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

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A B S T R A C T

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.

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.

Table 1
Experimental design of rheotaxis trials.

Experiment	Type of stimuli	Condition	Trials (N)	Individuals (N)	Mean trial time in minutes (SD)
Barbels-intact	Optomotor (visual)	Above	24	23	8.78 (0.96)
	Optomotor (visual)	Below	24	23	9.04 (0.63)
	Mechanical	Light	24	23	11.11 (1.76)
	Mechanical	Dark	24	23	10.92 (1.23)
Barbels-removed	Mechanical	Light	11	11	11.73 (0.59)
	Mechanical	Dark	11	11	11.67 (0.48)

Conditions twice; for the sake of conservatism, we have analyzed the data as though it was the same fish, although in all likelihood it was two different fish. Each of the flow trials began with a flow velocity of $1 \, ms^{-1}$; flow was increased in increments of $0.1 \, ms^{-1}$ every 15 s until a maximum of $2 \, ms^{-1}$ was reached. For the optomotor trials (composed of Conditions Above and Below), each trial began with the optomotor belt moving at $1 \, ms^{-1}$; the belt's speed was increased by $0.1 \, ms^{-1}$ every 15 s until a speed of $2 \, ms^{-1}$ was reached. Water velocity was measured using an electromagnetic velocity meter (Marsh McBirney, Inc., Flo-mate Model 2000). Average water temperature across trials was 20.9 °C ± 1.14.

Video recordings of the trials were made with MiniDV camcorders (Sony, Inc., DCR-TRV18) with "NightShot" infrared sensors and analyzed using Jwatcher (Blumstein et al., 2012). For the flow trials, the camera was positioned to the left side of the swim chamber (relative to the direction of flow) on a tripod at a distance sufficient to capture the entire chamber. Infrared LED lights were positioned around, above, and under the chamber to provide illumination during the Dark Condition. For the optomotor trials, a second camera was equipped with a wide-angle conversion lens (Sony, Inc., VCL-06305) and mounted either above or below the swim chamber, depending on the position of the optomotor belt. During analysis of the taped trials, specific keystrokes were assigned to mark change points between positive, neutral, and negative rheotaxis during a timed trial of an individual fish.

The range of degrees used to define positive, negative, or neutral orientation are displayed in Fig. 2. Impinging flow (either real physical flow in the water flow Conditions or the optomotor belt "flow" in the visual Conditions) was oriented 180° relative to the right side of the video frame. Positive rheotaxis was then defined as maintaining a body position in the water column where the fish's head was facing the oncoming flow at any orientation between 120° and 240° (Fig. 2). Negative orientation was defined as a body position oriented between 300°–360° and 0°–60° relative to the direction of flow or "flow". Neutral orientation was defined as maintaining body position between either 61° and 119°, or between 241° and 299°. In other words, with 120° possible for each of three orientations, we might expect to see mean

proportions of 0.33 for positive, neutral, and negative rheotaxis behavior across timed trials if rheotaxis response was random. The proportion of time spent in each orientation during each trial was calculated by tracking and summing the time elapsed between change points. Although the full dataset is provided in Supplementary materials, the analysis presented here concerns only the proportion of time spent positively oriented during a trial, and not that spent negatively or neutrally oriented.

In the barbels-removed experiment, eleven of the 23 fish from the barbels-intact experiment and two new individuals underwent 22 additional water flow trials (Conditions Light and Dark) to determine whether their barbels played an observable role in flow detection, and thus on rheotaxis behavior. Video recording and data analysis followed the same procedure as in the barbels-intact experiment.

