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Source: Northwestern Naturalist, 105(1) : 54-58

Published By: Society for Northwestern Vertebrate Biology

URL: <https://doi.org/10.1898/NWN23-11>

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STOP, CHOMP, AND ROLL: ROTATIONAL FEEDING BEHAVIOR IN MARINE SCULPINS

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ABSTRACT—In summer 2022 at the University of Washington Friday Harbor Laboratories on San Juan Island, Washington, we recorded 4 species of marine sculpin, *Oligocottus maculosus*, *Leptocottus armatus*, *Clinocottus globiceps*, and *Clinocottus embryum*, performing rotational feeding behavior in which the fish rapidly rotates about the body axis in order to break off a manageable piece of a prey item. These recordings were made while filming prey-capture trials as part of another study. Although these behaviors have been observed in distantly related groups of primarily anguilliform fishes, these are the first filmed recordings of stout-bodied sculpin species performing rotational feeding behaviors consistently in a laboratory setting. The species observed in the study primarily prey upon small marine invertebrates and fish larvae that they bite or scrape off the substrate, or suction feed from the water column near the substrate. When offered large prey items, they are unable to obtain the food in their ordinary manner and instead bite off small pieces or perform the rotational behavior to assist in tearing off a manageable piece.

Key words: biting, Cottidae, feeding system, rotational, sculpin, spinning

Fishes have evolved many approaches to feeding including suction feeding, ram feeding, and biting (Mehta and Wainwright 2007; Ferry and others 2015). Whereas suction is an indirect method of prey capture that relies on a rapid drop in intraoral pressure to pull prey into the mouth, biting involves direct contact of the jaws with the prey. Ram feeding relies on swim speed to overrun prey and can be performed alone or in combination with the other modes (Ferry and others 2015). Within these approaches are specializations, and one such form of specialized biting is rotational feeding. In rotational feeding, also referred to as spin feeding or twist feeding, the fish or other organism bites onto a prey item too large to ingest and uses a rapid spinning or rotating movement to tear off a smaller-sized piece that is more easily ingested (Taylor 1987).

The ability to reduce a prey item to a more manageable size is especially helpful in organisms without other means of manipulating prey prior to mastication. Rotational feeding has been

observed in several fish taxonomic groups including: elasmobranchs (Springer 1961; Motta and Huber 2012), eels (Helfman and Clark 1986; Miller 1989; Helfman and Winkelman 1991; Mehta and Wainwright 2007; Moretto and others 2022), sculpins (Yoshiyama and others 1996), gobies (Angradi 2018), and other anguilliform fishes including stichaeids and pholids (Clark and others 2016). Some clades of aquatic and terrestrial tetrapods, including crocodylians (Fish and others 2007) and caecilians (Measey and Herrel 2006), also use rotational feeding. Social rotational feeding has even been observed in a species of icefish, *Pagothenia borchgrevinki* (Janssen and others 1992). In these bouts of social rotational feeding, 1 *P. borchgrevinki* individual will capture the prey and attract 1 or 2 conspecifics, which promotes synchronized twisting.

In the summer of 2022, we recorded rotational feeding in 4 species of marine sculpin: (1) Tidepool Sculpin (*Oligocottus maculosus*); (2) Staghorn Sculpin (*Leptocottus armatus*); (3) Mosshead Sculpin (*Clinocottus globiceps*); and (4) Calico Sculpin (*Clinocottus embryum*). Another species of intertidal sculpin, the Saddleback Sculpin (*Oligocottus rimensis*) was observed completing the rotational feeding behavior singly and in groups in the holding tank; however, we did not film this behavior. These opportunistic findings were observed during data collection for comparative studies of feeding kinematics in sculpins. All data presented here were from lab observations. Other species were held and/or filmed feeding in the lab, including 3 species of *Artedius* (*A. lateralis*, *A. fenestralis*, and *A. harringtoni*), *Oligocottus snyderi*, *Rhamphocottus richardsoni*, and *Blepsias cirrhosus*. None of these species exhibited rotational feeding behavior when offered larger pieces of prey.

