Abstract—Underwater cameras increasingly are being used on remotely operated, autonomous, or towed vehicles to provide fishery-independent survey data in areas unsuitable for bottom trawls. To observe and quantify avoidance and attraction behaviors of fish to these vehicles, we developed an observational test bed consisting of 3 benthic stereo cameras, set in a straight line, on a coral reef in the Gulf of Mexico. During one pass of a towed camera vehicle, one of the benthic cameras viewed a school of vermilion snapper (*Rhomboplites aurorubens*) that exhibited a variety of avoidance behaviors. Stereo analysis was used to position some these fish, and target tracking was used to estimate their swimming performance and schooling characteristics for each second from the time the research vessel had passed the benthic cameras to the time of arrival of the towed underwater vehicle. The fish showed little reaction to the tow vessel but responded to the tow cable by swimming laterally and downward, then rapidly increased their swimming speed and avoidance behavior when the towed vehicle came into view. The use of observational test beds, stereo photography, and target tracking allows quantification of the avoidance response and provides a means to determine which stimuli produced by the sampling process elicit fish avoidance behaviors.

Quantifying the behavior of fish in response to a moving camera vehicle by using benthic stereo cameras and target tracking

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For most commercial and recreational marine fish species in the United States, bottom trawl surveys provide fishery-independent indices of abundance needed for stock assessment modeling. However, bottom trawl surveys cannot be used in areas that are too steep or rocky, have fragile epibenthos, such as coral, or are legally closed to trawling. As an alternative to bottom trawling in such areas, optical assessment increasingly is being used, especially with the use of camera systems on stationary platforms (Campbell et al., 2015) or mobile platforms, such as remotely operated vehicles (Adams et al., 1995), autonomous underwater vehicles (Clarke et al., 2009), towed vehicles (Lembke et al., 2013), and manned submersibles (Yoklavich et al., 2007).

One concern that has been raised about fish density or abundance estimates produced by such camera systems is that they could be biased as a result of attraction, avoidance, and incomplete detection of fish (Trenkel et al., 2004; Stoner et al., 2008; Ryer et al., 2009; McIntyre et al., 2015). Studies have addressed such sampling bias by quantifying fish behavior as seen from the camera vehicles themselves. (Lorance and Trenkel, 2006; Yoklavich et al., 2007) or by estimating the relative sampling efficiency of different camera vehicles (Laidig et al., 2013). However, there have been few attempts to obtain independent estimates of sampling efficiency of camera vehicles or to conduct in situ observational studies of fish behavior in response to camera vehicles by using an independent observational method that is unlikely to elicit behavioral responses.

Similar concerns about sampling efficiency have been raised concerning survey bottom trawls. However, bottom trawls have been in use much longer than camera vehicles, and a variety of techniques have been developed to estimate components of trawl sampling bias, such as herding (Engås and Godø, 1989a) and escapement under the footrope (Engås and Godø, 1989b). In some cases, these

techniques have been applied to estimate the size selectivity of a survey trawl (Somerton et al., 2007) and even of the absolute catchability of a trawl survey (Somerton et al., 2013). Estimating the sampling efficiency of a survey method or the catchability of a survey can be important for stock assessments because estimates of these quantities can be incorporated into stock assessment models (Maunder and Punt, 2013) as Bayesian priors to improve model reliability. Inclusion of such priors in stock assessment models is especially important for developing surveys, like those envisioned for camera vehicles, because the survey time series will initially be too short to adequately inform the model (Somerton et al., 1999).

To help develop methods for estimating the sampling efficacy of camera vehicles and to understand better the stimuli produced by these vehicles that may influence sampling efficiency, the U.S. National Marine Fisheries Service initiated the Untrawlable Habitat Strategic Initiative, which conducts experiments to observe and quantify the reactions of fish to remotely operated vehicles, autonomous underwater vehicles, and towed camera vehicles. For the first experiment, which is considered here, an observational test bed was developed that consisted of unlit, bottom-mounted stereo cameras set in shallow, clear water to unobtrusively observe the responses of fish to various types of camera vehicles. The study site was a sponge and soft coral reef that is situated in the northeastern Gulf of Mexico and is inhabited by a variety of tropical fishes, including several species of snappers and groupers important to commercial and recreational fisheries (Coleman et al.[1]).

