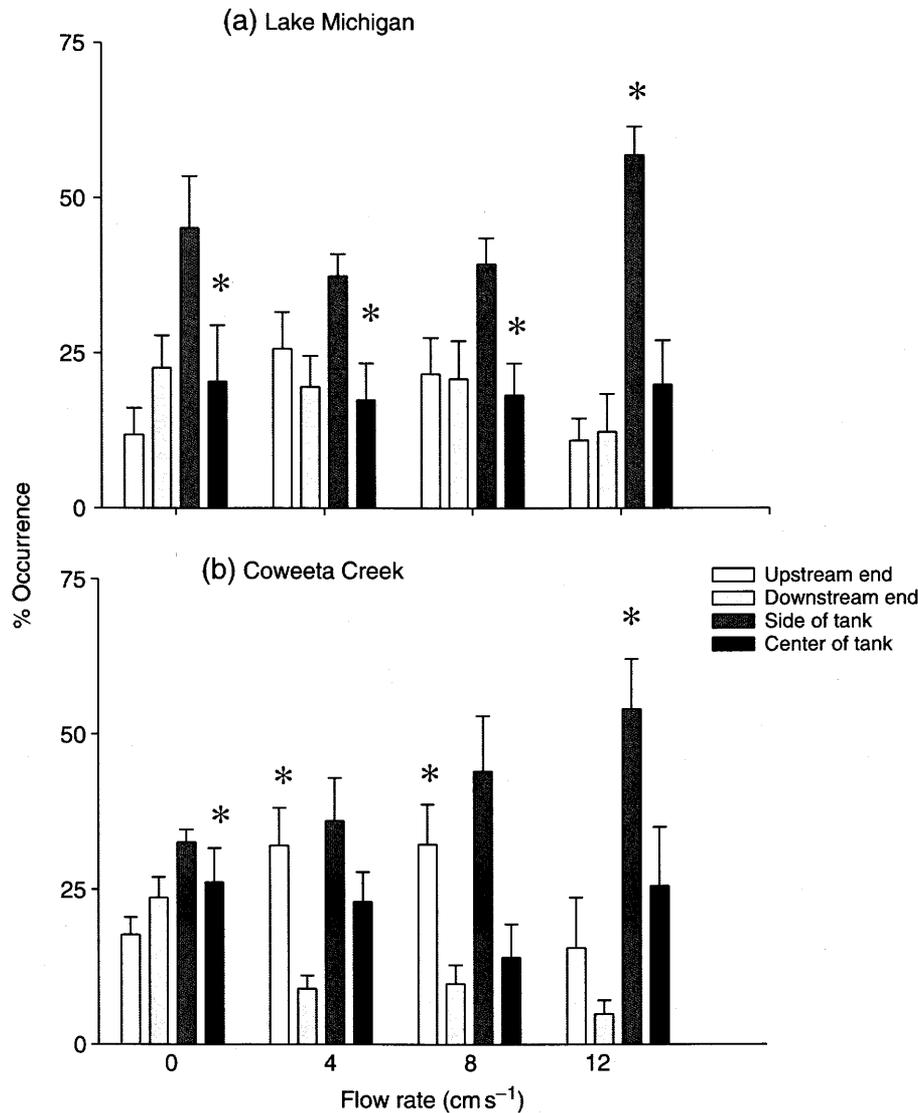


Figure 3. Mean percent occurrence of Lake Michigan (a) and Coweeta Creek (b) sculpin at different locations in the tank, during different velocity treatments. Data are pooled over all individuals in each population. Chi-square tests indicated that all distributions differed significantly from random (i.e. sculpin did not occupy locations based on their availability alone, all p 's < 0.01). The asterisk denotes the category with the highest marginal total (i.e. the category that contributes most to significance of the statistic).

other species, including the stream-dwelling torrentfish (*Cheimarrichthys fosteri*), the pool and the stream-dwelling blind cavefish (*Astyanax fasciatus*) and the cryopelagic antarctic fish (*Pagothenia borchgrevinki*) (Montgomery et al. 1997; Baker and Montgomery 1999a, b). In these species, the rheotactic response to current velocities below 10 cm s⁻¹ is not manifested when the superficial neuromasts of the lateral line system are pharmacologically blocked. Although we did not experimentally confirm that the rheotactic behavior of mottled sculpin was likewise mediated solely by the lateral line system, other mechanosensory candidates (i.e. tactile and inner ear senses) are unlikely to play a role at current velocities insufficient to displace the fish (Arnold 1974; Montgomery et al. 2000).