Fishes were collected through a combination of tidepooling, dip netting, beach seining, and tidepool bailing alongside the Friday Harbor Laboratory Fish Functional Morphology course participants in the San Juan Islands, Washington, USA. *Oligocottus maculosus* were collected at

Deadman Bay (UTM: Zone 10, 48.514240, -123.144534) and Cattle Point (UTM: Zone 10, 48.452356, -122.962320) on San Juan Island. *Leptocottus armatus* were collected via seine at Jackson Beach (UTM: Zone 10, 48.519605, -123.010148) and Eagle Cove (UTM: Zone 10, 48.461562, -123.032536) on San Juan Island. *Clinocottus globiceps* were collected at Cattle Point. *Clinocottus embryum* were collected at Iceberg Point (UTM: Zone 10, 48.419880, -122.892899) on Lopez Island. Fish were housed in flow-through sea tables and separated into labeled flow-through containers during filming to keep track of individuals across multiple days. Fish were left to acclimate in the filming tank until they appeared calm and willing to feed. The filming setup used 2 synchronized Edgertronic cameras (SC1, Sanstreak Corp., Campbell, CA) mounted on tripods, 1 camera mounted for a dorsal view and the other setup for a lateral view, to allow for calculating 3D kinematics of feeding and swimming behaviors. In trials where rotational feeding was observed, the individual was offered a large piece of thawed shrimp held in place with long forceps. Videos were recorded at 500 fps for *L. armatus* and *O. maculosus* and 700 fps for *C. embryum* and *C. globiceps*. All animal use and care procedures and guidelines follow University of Washington IACUC protocol #4238-18.

The species recorded in the study, and other similarly sized cottid fishes, generally feed on small benthic invertebrates and larval fishes, often doing so on or near the substrate and sometimes feeding on suspended prey items (Norton 1991; Buser and others 2019). *Oligocottus maculosus* feeds mainly on marine invertebrates including isopods, amphipods, snails, and worms (Norton 1991; Buser and others 2019). *Leptocottus armatus* is known to consume salmon fry (Mace 1983) in addition to benthic invertebrates including amphipods, polychaetes, mysids, and isopods (Norton 1995; Visintainer and others 2006; Buser and others 2019). *Clinocottus embryum* is also primarily a benthic invertivore (Miller 1980; Buser and others 2019) and has even been observed to be cannibalistic in a laboratory setting (Pfister 1999). *Clinocottus globiceps* specializes in anemone feeding with its diet also including algae and small pelagic invertebrates (Yoshiyama and others 1996; Buser and others 2019).

Initial expectations during feeding trials with large prey items were that the sculpins would bite off small pieces of the shrimp as previously

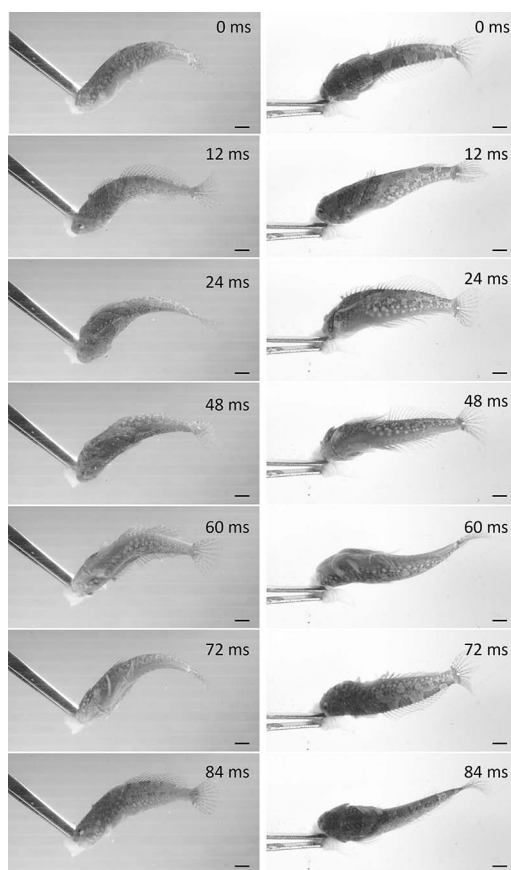


FIGURE 1. Lateral (left) and dorsal (right) views of 1 full rotation of *Oligocottus maculosus*; rotation is the 2nd full rotation from a sequence of 9 continuous rotations. Scale bar = 10 mm.

observed while feeding fish in the holding tanks. Although many individuals did take small bites from the larger piece, some used the spinning behavior to shear off small enough pieces to ingest (Fig. 1). When performing the rotational behavior, fish rotated along the long axis and fins were kept flush to the body at the beginning of all rotational bouts. Rotations were never the first attempt to obtain food. Instead, the sculpins would bite first, unsuccessfully, and then return to attempt to remove a manageable piece of food through rotational feeding. In some trials the fish would take multiple bites at the same site, seemingly to get a good grasp on the prey item before beginning to rotate.