Several independent strategies were used to quantify the responses of fish. One of these was to measure changes in the relative density of fish in the area viewed by single cameras (Campbell[2]) and by DIDSON[3] imaging sonars (Sound Metrics, Bellevue, WA) (Wakefield[4]) as the benthic cameras were approached by camera vehicles. Another strategy, described here, was to quantitatively assess fish behavior in response to the camera vehicles by using stereo images to repeatedly measure the 3-dimensional positions of individual fish over time (i.e., target tracking). This type of information, in turn, allowed measurement of changes in swimming speed and direction of individual fish as

well as attributes of school structure indicative of their behavioral state.

Target tracking methods have been used previously to quantify changes in fish behavior in several settings. For laboratory studies, stereo photography has been used, with both target tracking and other analytical techniques, to quantify the movement of individual fish and the coordinated movement of fish schools (Tien et al., 2004; Viscido et al., 2004). For in situ studies, several acoustic methods have been used for target tracking. These methods include the use of buoy-mounted, split-beam sonars to track the avoidance of fishing vessels or bottom trawls by individual cod (Handegard and Tjøstheim, 2005) and the use of DIDSON imaging sonars to track the escapement of individual walleye pollock (*Gadus chalcogrammus*) from a pelagic trawl (Williams et al., 2013). Optical methods are rarely used for aquatic in situ experiments because 1) water clarity typically limits the feasible range that cameras can image objects and 2) artificial lighting, which can itself alter fish behavior, is needed in other than very shallow water.

Our initial intention was to use optical target tracking on several species of snappers and groupers that are relatively solitary, benthic-oriented, and commonly seen in the study area. However, at one location, a school of vermilion snapper (*Rhomboplites aurorubens*) was viewed repeatedly by the benthic stereo cameras, and, during one pass of the towed camera vehicle (Lembke et al., 2013), the school was viewed during the entire period between the transits of the tow vessel and the camera vehicle. Here we focus on this single observation of a schooling species rather than on our more numerous observations on solitary species because our intent is to demonstrate that in situ optical target tracking with stereo cameras can be used to quantify changes in individual and group behaviors that are often associated with predator avoidance (Parrish et al., 2002; Viscido et al., 2004) are also displayed in response to a camera vehicle. To aid the development of stealthier camera vehicles, we consider the linkages between these behavioral changes and the stimuli produced by the camera vehicle and its tow vessel that could have triggered the changes. In addition, we provide an example of how target tracking can be used to estimate sampling efficiency of camera vehicles.

Materials and methods

Description of the study

The experiment was conducted from 17 through 19 July 2014 on the Florida Middle Grounds, which is a reef of calcareous sponges and soft corals situated in the northeast Gulf of Mexico (Coleman et al.[1]; Wakefield[4]). This reef has a relatively flat top, at a depth range of 23–32 m, and steep slopes. The highest fish abundance and diversity concentrated near the junction of the reef top and slope. The target species, vermilion snapper, is

[1] Coleman, F., G. Dennis, W. Jaap, G. P. Schmahl, C. Koenig, S. Reed, and C. Beaver. 2004. Part I: Status and trends in habitat characterization of the Florida Middle Grounds. Final report to the National Oceanic and Atmospheric Administration Coral Reef Conservation Grant Program, 135 p. [Available from website.

[2] Campbell, M. D, 2016. Unpubl. data. Mississippi Laboratories, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 3209 Frederic St. Pascagoula, MS 39567.