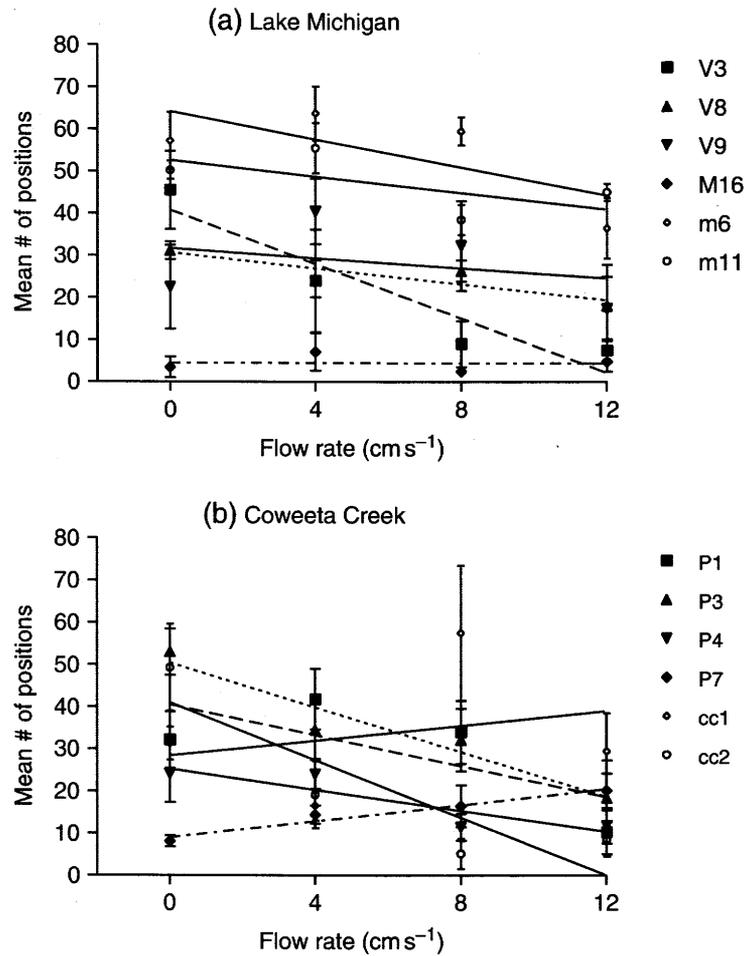


Figure 4. Mean repositioning frequency (number of positions/5 min) as a function of flow rate for Lake Michigan (a) and Coweeta Creek (b) sculpin. We present the regression lines, points and 95% CI around the points for each regression. Regression statistics are summarized in Table I.

Table I. Regression statistics for repositioning frequency of sculpin *vs.* flow rate. Slope of regression line, goodness of fit (r^2) and p -values for slopes significantly different from zero.

	V3	V8	V9	M6	M11	M16
Lake Michigan population						
Slope	-3.2	-0.9	-0.6	-1.7	-1.01	-0.0
r^2	0.36	0.1	0.01	0.25	0.18	0.00
P	0.002	>0.05	>0.05	0.05	>0.05	>0.05
	P1	P3	P4	P7	CC1	CC2
Coweeta Creek population						
Slope	-1.8	-2.6	-1.2	1.0	0.9	-3.4
r^2	0.18	0.39	0.21	0.14	0.02	0.42
P	0.04	0.001	0.02	>0.05	>0.05	0.0006

Flow velocities in this study did not displace fish downstream, a result that is consistent with measured slip speeds for different stream populations of mottled sculpin (Webb et al. 1986; Facey and Grossman 1990). Moreover, physiological studies show that superficial neuromasts are exceedingly sensitive to low velocity currents (Montgomery et al. 2000; Englemann et al. 2002) and thus, well-suited for the task.