The data presented here represent 8 rotational feeding trials observed across the 4 species (Table 1). The specimens filmed ranged in size from 4.2 to

TABLE 1. Summary of individuals used in this study.

Species	Individual identification number	Total length (cm)	Number of trials analyzed	Number of rotations	Average angular speed \pm SD (ms rotation ⁻¹)	Range (ms)
<i>Leptocottus armatus</i>	Larm08	10.6	1	7	90.57 \pm 16.36	76.00–124.00
	Larm09	10.1	3	2.5	114.00 \pm 14.14	104.00–124.00
				4	104.00 \pm 23.04	88.00–138.00
				1	146.00	—
<i>Oligocottus maculosus</i>	Omac03	9.4	1	8	78.50 \pm 10.73	64.00–92.00
	Omac05	7.4	1	14	65.00 \pm 11.58	54.00–92.00
<i>Clinocottus globiceps</i>	Cglob03	4.2	3	11	131.30 \pm 39.35	75.71–194.29
				11	140.52 \pm 15.92	120.00–168.57
				4	86.79 \pm 25.11	71.43–124.29
<i>Clinocottus embryum</i>	Cemb01	7	2	9	120.00 \pm 30.59	85.71–182.86
				10	88.00 \pm 15.20	51.43–104.29

10.6 cm in total length. Owing to the complex orientation of fish and limited number of cameras, 3D kinematic analyses of spins were not possible and the descriptions we present are limited to basic qualitative and quantitative analyses. Angular speed for each spin was calculated by determining the elapsed time for the fish to complete a 360° rotation.

Across species, we observed rotations to the left and to the right, but owing to the small sample size it was unclear whether individuals had directional preferences or responded to some aspect of prey presentation. Another variation observed among species was the amount of axial bending during rotations. *Leptocottus armatus* showed the least bending along the midline and *O. maculosus* exhibited the most sinusoidal axial bending, with bending in *C. embryum* appearing to be between the 2 previous species but more similar to *O. maculosus* in the amount of bending. *Clinocottus globiceps* showed the most diversity in movements, varying axial bending with angular velocity and would be of particular interest in further work using an updated camera arrangement to capture movement more accurately.

The number of rotations per trial varied within and between species. Overall, *L. armatus* had the smallest number of rotations per trial, ranging from 1 to 7. In contrast, *C. embryum* performed 9 and 10 rotations in each trial, whereas *C. globiceps* performed 4 rotations in 1 trial and 11 in the other 2 trials, and *O. maculosus* performed 8 and 14 rotations. In trials for *O. maculosus* and *C. embryum*, the fish splayed their pectoral fins out to the side during the last rotation, which caused a rapid decrease in rotational speed (Fig. 2). *Leptocottus armatus* did not splay pectoral fins out at the end

of the rotations. Instead, these individuals turned their body away from the prey item, leading with the head to remove their bite of food.

Species varied in average angular speed, with the fastest rotations seen in *O. maculosus* (mean = 69.91 ms rotation⁻¹, SD = 12.87). Intermediate speeds occurred in *L. armatus* (mean = 101.71 ms rotation⁻¹, SD = 22.45) and *C. embryum* (mean = 103.16 ms rotation⁻¹, SD = 28.30). The slowest average angular speed was seen in *C. globiceps* (mean = 128.35 ms rotation⁻¹, SD = 33.79). These averages do not include the final rotation when fins were splayed out, slowing the rotation in *C. embryum* or *O. maculosus*. *C. globiceps* exhibited the greatest range in angular speed, with the fastest rotations reaching 195 ms. Axial bending in *C. globiceps* varied at different rotational speeds; at the faster rotations, the body was kept straighter, more rigid, whereas the slower rotations included pauses mid-rotation and increased axial bending.

These observations show that rotational feeding behaviors are readily employed in the lab by multiple sculpin species when offered prey items larger than their typical prey types. This affirms that rotational feeding is not limited to primarily elongate fishes and suggests that rotational feeding might be an important feeding mode in sculpins that has been largely overlooked and is more widespread than initially known. However, comparisons of biting versus rotational feeding proportions were not possible with the current data set. Further investigation is necessary with an updated filming scheme and a broader recording approach. Using at least 4 views would allow for a better comparison of movement during rotational feeding, including undulation amplitude and