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Wakefield, W. W., II. 2015. Unpubl. data. Newport Facility, Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., 2032 SE OSU Dr., Newport, OR 97365-5275.
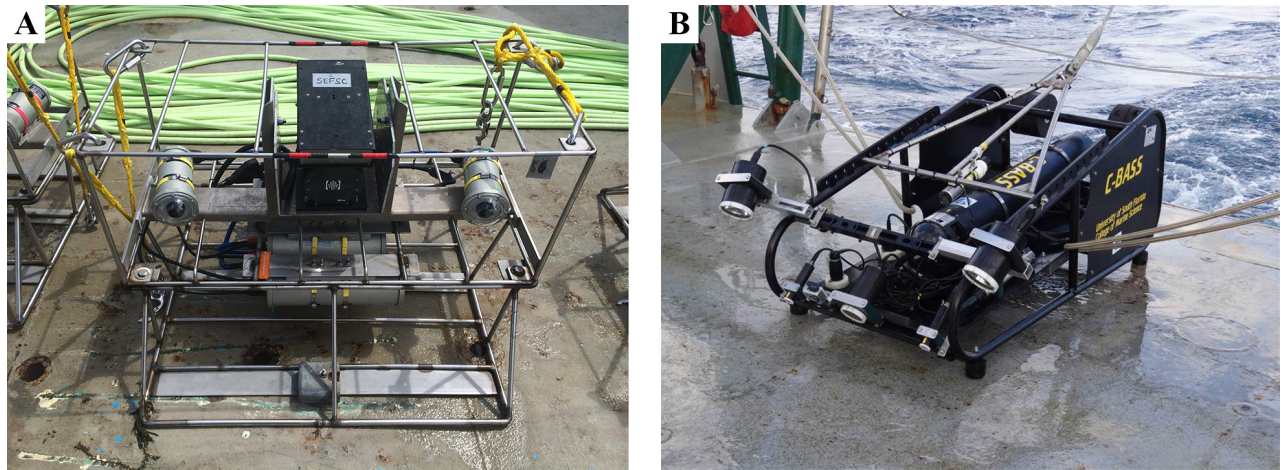
Figure 1

Photographs of (**A**) an observation cage, containing the Modular Optical Underwater Survey System, a DIDSON imaging sonar (black rectangular box), and the bridles used to attach the cage to the longline (yellow lines at the top), and (**B**) the camera-based assessment survey system (C-BASS) towed camera vehicle shown before being launched from the stern of the RV *Pelican*. The cage and camera vehicle were used in an experiment conducted in July 2014 in the northeast Gulf of Mexico.

an important commercial and recreational species and is a dominant component of the reef fish assemblage in the southeastern United States. During the night, vermilion snapper forage on planktonic and benthic prey on both reefs and their adjacent sand flats. However, during the day, they are reported to form resting schools on the tops of reefs (Grimes, 1979; Sedberry and Cuellar, 1993). Viewed from our cameras, the behavior of the school of vermilion snapper in the study area was consistent with this notion.

To quantify changes in fish behavior, an observational test bed was set up at select locations on a daily basis. The test bed consisted of 3 observation cages (Fig. 1) measuring 94 cm wide, 94 cm long, and 67 cm high. The cages were attached at 61 m intervals along a groundline with anchors and buoy lines at each end of the groundline separated by 61 m from the nearest cage (Wakefield[4]). The groundline was set off the stern of the tow vessel (RV *Pelican*) under tension, from anchor to anchor, so that the line was straight and all camera cages had the same general geographic orientation. Each of the cages had an unlit, monochrome stereo camera system, known as the Modular Optical Underwater Survey System, equipped with 2 Prosilica GT 1920 cameras with 2.82-MP resolution (Allied Vision Technologies, Stadtroda, Germany) that were rigidly attached to an aluminum frame with a baseline separation of approximately 75 cm. Once filming was initiated, synchronized stereo photos were taken at 5 Hz continuously for up to 8 h. In addition, each cage contained a dual-frequency acoustic imaging system (DIDSON; Belcher, 2002), and the 2 end cages also contained a long baseline acoustic beacon to obtain in-

formation on cage position and to aid navigation of the vehicles to within visual range of the camera cages.

The towed camera vehicle used in the experiment collected both video and still optical imagery with forward- and side-mounted cameras that were angled downward approximately 45° from level and illuminated with 4 continuous 85-W LED lights. The camera vehicle frame measured 1.2 m wide by 0.7 m tall by 1.7 m long and was designed to be towed at approximately 1.8 m/s with a target off-bottom distance of 2.5 m (Fig. 1; Lembke et al., 2013). The towing cable was standard 10.8-mm hydrographic wire that passed over an A-frame along the centerline of the vessel. At the depths in the experimental area and at a towing speed of 1.5–2.0 m/s, the camera vehicle trailed behind the vessel by ~40–50 m.

At each sampling site, the observation cages were deployed, then the positions of the end cages were estimated by using a long-baseline system after circling the entire array with the vessel. Approximately 1–2 h after cage deployment, depending on the time required to obtain quality positions, the camera vehicle was launched and towed near the cages with a target horizontal distance of 3–5 m at closest approach to each camera. Towing always occurred in the same direction when the camera vehicle passed by the cages, and replicate passes were separated in time by ~20–25 min.