Our results also show that the strength and in some cases, the polarity of the rheotactic response varies as a function of flow velocity. The rheotactic responses of the Lake Michigan population generally increased in vector strength with increasing flow velocity. These results are similar in principle to those obtained from torrentfish, blind cavefish, and Antarctic fish, in that rheotactic strength (in this case, measured by the percentage of fish showing positive rheotaxis) generally increased with increasing flow rates up to 8 cm s^{-1} (Montgomery et al. 1997; Baker and Montgomery 1999a, b). In contrast, the rheotactic vector strength of Coweeta Creek mottled sculpin varied with flow rate in a non-linear fashion and with higher degrees of inter-individual variability. At higher flow rates, the rheotactic responses of Coweeta Creek mottled sculpin tended to be either reduced in strength or reversed in polarity (from positive to negative) relative to that at lower flow rates. Because negative rheotaxis in Coweeta Creek mottled sculpin occasionally has been observed in the field (Grossman, personal observation), it appears to be a real phenomenon. Other species have shown polarity changes as a function of flow velocity, but in opposite directions. That is, salmon fry from the Stellako River progressively changed from upstream to downstream orientations when current velocity was reduced from 15.2 to 2.8 cm s^{-1} in an artificial stream (Brannon 1972).

In cases where rheotaxis plays a major role in the spawning migrations of fish, differences in the polarity of rheotactic preferences can be understood in light of the migration direction. Brannon (1967), for example, demonstrated that Chilko River fry, an upstream migrant population of salmon, moved predominantly upstream when placed in an artificial stream with low current velocities, whereas Stellako River Fry, normally downstream migrants, moved downstream. Whereas positive rheotaxis in non-migrating benthic species like mottled sculpin may benefit fish in terms of energy conservation, the function of negative rheotaxis is unclear. Low frequencies of negative rheotaxis in Coweeta Creek sculpin may simply reflect an absence of benefits accrued by positive rheotaxis (see discussion below), or situations in the field where the fish is still within the benthic microzone and hence, sheltered from strong current effects (Grossman and Ratajczak 1998).

Both Coweeta Creek and Lake Michigan mottled sculpin appeared to avoid the central portion of the flow tank and typically preferred tank sections adjacent to a wall (i.e. sides, upstream or downstream). This may represent an adaptation for reducing the energetic costs of holding position, because boundary layer effects (i.e. the slowing down of water near the surface of a solid) are likely to reduce the true velocities experienced by mottled sculpin. These findings are also in concordance with long-term field studies of microhabitat use by Coweeta Creek mottled sculpin, which demonstrate that this species is almost always found under shelter or resting on the substratum, at focal point velocities (i.e. velocity at the fish's head) substantially lower (i.e. $<5 \text{ cm s}^{-1}$) than the average velocities observed in the water column ($>22 \text{ cm s}^{-1}$, Grossman and Ratajczak 1998). It is unlikely that these responses are a consequence of predator avoidance, because predators have little effect on microhabitat use by mottled sculpin in Coweeta Creek (Grossman et al. 1998). Rheotaxis and thigmotaxis are likely to result in decreased energetic costs of holding position for Lake Michigan mottled sculpin, which also inhabit sheltered areas in the lake (Hoekstra and Janssen 1985). Though lake mottled sculpin may not encounter continual, unidirectional

currents like those found in lotic systems, the lake does possess bulk currents and flows created by seiches, wind effects, and temperature-related mixing in lake ecosystems (Goldman and Horne 1983). Coweeta Creek mottled sculpin appeared to show a stronger negative relationship between the velocity and the repositioning frequency than Lake Michigan sculpin – a finding that may very well arise from the former population's greater experience with and exposure to continuous currents more or less in the same direction.