2.3. Statistical analysis

A series of multilevel beta regression models were first fit to the data and then compared using the *rethinking* package (McElreath, 2015) for the *rstan* package (Stan Development Team, 2014) in the statistical software R (R Core Team, 2016). Models were sampled with Hamilton Monte Carlo (HMC) estimation. All non-adaptive priors used were only weakly informative. HMC chains were verified to be well-mixed and stationary, and model comparison was performed using Widely Applicable Information Criterion (WAIC). WAIC is a generalized Bayesian version of AIC and can, in this analysis, be interpreted similarly (McElreath, 2015; Watanabe, 2010). A full justification of the Bayesian approach, as well as the code and data used to fit the models, is provided in supplementary materials.

The response variable modeled was the proportion of time spent positively oriented during a given trial. Accordingly, the beta distribution was selected for its ability to model continuous data restricted to the interval (0,1) (Ferrari and Cribari-Neto, 2004). One zero was present in the observed response values, and models were run first with this value excluded and then with this value reassigned to 0.0001; after determining the results did not change with its inclusion, it has been
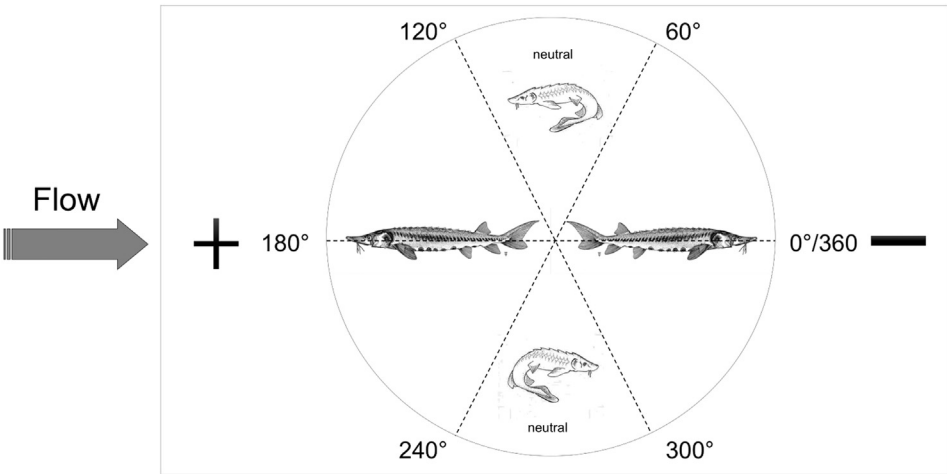
Fig. 2. The range of degrees used to define positive, negative, or neutral orientation. Impinging flow (either real physical flow in the water flow Conditions or the optomotor belt "flow" in the visual Conditions) went from left to right across the frame. Positive rheotaxis was then defined as maintaining a body position in the water column where the fish's head was facing the oncoming flow at any orientation between 120° and 240°. Negative orientation was defined as a body position oriented between 300°–360° and 0°–60°. Neutral orientation was defined as maintaining body position between either 61° and 119°, or between 241° and 299°.

left in the final dataset with its reassigned value. Reported model coefficient estimates have been converted from the model output scale of log-odds back to the proportional scale for easier interpretation. The predictor variables considered for inclusion in model likelihoods for the barbels-intact experiment were: individual fish (1 through 23), Condition (Above, Below, Light, or Dark), and the presence or absence of flow (a dummy variable codified by pooling the flow Condition trials as "1" and the visual Condition trials as "0", respectively). Eleven models were fit to the data from the barbels-intact experiment. For the barbels-removed experiment, eight candidate models were structured to fit the data for the 44 total velocity trials of the 11 fish used in both experiments, so that the effect of barbel removal on individual rheotaxis might be examined. Predictors for inclusion in this model set were: presence or absence of barbels, Condition (Light or Dark), and individual fish. Full specifications and mathematical notation for all models are provided in supplementary materials.