Stereo camera calibration

Accuracy of estimates of fish position depend on the quality and precision of the calibration of the stereo camera. Calibration of the Modular Optical Underwa-

ter Survey System cameras proceeded according to the methods described in Williams et al. (2010, 2013) with the Camera Calibration Toolbox for Matlab (Bouguet, 2014). Calibration images of a submerged (freshwater) checkerboard test pattern (9 by 7 matrix of 108-mm squares) were captured by each camera of the Modular Optical Underwater Survey System at a distance of about 3 m. The checkerboard was tilted and rotated along all 3 axes into 25 poses, which were held stationary for ~5 s. Paired stereo images were later viewed and 1 paired image from ~25 paired images in each pose was selected for analysis on the basis of image clarity and the required presence of all 4 corners of the checkerboard in both images. By using the camera calibration software, each of the paired images was sequentially displayed, and the 4 external corners of each checkerboard image were manually identified. This information was then used to estimate the optical distortion of each camera and the translation and relative rotation of the camera pair to define a measurement coordinate system.

Once calibrated, the 3-dimensional position within this coordinate system can be determined for any object in the joint (i.e. overlapping) field of view of the stereo cameras. The axes of this coordinate system are the y-axis, increasing monotonically with distance from the lens of the left camera (optical axis), and the x-axis and z-axis, which are measured perpendicular to the y-axis in the horizontal (positive to the left, as seen by the camera) and the vertical planes (positive upwards).

Measuring fish positions

Fish positions were measured from images recorded during 2 time periods. The first time period (disturbed case) consisted of a 22-s period between the time when the tow vessel was at its shortest distance to the benthic camera (i.e., passage time) and the time when the camera vehicle just entered the field of view of the benthic camera and the last tracked vermilion snapper completely exited the field of view. The second time period (undisturbed case) consisted of a 10-s period taken 20 min after the previous vessel passage time (an interval which was assumed to be sufficiently long to allow disturbed fish to return to their undisturbed state) and 5 min before the passage time of the disturbed case. During the 2 cases, the same school was viewed with the same camera under nearly identical viewing conditions; consequently the cases were essentially one sequence with a 5-min break to reduce video processing time.

For each of these 2 periods, paired stereo images were processed as follows. During each second, 5 stereo paired frames were collected, but only frames 2–4 were used to estimate fish position (although fish position in each second can be estimated with only a single frame, estimation of swimming velocity required 3 successive frames). Starting with the first of these frames, 25 fish were selected at progressively increasing distances from the camera. Each fish was then followed

and positioned (i.e., x, y, z coordinates) sequentially through the 3 frames by using the Stereo Tracker stereo measurement software (Fig. 2; Williams et al.[5]) and techniques described in Williams et al. (2010, 2013). In all cases, the fish snout was used as the reference feature for measurement because it was the easiest feature to consistently locate. Therefore, for each second, in both the disturbed and the undisturbed cases, the data available for target tracking were the x, y, and z coordinate positions of 25 fish individually followed through 3 successive frames. To reduce the influence of possible random measurement errors, these data were smoothed by fitting a straight line to the 3 positions of each fish on each coordinate axis as a function of time (function lm in R statistical software, vers. 3.3.1; [R Core Team, 2016]), then by using the fitted model to predict the positions at the 3 times. The position of each fish during each second was subsequently based on its smoothed position during the second frame.

Distance off the bottom

Because the benthic cameras imaged the bottom, as well as the fish, from a fixed position, it was possible to construct a topographical map of the bottom expressed in the same coordinate system as that used to view the fish and then to use this map to determine the distance of each fish from the bottom. First, the coordinates of 30 locations on the bottom were measured with the software, and then a topographic map of the bottom was estimated by fitting the z coordinates of these positions as a smooth function of the x and y coordinates by using generalized additive modeling (function gam in the mgcv package for R). The fitted function was then used to predict the z coordinate of the bottom at the x and y coordinates of every fish position, and that z coordinate, when negated and added to the z coordinate of the fish itself, produced the distance off bottom (d) in each frame for every fish. The group distance off bottom (D) during each second was then calculated as the mean of the d values for all the fish in the group.