Prey-orienting experiments

The majority of Lake Michigan mottled sculpin met our feeding criterion for signal testing in the experimental tank. In the absence of visual and chemosensory cues, Lake Michigan mottled sculpin responded to the 50 Hz vibrations of a nearby sphere with an unconditioned orienting and feeding behavior, as has been reported previously in numerous studies (Hoekstra and Janssen 1986; Coombs and Janssen 1990; Coombs 1995; Coombs and Conley 1997a, b). Unlike Lake Michigan mottled sculpin, Coweeta Creek fish failed to meet our feeding criterion for signal testing in the experimental tank. These results are consistent with those obtained from Rob Roy Creek mottled sculpin, which, after feeding successfully in their home tanks, failed to feed in the experimental tank for up to 1 month (12 sessions) (Coombs, unpublished data). Given that the majority of both Coweeta Creek and Lake Michigan sculpin readily fed on squid in their home tanks, indicating that this feeding capability was present in both groups, it is unlikely that our home-tank feeding criterion led to a biased sample of the experimental animals.

The failure of Coweeta Creek sculpin to meet the feeding criterion in the experimental tank meant that we could not test their responsiveness to the mechanosensory cues alone, in a way that was comparable to the previous experiments on Lake Michigan individuals. Hence, we could not eliminate the differential feeding motivation as a confounding factor affecting our results. Nonetheless, our failed attempts to evoke orienting responses from Coweeta Creek sculpin in their home tanks, where normal feeding behavior was observed, argues against differential feeding motivation as an important factor influencing our results.

General discussion

The biological significance, if any, and underlying mechanisms of these population (or interspecific) differences remain unknown, but there are at least two major possibilities: innate differences in sensory abilities at the level of the peripheral nervous system (the sense organs and their neural connections to the brain) and either innate or learned differences in the way that sensory information is processed and used by the central nervous system to effect behavior. The lateral line sensory abilities of Lake Michigan mottled sculpin have been well studied at different levels of the nervous system, including neurophysiological studies of peripheral lateral line nerve fibers (Coombs and Janssen 1990) and central brainstem cells (Coombs et al. 1998), as well as behavioral measures of the motor output (orienting response) of the central nervous system (Coombs and Janssen 1990, Coombs and Fay 1993; Coombs 1999). In contrast, little is known about the lateral line sensory abilities of Coweeta Creek mottled sculpin or auditory, visual, or chemosensory abilities in either group. Coweeta Creek and Lake Michigan mottled sculpin do show minor differences in the peripheral distribution of the lateral line canal neuromasts. Whereas the lateral line trunk canal on Lake Michigan mottled sculpin typically extends between 1/2 and 2/3 of the trunk length, the trunk canal on Coweeta Creek sculpin extends much further (personal observation of the authors). Nevertheless, the gap between the end of the trunk canal and the caudal peduncle is filled by a line of large superficial neuromasts in both species. Despite

these minor differences, it is unlikely that members of the two groups differ significantly in peripheral lateral line abilities – i.e. in threshold levels of sensitivity or frequency range of detection. In fact, even fish from different genera and with far more drastic differences in lateral line canal morphology than found among different groups of mottled sculpin have failed to show significant differences in response properties at the level of peripheral lateral line nerve fibers (Montgomery et al. 1994). Rather, it is more likely that differences arise from how the central nervous system deals with the incoming sensory information.

Because Lake Michigan mottled sculpin are largely nocturnal (Emery 1973; Hoekstra and Janssen 1986), whereas the Coweeta Creek mottled sculpin are active during both diurnal and nocturnal periods (Grossman et al. 1995), inter-population/specific differences may arise from different sensory hierarchies governing the prey capture and rheotactic behaviors. That is, the mechanosensory system may play a much larger role in eliciting these behaviors in nocturnal lake populations than it does in diurnal stream populations. Differences in the sensory hierarchies and adaptations for nocturnal *versus* diurnal feeding might also explain why Lake Michigan sculpin, when blinded, fed readily in the test tank after being transferred from their home tanks, whereas Coweeta Creek sculpin did not. Given that the distance range for mechanosensory detection of small invertebrate prey is likely to be quite short (e.g. <1 cm for *Daphnia* detection, Hoekstra and Janssen 1986), Coweeta Creek sculpin may enjoy a greater prey capture success by relying more heavily on visual cues to expand the distance range. Visual deprivation may have also had a much more profound effect on Coweeta Creek sculpin than the Lake Michigan sculpin in more general ways (e.g. on the ability or proclivity to explore foreign environments) that would also impact feeding behavior in novel test environments.

