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Experimental evaluation of the use of vision and barbels as references for rheotaxis in green sturgeon

Myfanwy E. Johnston[a,*], John T. Kelly[b], M. Emilia Lindvall[a], Richard McElreath[c], A. Peter Klimley[a]

[a] Department of Wildlife, Fish, and Conservation Biology, University of California, 1 Shields Ave, Davis, CA 95616, USA
[b] Department of Biology and Environmental Science, University of New Haven, 300 Boston Post Rd., West Haven, CT 06516, USA
[c] Max Planck Institute for Evolutionary Anthropology, Department of Human Behavior, Ecology and Culture, Deutscher Platz 6, 04103 Leipzig, Germany

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ABSTRACT

Rheotropism (the ability to detect and respond to a current) and rheotaxis (deliberate orientation relative to a current) are widespread in fishes and aquatic organisms, but the relative importance of different sensory modalities as references for the rheotaxis response in fishes is largely unknown. While mechanical stimuli (including water flows) have been used to evaluate rheotaxis behavior in fishes, comparison between sensory modalities is rare, and there has been little or no investigation into the mechanosensory role of barbels in rheotaxis for bottom-oriented fish. We conducted two experiments to evaluate the role of visual stimuli (in the form of an optomotor belt) and barbels in juvenile green sturgeon rheotaxis behavior. The green sturgeon did not exhibit a clear optomotor response, and spent a higher proportion of time positively oriented toward a flowing current than they did toward a moving background in the absence of flow. Removal of barbels increased the average individual tendency to orient positively in the presence of flow. While visual cues almost certainly play a role in rheotaxis behavior at large, individuals vary greatly in their degree of responsiveness to stimuli, and the optomotor stimuli used in our experiments were not as effective as the mechanosensory stimuli in provoking positive rheotaxis. Further, the barbels of green sturgeon do not appear to influence their ability to display positive rheotaxis in the presence of water current.

1. Introduction

Rheotropism, the ability to detect and respond to a current, and rheotaxis, orientation into or away from a current, are widespread in aquatic organisms and were first studied in detail in fishes by Lyon (1904). Most fish exhibit innate rheotaxis, and the behavior plays an important role at every stage of life history (Arnold, 1974). Movement of water is detected when the current stimulates superficial neuromasts – hair cells of the lateral line system distributed across the head and body of the fish (Baker and Montgomery, 1999). However, based on neuromast output alone, the fish cannot distinguish between a current and its own movement. Additionally, if the fish is drifting passively in a current, it may receive no output at all from its neuromasts and not feel as if it were moving. In order to detect movement – its own or that of the water around it – the fish must have a frame of reference. As described by Arnold (1974), there are several sensory cues that fish may utilize for this purpose, and principal among these is the visual system. In early experiments, Lyon (1904) showed that fish (*Fundulus* spp.) reacted to a striped strip of cloth being drawn underneath the bottom of their tank in the same manner as they would react to current. The fish showed positive rheotaxis, turning to face the direction of movement of the visual field. This "optomotor response" has been described to varying degrees in a host of fish species (e.g. Pavlov et al., 1969). Indeed, Arnold (1974) believes that the optomotor response occurs in "nearly all fish, with the exception of a few sessile forms" (p. 526).

The relative importance of different sensory modalities to the rheotaxis response in fishes is largely unknown. For fish that can see the bottom, the optomotor response may be sufficient; however, many fish make lengthy oriented movements while swimming up in the water column or in turbid conditions, despite the apparent absence of benthic visual cues. Additionally, fish may be utilizing tactile inputs as an external frame of reference for rheotropism. For example, in species that utilize sensory barbels for foraging and sensing the substrate below them, including *Acipenser medirostris* (green sturgeon), their barbels may provide a tactile reference point to the direction of water currents when a visual reference is unavailable.

* Corresponding author.
E-mail addresses: merowlands@ucdavis.edu (M.E. Johnston), jkelly@newhaven.edu (J.T. Kelly), melindvall@ucdavis.edu (M.E. Lindvall), richard_mcelreath@eva.mpg.de (R. McElreath), apklimley@ucdavis.edu (A.P. Klimley).

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Rheotaxis behavior is present in different forms and degrees in green sturgeon at almost every life stage, but there has been very little investigation regarding the rheotropic cues used in these orientations. Green sturgeon larvae display nocturnal behaviors and migrate downstream (Van Eenennaam et al., 2001), but their downstream movement is often interrupted with short foraging bouts upstream (Kynard et al., 2005). As green sturgeon mature to juveniles, deliberate rheotaxis is evident (Poletto et al., 2014). Adult green sturgeon display strong rheotaxis, negatively orienting to currents at the top of the water column and positively orienting to those nearer to the bottom (Kelly and Klimley, 2012). Still unknown is whether green sturgeon primarily attend to visual cues (for example, the substrate beneath them or celestial cues above them, among others), mechanosensory ones (their barbels), or geomagnetic cues for rheotaxis.

To investigate the source of the rheotaxis response in green sturgeon, we conducted two experiments investigating the role of visual stimuli (in the form of the optomotor response) and barbels as a tactile reference point, respectively. The goal of this design was not to determine whether juvenile green sturgeon orient to current (we expected the fish would orient to current, as has been found in other fish taxa (Arnold, 1974; Münz, 1989; Montgomery et al., 1997, Moyle, 2002)), but was instead to determine how important visual stimuli are as a frame of reference for rheotaxis. If juvenile green sturgeon rely upon tactile cues (via their barbels, or other points of contact) to provide a stationary reference point, then water flow detected by their superficial neuromasts should be adequate to elicit rheotaxis. If, however, a juvenile green sturgeon uses vision to perceive that it is stationary relative to its background, then the reverse movement of the background would signal forward movement (see bottom panel, Fig. 1) and provoke a compensatory optomotor response.