Tracking the camera vehicle to determine its sampling path

The stereo cameras were used to position the forward, right-hand corner of the camera vehicle frame at 3 times during its passage through the field of view of the benthic camera to calculate its trajectory on the horizontal plane. The trajectory, which was assumed to follow a straight line, was estimated by fitting straight lines to the x and y coordinates individually as a function of time. Because the trajectory was nearly parallel to the x-axis, the trajectory of the camera vehicle center line was estimated by adding the half width of

[5] Williams, K., R. Towler, P. Goddard, R. Wilborn, and C. Rooper. 2016. *Sebastes* stereo image analysis software. AFSC Processed Rep. 2016-03, 42 p. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115. Report
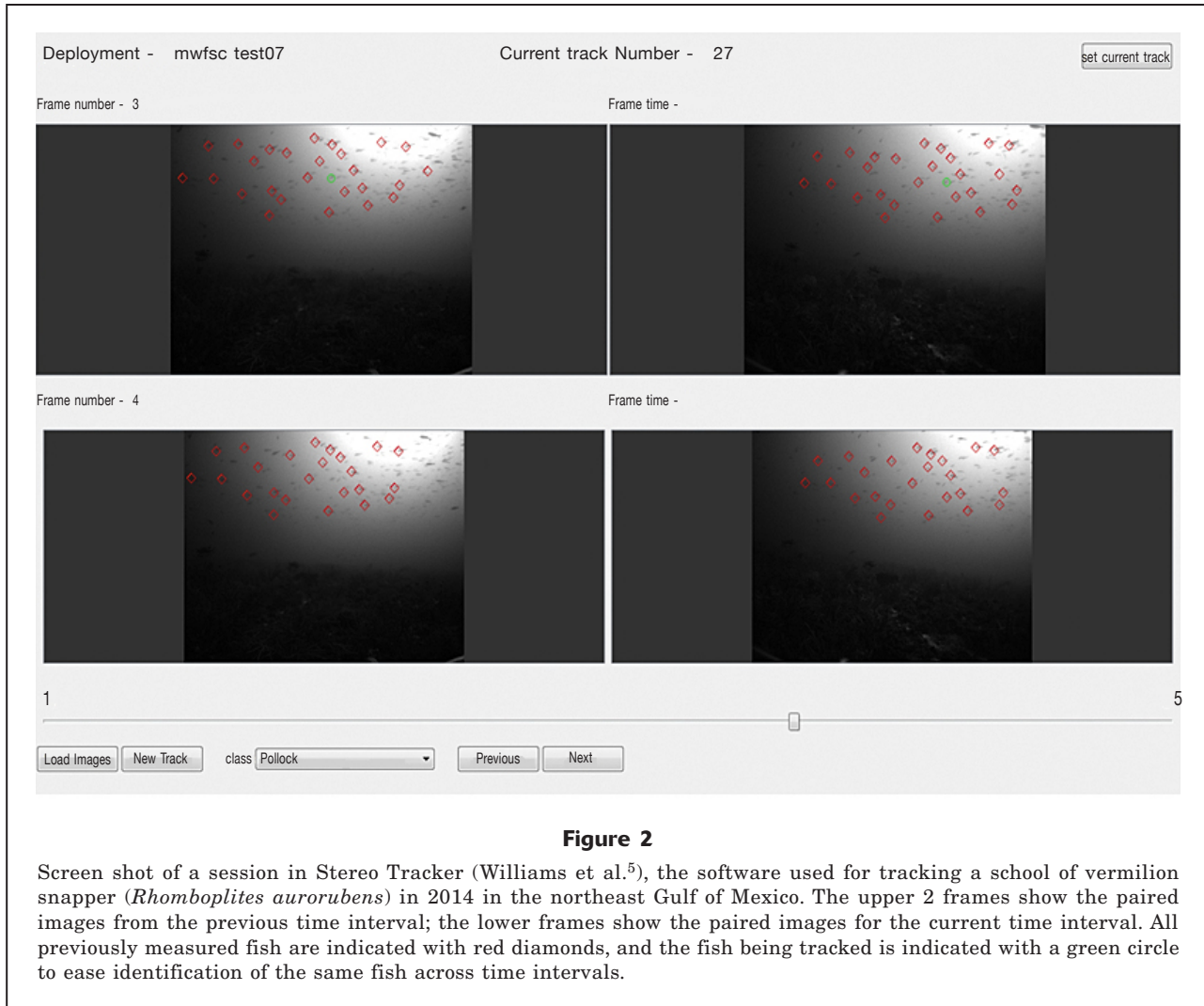
Figure 2