Whether or not observed differences in rheotactic and prey-orienting behaviors in fluvial and lacustrine mottled sculpin are innate or learned (adaptive changes in the brain over time) is a matter of speculation. The rheotactic response exhibited by several different species of newly hatched juveniles to flowing water (e.g. Jonsson et al. 1994; Kaya and Jeanes 1995, reviewed by Arnold 1974) has long been held as evidence that rheotactic preferences (whether positive or negative) are innate and independent of experience. Even more compelling are studies showing that fluvial species, even when raised from hatching in lacustrine environments, show innately greater tendencies for positive rheotaxis than lacustrine populations (Kaya 1991; Kaya and Jeanes 1995).

Nevertheless, recent studies indicate that three-spined sticklebacks can learn to use flow direction as an orientation cue (Girvan and Brathwaite 2000) and that juvenile gobies can rapidly learn to override their upstream rheotactic preference when exposed to backwaters flowing in directions opposite to their intended migratory direction (Smith and Smith 1998). Lake Michigan mottled sculpin can likewise override their positive rheotactic preference when orienting away from the upstream direction and towards an artificial prey to their left or right (Kanter and Coombs 2003).

Based on laboratory studies, the orienting response of Lake Michigan mottled sculpin to artificial prey is an unconditioned response (unconditioned by us, at least) that can be evoked from naïve animals at high frequencies (>70%) without any food or odor cues being delivered (Coombs et al. 1995). However, the rate of response declines to less than 50% if animals are satiated before testing begins and over a longer time period (several days), if the food is not consistently associated with the orienting response (Coombs et al. 1995). Thus, food reward is needed to maintain, but not condition initial orienting responses from Lake Michigan mottled sculpin in the lab. Nonetheless, it is also possible to train Lake Michigan mottled sculpin to orient toward the vibrating source if, and only

if, the vibration amplitude increases (Coombs and Fay 1993). In these studies, we took advantage of the fact that the orienting behavior extinguishes over time when not maintained with food reward and subsequently shaped the new behavior by rewarding the fish with food only when they responded to the amplitude increases. Thus, it is clear that learning can take place, making it possible that the orienting response of Lake Michigan mottled sculpin towards mechanosensory cues alone is learned. Given that lacustrine and fluvial mottled sculpin inhabit different environments, it is quite likely that they are exposed to different stimuli and have different learning experiences over their life history.

In addition to hydrodynamic differences between lentic and lotic habitats, light penetration at the shallow depths (generally <1 m) where Coweeta Creek sculpin reside (Grossman and Ratajczak 1998) is likely to be better than at the deeper habitats occupied by Lake Michigan mottled sculpin (~3–30 m). Most importantly, light availability to diurnally active Coweeta stream sculpin will differ markedly from that for nocturnally active Lake Michigan sculpin.

Finally, the natural prey encountered by Lake Michigan and Coweeta Creek mottled sculpin also differ substantially. Both gut content and prey availability data for Coweeta Creek mottled sculpin indicate that benthic macroinvertebrates such as trichopterans (e.g. hydropsychids), ephemeropterans (e.g. heptageniids), and plecopterans (e.g. leuctridae) dominate their diet energetically (Stouder 1990), and that epibenthic prey such as amphipods and cladocerans are not generally available (Petty and Grossman 1996). By contrast, epibenthic or sporadically swimming prey (e.g. the amphipod *Gammarus* and the cladoceran *Eurycercus*) make up a significant portion of Lake Michigan mottled sculpin's diet (Hoekstra and Janssen 1985) and the lateral line clearly contributes to the ability of sculpin to detect and localize the vibrations caused by these kinds of prey (Hoekstra and Janssen 1986), as well as those from prey buried in the substrate (Janssen 1990). Although further study is clearly needed, it is quite possible that the benthic macroinvertebrate prey of Coweeta Creek mottled sculpin (being slower and more sedentary in nature) produce weaker mechanosensory cues than those produced by the dominant prey of Lake Michigan sculpin.