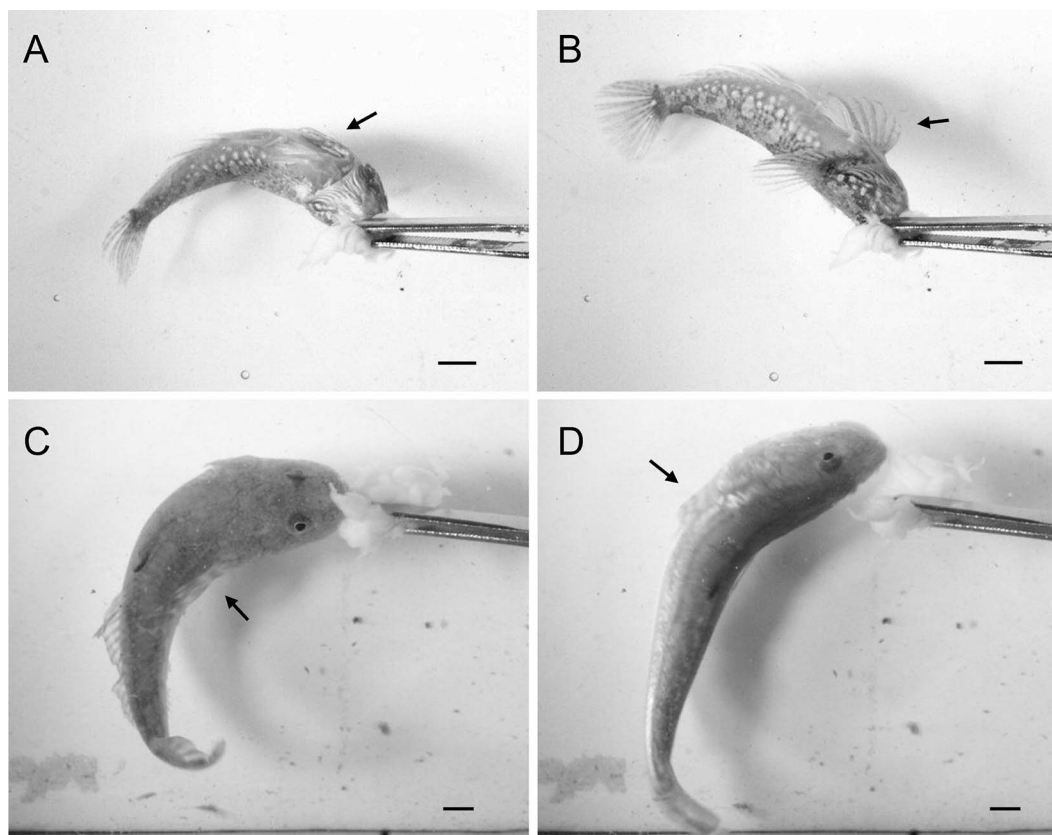


FIGURE 2. Representative images showing pectoral fin use during a final roll. (A) *Oligocottus maculosus* before with their pectoral fins flush against the body and (B) while splaying pectoral fins, slowing rotations; and (C–D) *Leptocottus armatus* keeping fins flush against body and ending rotation by turning away from food parcel. Scale bar = 10 mm. Arrows indicate pectoral fin placement.

changes in rotation along the body. Standardization of prey placement using a clamp instead of hand-held forceps will remove the influence of hand movements and should support a more standardized approach for the fish towards the prey.

Oligocottus maculosus, *L. armatus*, *C. embryum*, *C. globiceps*, and *O. rimensis* were the only species observed completing rotational feeding in this study. Interestingly, *Oligocottus* and *Clinocottus* are closely related intertidal genera, whereas *L. armatus* is a more distant subtidal species (Buser and others 2019). It is unclear whether this behavior is a factor of habitat of origin, life stage, or other traits, as not all species performed rotational feeding. An increase in the number of species studied, a range of individual body size, and adjustments to the filming scheme will greatly increase our understanding of this behavior. Additionally, we expect that in specific conditions and

motivations, other species may also be capable of this behavior, and it may be more widespread across aquatic vertebrates than previously reported.

Acknowledgements.—We thank the Friday Harbor Laboratory 2022 Functional Morphology and Ecology of Marine Fishes course students, instructors, and guests who participated in fish collection throughout the summer. Specifically, we wish to thank SD Arnette, LL Lungstrom, and MA Kolmann for their help with collecting *C. globiceps* from San Juan and *C. embryum* from Lopez Island. Funding: Company of Biologists Traveling Fellowship (JEB) awarded to CHC; NSF graduate research fellowship DGE-1746914, Stephen and Ruth Wainwright Endowment Fellowship (from FHL), and Wilbur V Harlan Research Fellowship (from GWU) awarded to JMH; and FHL New Faculty Fellowship awarded to EAK and EAK startup at University of Louisiana at Lafayette.

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