Screen shot of a session in Stereo Tracker (Williams et al.[5]), the software used for tracking a school of vermilion snapper (*Rhomboplites aurorubens*) in 2014 in the northeast Gulf of Mexico. The upper 2 frames show the paired images from the previous time interval; the lower frames show the paired images for the current time interval. All previously measured fish are indicated with red diamonds, and the fish being tracked is indicated with a green circle to ease identification of the same fish across time intervals.

the vehicle frame (0.6 m) to the y coordinates. The distal and proximal edges of the vehicle sampling path, spanning the width of the area for counting fish, were then calculated as the center line path (± the approximate half width of the estimated field of view of the vehicle [~3.7 m]). The sampling path was used, in conjunction with the measured fish positions on the horizontal plane, to determine whether vermilion snapper occupied the sampling path prior to the arrival of the camera vehicle and, if so, when they left the path.

Individual velocity, mean speed, and direction of swimming Individual swimming velocity (V_j) in each coordinate direction ($V_{x,j}$, $V_{y,j}$, $V_{z,j}$) was calculated for each fish (indexed by j) during each second as the difference in the smoothed beginning and ending positions divided by the elapsed time (0.4 s). Mean individual speed and direction were calculated from the velocity vectors both in 3 dimensions, as well as from projections on the x–y plane and the z-axis separately to better visualize the lateral and vertical movements associated with

avoidance behavior. Mean swimming speed (S) during each second was calculated first by determining the individual speeds from the estimated velocity vectors and then by determining the means of these values; that is,

$$S = \overline{sqrt(V_{x,j}^2 + V_{y,j}^2 + V_{z,j}^2)}, \qquad (1)$$

where V_z was omitted in this equation for horizontal speed, and V_x and V_y were omitted for vertical speed. Mean swimming heading, on the x–y plane, was calculated as the mean of the individual swimming headings, expressed in degrees counter clockwise from the direction of vehicle travel, after correcting for the slight misalignment between the direction of travel and the x-axis of the camera coordinate system.

Group velocity, speed, and swimming polarity Group velocity (U) on each coordinate axis (U_x, U_y, U_z) was calculated each second from the difference in the mean positions of the 25 fish between the second and fourth frames, divided by the elapsed time. Group speed (S_g)

was then calculated from the 3 coordinate velocity vectors as

$$S_g = sqrt(U_x^2 + U_y^2 + U_z^2). \qquad (2)$$

Swimming polarity, which is a measure of the alignment in swimming direction of individuals relative to that of the group, was calculated as the mean of the angular deviations (θ_i) between the individual velocities (V_j) and the group velocity (U) (Viscido et al., 2005):

$$\theta_j = \cos^{-1}\left[\frac{V_j \cdot U}{|V|_j |U|}\right], \qquad (3)$$

where "·" is the vector dot product; and "| |" is the absolute value.

The individual swimming polarities were then converted to a nondimensional mean value to simplify interpretation (Viscido et al., 2004) as:

$$\Phi = \frac{\overline{(90° - \theta_j)}}{90°}. \qquad (4)$$

In this notation, fish swimming directions become increasingly parallel as Φ approaches 1.0.

Nearest neighbor distance   Nearest neighbor distance of each individual fish to other group members is defined in the following manner (Viscido et al., 2005):

$$NND_j = \min^{f()}(d_{j,1}, d_{j,2}...d_{j,p}), \qquad (5)$$

where $d_{j,k}$ = the distance between the jth fish and each of the p remaining fish.

Nearest neighbor distance of the group is the mean over the p+1 members of the group.

   The above metrics of group behavior were calculated identically for both the disturbed and undisturbed periods, but the use of those descriptors differed between these periods. For the disturbed period, we were interested in the temporal change of the metrics in response to the tow vessel and camera vehicle. In contrast, for the undisturbed case, we used the metrics to set a reference level to use as a baseline for comparison with the disturbed case. We assumed that the values of each metric were relatively constant over the 10-s interval and that they characterized the undisturbed state of each metric as its mean and standard deviation.