3. Results

The empirical observations of the proportion of time spent positively oriented from the barbels-intact experiment (fish with barbels, exposed to the four Conditions: Above, Below, Light, and Dark) are graphed in Fig. 3, and summary statistics are presented in Table 2. The sample mean and standard deviation of proportion of time spent positively oriented in the flow trials (Conditions Light and Dark) was 0.59 ± 0.37 (median 0.77) and 0.65 ± 0.29 (median 0.76), respectively. The sample mean and standard deviation of proportion of time spent positively oriented in the visual, no-flow trials (Conditions Above and Below) was 0.32 ± 0.12 (median 0.31) and 0.35 ± 0.17 (median 0.35), respectively. Both mean and median values from the visual trials are very close to 0.33, which would be the value expected if the fish moved equally in all directions within the tank (see dotted line, Fig. 2). In contrast, the mean and median values during flow trials are well above 0.33. Variability was present both within and across individuals between Conditions, especially in the flow trials, where proportion positive rheotaxis ranged from 0.00 to 0.996 within the Light Condition and from 0.033 to 0.987 within the Dark Condition.

From the set of eleven models fit to the data, a single model (m2NC) was assigned the full WAIC weight; this model estimated a fixed effect for each Condition, as well as varying effects for each fish and Condition combination. The reader can then interpret the Condition

coefficient estimates reported in Table 3 as "the mean proportion of time spent positively oriented under this Condition, before adding variation in responses between and within fish." Overall, model estimates were very close to the empirical observations, and 95% Confidence intervals for all four fixed Condition coefficients, presented in Table 3, indicate that Condition had a clear effect on the proportion of time spent positively oriented for individual fish. Contrast values between each of the four Conditions (calculated by subtracting the posterior probability of one Condition from that of another, and similar in interpretation to post-hoc multiple comparison analysis) were small between similar types of trials, and larger across different types of trials. The contrasts estimate that respectively, fish spent approximately 31% more time positively oriented under Condition Dark and approximately 23% more time positively oriented under Condition Light than during either of the optomotor Conditions (Above or Below).

In the barbels-removed experiment, removal of barbels correlated with an increase in mean proportion of time spent positively oriented. Most barbelectomized fish (64%) increased in their mean proportion of time spent positively oriented between the two flow Conditions relative to the barbels-intact experiment (Fig. 5). The difference in mean proportion of time spent positively oriented from barbels-intact to barbels-removed was + 0.12 (from 0.60 ± 0.34 to 0.72 ± 0.23, respectively). Four models in the set of eight candidate models fit to the data for the barbels-removed experiment shared 89% of the WAIC weight, and implied nearly identical predictions. Table 4 displays the coefficients of main effects parameters for these top-weighted models.

4. Discussion

Empirical results from these experiments suggest that for juvenile green sturgeon, the presence of (or absence) water flow has a greater effect on the tendency to spend time positively oriented than rheotaxis behavior provoked by an optomotor response. The top-weighted model in the barbels-intact experiment captured the bimodality of the empirical data very well; Fig. 4 shows that the peaks of the distribution density curves are distinct between the optomotor trials (Conditions Above and Below, shown in black and purple) and the flow trials (Conditions Light and Dark, shown in blue and orange). However, results from the model comparison process indicate that although this effect of Condition was clear, high variability in rheotaxis *within* fish, as well as variability across Conditions *between* fish, also strongly