2. Methods

2.1. Experimental apparatus

A partitioned tank (Fig. 1, left) was built to provide two different kinds of experimental flows: 1) physical water current with a stationary background, and 2) optomotor visual “flow,” in the form of a moving background and in the absence of physical water current. It contained an experimental chamber in which the subject was held (water depth in the chamber was 45 cm), which was 60 cm in width, 51 cm in height, and 148 cm in length. An electric outboard motor with a rotating propeller that generated a diffuse current for the experimental flow trials was mounted on the far side of the partition adjacent to the experimental chamber. As this was not a respirometer study, we did not require flow in the chamber to be perfectly laminar – we did require that all the water in the chamber flow the same direction, and that the flow would not change from positive to negative during the trials. A Marsh McBirney flow meter was used to take readings at three depths (top, middle, and bottom of water column), three widths (left, middle, and right), and seven locations along the length of the chamber for a total of 63 locations. To verify that flow did not change direction in the tank during the trials, these readings were taken at potentiometer settings 1, 2, 3, 4, and 5 with the diffuser screen in place.

For the experimental visual trials, the moving background (hereafter termed the optomotor belt) was a canvas belt with alternating, 5 cm-wide, horizontal black and white stripes that could be placed either above or below the subject of the experiment and set to move with an electronic motor, so that the pattern of alternating stripes advanced, in the same way the belt on a treadmill advances. The optomotor belt is shown at the bottom of the flow chamber in the two illustrations of the apparatus (Fig. 1, right).

For all timed trials in both experiments, a juvenile sturgeon was placed in the experimental chamber, where its swimming behavior was observed under one of four possible Conditions. The first two Conditions comprised the optomotor trials, and were conceived to isolate just the visual sensory modality, and to determine if the fish attended to a certain visual field (above for potential surface or interface cues, or below for benthic cues). The first Condition, termed ‘Above’, occurred under daylight and consisted of the striped optomotor belt moving above the subject, with no flow present in the chamber. The second Condition, ‘Below’, occurred under daylight and consisted of the belt moving below the subject with no flow of water. The third Condition, ‘Light’, occurred under daylight and in the presence of water flow in the chamber, with no optomotor stimulus. The fourth and final ‘Dark’ Condition took place in darkness and in the presence of water flow in the chamber, also with no optomotor stimulus present, and was designed to remove all visual reference cues. By organizing the Conditions this way, the Light Condition essentially served as a control for the other Conditions' isolation of response to visual cues.

2.2. Experimental design

There were two sets of trials, referred to throughout as the “barbels-intact” experiment and the “barbels-removed” experiment. In the barbels-intact experiment, all four experimental Conditions (Above, Below, Light, and Dark) were conducted on juvenile green sturgeon with their barbels in place. For the barbels-removed experiment, barbels were removed surgically (details of surgical procedure are provided in Supplementary materials), and trials for Conditions Light and Dark were repeated in order to determine if barbels were providing a tactile frame of reference for rheotaxis. An overview of the experiments, trials, and Conditions are given in Table 1. Twenty-four juvenile green sturgeon (from 49 to 64 cm in total length) underwent a total of 118 timed swimming trials in the two experiments (96 trials in the barbels-intact experiment, and 22 trials in the barbels-removed experiment). In each experiment, a subject was allowed to acclimate to the tank environment for a minimum of 35 min prior to completing a single trial with either flow or visual Conditions. With their barbels intact, twenty-three fish underwent each of the four experimental Conditions. The sequence of Conditions was determined by Latin square design. A labeling mishap gave the appearance of a single fish (ID #20) undergoing all four

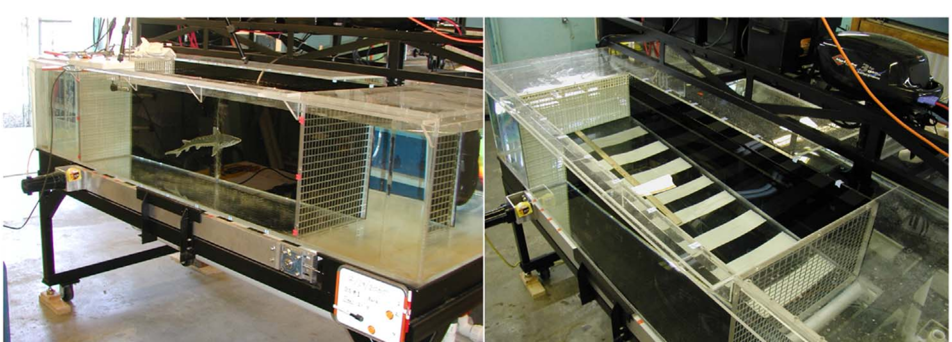

Fig. 1. Photographs of a juvenile green sturgeon subject in the apparatus built for experiments (left), showing the diffuser screen and experimental chamber; and the physical setup for Condition Below (right), where the striped optomotor belt is placed below the experimental chamber. In Condition Above, the optomotor belt is moved to the top side of the experimental chamber.