Results

The response of the vermilion snapper to the vessel, tow cable, and camera vehicle can be considered from the perspective of individual behavior, but, because this is a schooling species, response can also be considered from the perspective of the group behavior of the school. First, we considered the movement attributes of individual fish. These attributes are best seen as a time series of mean swimming vectors, which, in Figure 3, are represented by the mean speed and direction and were projected separately on the horizontal plane (x- and y-axes) and vertical direction (z-axis). At the moment that the tow vessel passed the camera (t=0), the mean horizontal swimming direction was aligned with and almost directly away (180°) from the tow direction; however, the swimming direction abruptly changed to 270° at 11 s, so that the fish were swimming perpendicular to the tow path, and again at 20 s to approximately 315°, so that they were swimming obliquely away from the towed camera. Horizontal swimming speed, indicated by the lengths of the movement vectors in Figure 3, increased at 11 s and again at 20 s in accordance with the directional changes. Therefore, as expressed on the horizontal plane, there were 2 changes in swimming speed and direction that essentially partitioned the time series into 3 distinct periods.

   Vertical swimming speed and direction changed in a similar pattern. The vertical swimming direction is initially slightly upward until 10 s, when it shifts abruptly downward for 1 s before a horizontal shift in direction (Fig. 3). The downward shift in vertical swimming direction was also accompanied by an increase in swimming speed.

   These changes in vertical swimming speed led to changes in the mean distance of the fish from the bottom (Fig. 4). The initial upward speed of the fish resulted in a gradual increase in distance off bottom. However, synchronously with the changes in horizontal and vertical swimming direction, the distance off bottom rapidly decreased from a maximum of ~4 m at 8 s after vessel passage to ~1 m at 22 s. Perhaps the reduction in vertical swimming speed seen in the last 2 s of the series (Fig. 3) is the result of the school reaching this close proximity to the bottom.

   Next, we considered the descriptors of group behavior: group speed; individual speed; and swimming polarity. These descriptors also displayed a temporal pattern with 3 distinct periods. Group speed (i.e., movement of the school itself), over the entire period after vessel passage, was elevated considerably above its value during the undisturbed case, and 2 distinct increases were observed, one starting at ~11 s and another starting at ~18 s (Fig. 5A). These changes in group speed are related to changes in individual speed and swimming polarity, but the relative influence of each factor changes over time. Mean individual swimming speed (now expressed in 3 dimensions) was barely elevated above its value in the undisturbed case and increased only gradually during the first 17 s after vessel passage, but the rate of increase distinctly accelerated starting at ~18 s (Fig. 5B). In contrast, swimming polarity (i.e., the alignment of individuals) was elevated greatly above its value in the undisturbed case over the entire record and a distinct rate of increase was observed at ~11 s (Fig. 5C). Therefore, changes in group speed (i.e., movement of the school) were primarily determined by changes in swimming polarity until the last few seconds when individual swimming speed greatly increased.
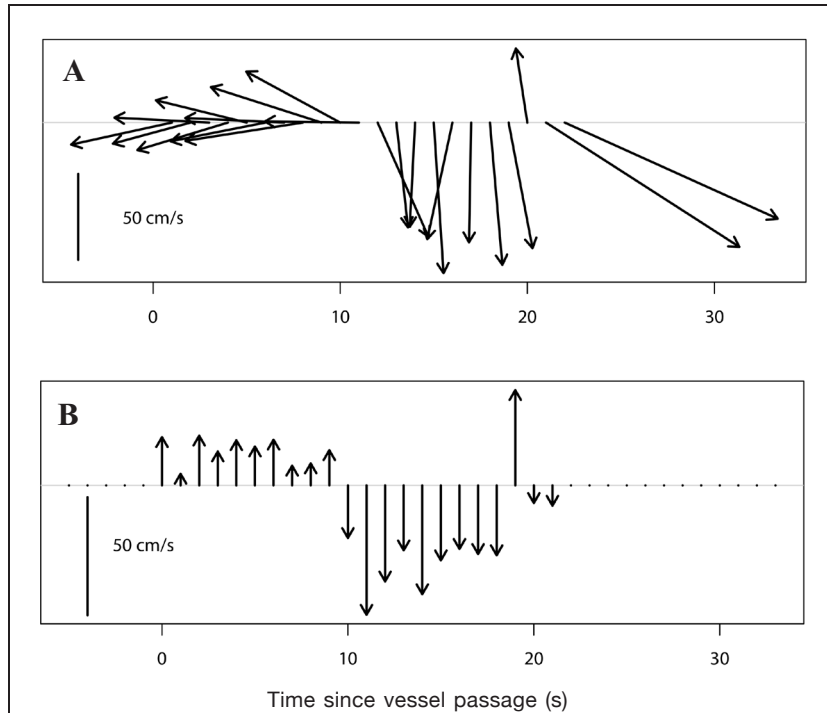
Figure 3