Proportion of Time Spent Positively Oriented by Condition: Barbels-Intact Experiment
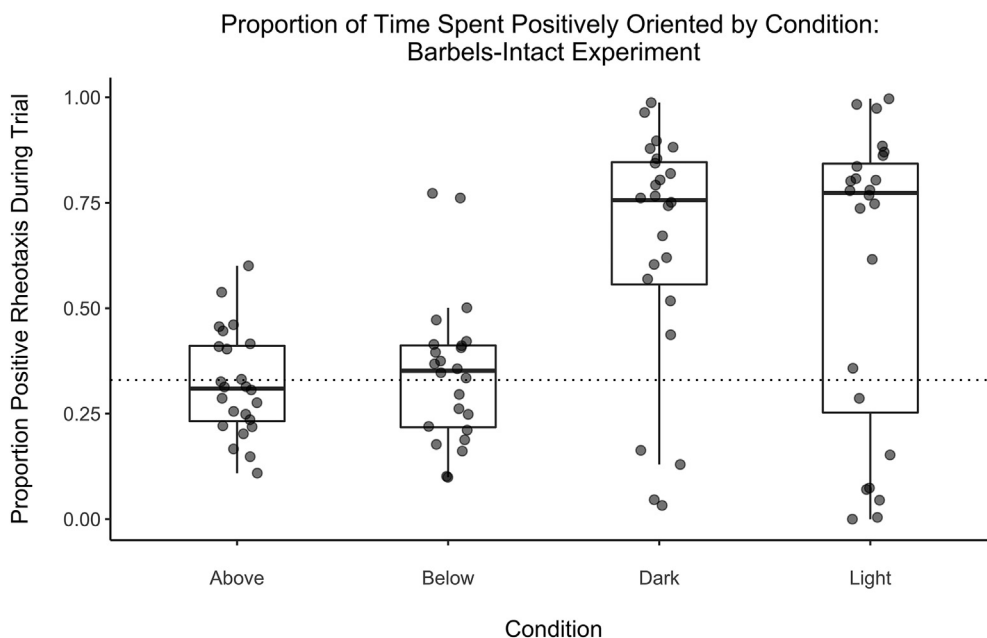
Fig. 3. Empirical data from the barbels-intact experiment. Each dot is the measured proportion of time that a single fish spent positively oriented during that trial (observations have been "jittered" on the x-axis within Conditions to improve visibility).

Table 2
Summary of empirical results, barbels-intact experiment.

Type of stimuli	Condition	Mean proportion of time spent positively oriented (SD)	Mean proportion of time spent negatively oriented (SD)	Mean proportion of time spent neutrally oriented (SD)
Optomotor (visual)	Above	0.32 (0.12)	0.32 (0.14)	0.36 (0.21)
Optomotor (visual)	Below	0.35 (0.17)	0.29 (0.16)	0.36 (0.21)
Mechanical	Light	0.59 (0.37)	0.25 (0.35)	0.16 (0.16)
Mechanical	Dark	0.65 (0.29)	0.13 (0.26)	0.22 (0.19)

Table 3
Estimates of the five main effects parameter coefficients from m2NC, the top-weighted model of the barbels-intact experiment. A population average estimate of positive rheotaxis for each condition is represented by parameters "Condition Above", "Condition Below", "Condition Light", and "Condition Dark", respectively. Within the model, the effects of condition and individual fish were allowed to covary.

Parameter	Mean (SD)	95% CI	Effective samples (N_eff)	$\hat{R}$
Condition Above	0.32 (0.53)	0.27–0.38	9000	1
Condition Below	0.34 (0.54)	0.27–0.42	4881	1
Condition Light	0.57 (0.60)	0.37–0.75	4196	1
Condition Dark	0.65 (0.58)	0.50–0.77	4280	1

Table 4
Coefficient estimates from four models of the barbel removal experiment, which collectively shared 89% of the WAIC weight of the set of eight candidate models fit to the data. The "Barbels Present" parameter represents the fixed effect of the presence of barbels, while the "Condition Present" parameter represents the fixed effect of water flow present during the trial. "Sigma Fish" represents the effect of an average individual fish on positive rheotaxis, and Sigma Condition represents the average effect of Condition on positive rheotaxis. In models mB7 and mB8, the effect of the presence of barbels was allowed to covary with the effect of condition and individual fish, respectively.