Although not directly tested in this study, it is conceivable that the multisensory interaction of mechanosensory, chemosensory, and visual cues may contribute to the observed differences between the two groups. For example, some species exhibit odor-gated rheotaxis in which the presence of a food odor initiates or conditions a lateral-line or visually mediated rheotaxis to help animals find the upstream odor source (Baker and Montgomery 1999; Baker et al. 2002; Carton and Montgomery 2003). In these cases, the current velocity at which the positive rheotaxis is initiated is lower in the presence of the odor than in its absence. In this regard, we should point out that whereas initial tests (first signal trial of each experimental session) of Lake Michigan sculpin to the artificial prey were conducted in the absence of any food odor, the subsequent reinforcement of orienting responses with squid meant that food odor was diffusely present in the tank after the first orienting response occurred. Thus, although it is clear that chemosensory cues are not necessary for the initiation or the directional nature of the response, the chemosense may still contribute to the response in some, as yet unmeasured way. As with odor-gated rheotaxis, food odor may increase the fish's state of alertness or motivation, resulting in an increased probability of the prey-orienting response. Increased probabilities of rheotactic or prey-orienting responses when odors are present may involve multisensory enhancement mechanisms in parts of the brain (optic tectum in fish, superior colliculus in mammals) where information from multiple senses is integrated and orienting responses are orchestrated (Stein and

Meredith 1993). Multisensory cells in this region of the brain can respond to a single sensory cue, but their response magnitude and reliability are enhanced when cues from different sensory modalities (e.g. vision and audition) are combined. Although multisensory enhancement effects can be quite large when the sensory cues for each modality are barely detectable and near threshold, they tend to decline at suprathreshold levels. Given that mechanosensory vibrations in our study were well above threshold levels of detection by the lateral line (Coombs and Janssen 1990), it is unlikely that multisensory enhancement through the addition of both odor and mechanosensory cues for Lake Michigan, but not Coweeta Creek mottled sculpin can account for the observed differences. Furthermore, since squid odors in our study were neither temporally nor spatially linked to the vibrating source, it is difficult to see how they could contribute to the multisensory enhancement.

To summarize, both Lake Michigan and Coweeta Creek mottled sculpin exhibit mechanosensory based rheotaxis in the absence of visual or chemosensory cues, but the vector strength of the rheotactic response of the Coweeta Creek population was suppressed at high flow rates relative to that in the Lake Michigan population. Moreover, prey-orienting behaviors, present in visually deprived Lake Michigan mottled sculpin, could not be elicited from visually deprived Coweeta mottled sculpin with mechanosensory cues alone. The most parsimonious explanation for these results is that behavioral differences have been shaped by different learning experiences in different environments and as a result, visual (and/or chemosensory) cues may play a larger role in the sensory guidance of these behaviors in Coweeta Creek sculpin, whereas mechanosensory cues dominate these behaviors in the Lake Michigan mottled sculpin.

Acknowledgments

The authors thank Jennifer Wasik and Robert Ratajczak for their assistance in collecting animals, conducting behavioral experiments, analyzing data, and maintaining animals. The long-term site access and the logistical support to GG were provided by James Vose, and the staff of the U.S.D.A. Forest Service Coweeta Hydrologic Laboratory. This work was supported by grants from NIH to SC and the U.S.D.A. Forest Service McIntire-Stennis program (GEO-0086-MS) and National Science Foundation (DEB-2018001) to GG. Additional support was provided by the Daniel B. Warnell School of Forest Resources (University of Georgia) and the Parmly Hearing Institute (Loyola University of Chicago). The authors would also like to thank the two anonymous referees for their helpful and constructive comments.

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