Model	WAIC weight	Parameter	Mean (SD)	CI (95%)	Effective samples (N_eff)	$\hat{R}$
mB8	0.27	Barbels Present	0.43 (0.59)	0.26–0.62	3707	1
mB5	0.27	Barbels Present	0.42 (0.60)	0.31–0.56	5198	1
mB6	0.20	Barbels Present	0.37 (0.57)	0.26–0.52	6825	1
		Condition Present	0.59 (0.55)	0.49–0.68	3557	1
		Sigma Fish	0.73 (0.73)	0.50–0.95	9000	1
mB7	0.15	Barbels Present	0.46 (0.64)	0.22–0.72	4875	1
		Sigma Fish	0.73 (0.73)	0.50–0.95	9000	1
		Sigma Condition	0.73 (0.73)	0.50–0.95	9000	1

characterize these data. This is worth emphasizing, because although the empirical results from these experiments were relatively straightforward, future experiments on subtler or overlapping sensory modalities may miss quieter signals of Condition (or other experimental treatment) among the "noise" of individual variability unless it is explicitly accounted for in the statistical analyses. Reliance on different types of rheotropic cues used by individual fish may also vary in degree, in much the same way that the effectiveness of medication in humans varies from individual to individual. While we did not measure this directly, the wide range in behavioral responses we observed between individuals and across different Conditions are consistent with other studies of green sturgeon behavior (Poletto et al., 2014), and may merit further investigation of this hypothesis.

The highest variation in response occurred in the Light Condition. This can be observed visually in both the empirical data (Fig. 2) and the posterior probability distribution of m2NC, where repeat samples from the posterior probability of Condition Light (shown in light blue in Fig. 4B) spans the largest range of values and has the greatest overlap with the density curves of the other Conditions. Additionally, there was a larger difference in posterior probability contrast values between Condition Dark and Conditions Above and Below (0.32 and 0.30, respectively) than there was between Condition Light and the Conditions Above and Below (0.24 and 0.22, respectively). One possible explanation for this is that Light is the only Condition where fish receive both visual and mechanosensory cues at the same time - since this Condition approximates a mixture of the two modes (both visual and mechanosensory), we might have captured a corresponding blend of the typical responses in fish to either visual or mechanosensory Conditions.

The results from the barbels-removed experiment suggest that juvenile green sturgeon do not use their barbels primarily to receive and interpret mechanosensory stimuli. While we did not measure time spent on the bottom directly, all four video reviewers have separately confirmed that anecdotally, fish did not spend a remarkable amount of time on the bottom or touching the sides during any of the four experimental Conditions, but when they did so their entire ventral side was touching the bottom, not just their barbels. Regardless, if barbels played a significant role in providing a tactile reference point for the detection of water current, we would not expect the overall increase in positive rheotaxis after barbel removal that we observed (Fig. 5). This overall increase in average proportion of time spent positively oriented from barbels-intact to barbels-removed may have lent undue weight to the presence or absence of barbels as an important predictor of rheotaxis behavior during the model comparison process in the barbels-removed analysis, simply because the barbel predictor became a de facto indicator separating the first experiment from the second. In other words, the barbel predictor may have captured an individual "learning" effect for the water flow trials, rather than an actual effect of barbel removal on rheotaxis behavior. However, further experiments should be conducted to determine whether juvenile green sturgeon use their entire body as a tactile reference point for orientation to current.

5. Conclusions

While visual cues almost certainly play a role in rheotaxis behavior at large (Montgomery et al., 1997), 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.
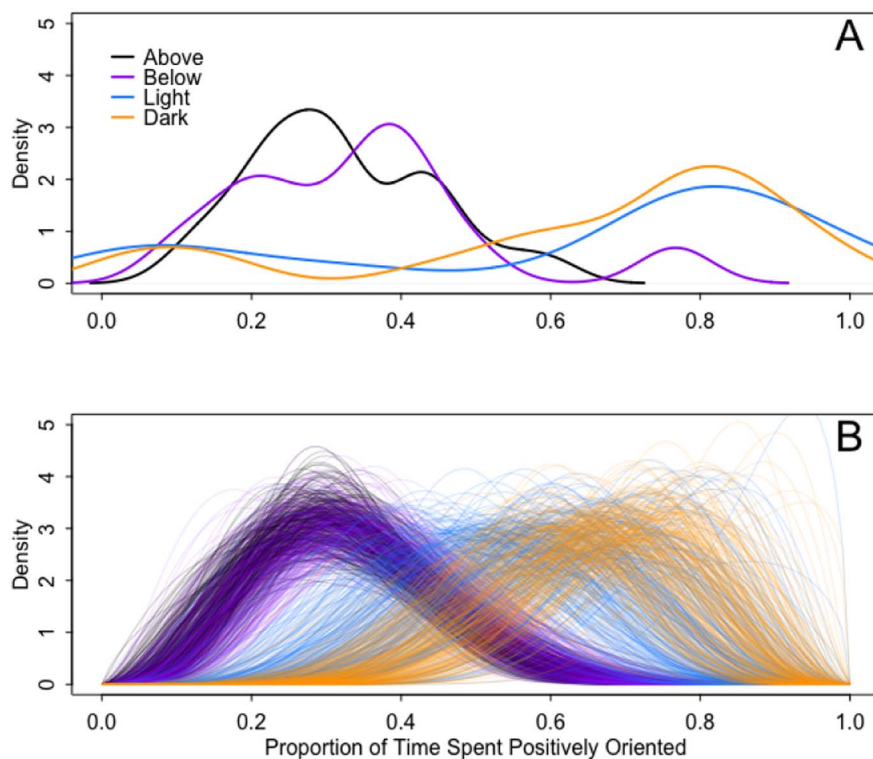
Fig. 4. (A) The density curves of the empirical observations (96 trials) by Condition from the barbels-intact experiment, to compare with density curves (B) of each Condition, drawn by repeat sampling of the posterior probability distribution of the top-weighted model. The visual Conditions (Above and Below) are shown in black and purple, respectively; the flow Conditions (Light and Dark) are drawn in light blue and orange, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
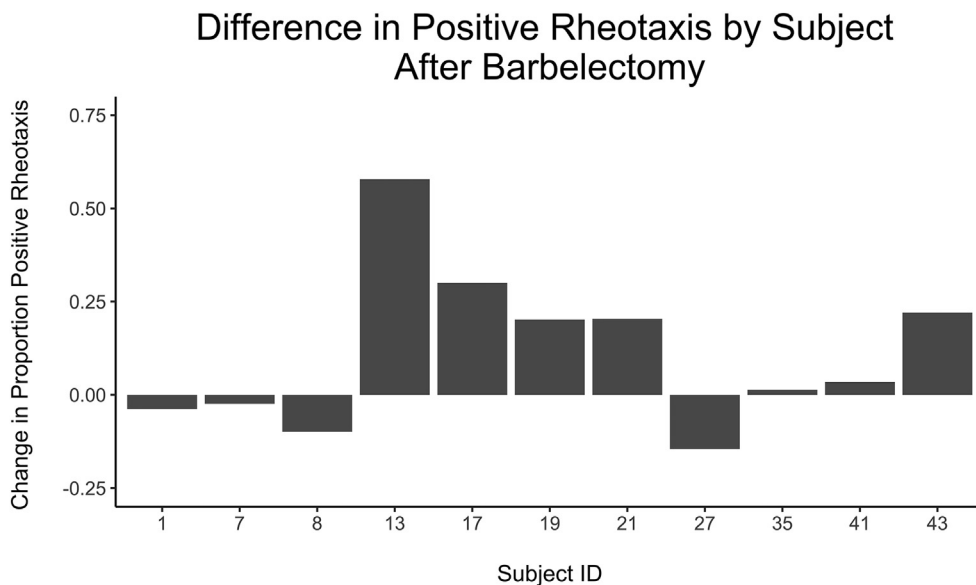

Fig. 5. Eleven subjects were used in both the barbels-intact experiment and the barbels-removed experiment. For each individual, the bar represents the difference in the average proportion of time spent positively oriented during flow trials (Light and Dark Conditions) between the two experiments.

providing constructive, thoughtful comments on the first draft of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2017.04.002.

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