Mean individual swimming speed and direction of vermilion snapper (*Rhomboplites aurorubens*) in the northeast Gulf of Mexico in 2014, expressed as either (**A**) degrees counter clockwise relative to the camera vehicle tow path (toward the right) on the horizontal plane and as (**B**) degrees up and down in the vertical plane. Time is in seconds since the passage of the tow vessel was recorded by the benthic camera. On the horizontal plane, the direction of travel is from left to right; therefore, a left arrow is directed away from the tow vessel and toward the approaching camera vehicle. On the vertical plane, the horizontal line represents zero speed. The closest approach of the vehicle was at 23 s after the passage of the vessel, and the velocity of the camera vehicle was 1.5 m/s. Hence, the approximate distance in meters from the vehicle to the fish school can be calculated as $(23-t) \times 1.5$, where t is the time in seconds after vessel passage.

The nearest neighbor distance followed an almost inverse pattern, with a distinct, strong, decrease starting at about 11 s (Fig. 5D). Therefore, over the entire encounter with the camera vehicle and its tow vessel, the school increased its swimming speed initially by the individual fish aligning with each other and finally by increasing the individual swimming rate. In addition, as the alignment of individuals was increasing, their spacing became progressively tighter.

One important effect of these changes in behavior was a decrease in the abundance of vermilion snapper within the area that was subsequently transited by the camera vehicle during its survey (i.e., count path; Fig. 6). At the time of vessel passage (t=0) all 25 measured fish were within the count path of the camera vehicle, but later, in response to the various stimuli produced, the fish moved closer to the fixed camera and ultimately out of the count path. When the cam-

era vehicle actually occupied the count path, at t=23 s, no vermilion snapper remained in the count path and none were seen in the forward cameras used for counting (although some fish were seen by the laterally pointed cameras not used for counting). Therefore, in this particular case, the vermilion snapper avoided sampling by the camera vehicle.

Discussion

The school of vermilion snapper observed in this study experienced a variety of visual and auditory stimuli between their undisturbed state (5 min before passage of the tow vessel) and the arrival of the camera vehicle. These stimuli triggered responses both at an individual level (i.e., swimming speed and direction), as well as at a group level (i.e., alignment of and spacing
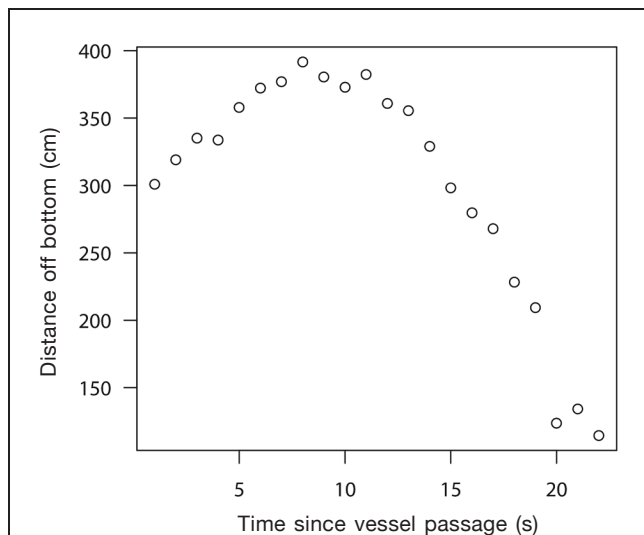
Figure 4

Mean distance of the vermilion snapper (*Rhomboplites aurorubens*) off bottom, measured in the northeast Gulf of Mexico in 2014, as a function of the time since passage of the tow vessel was recorded by the benthic camera. The closest approach of the vehicle was at 23 s, and the vehicle velocity was 1.5 m/s; therefore, the approximate distance in meters of the vehicle to the fish school can be calculated as $(23-t) \times 1.5$, where t is the time in seconds after vessel passage.

characterized by abrupt changes in horizontal direction from nearly parallel to nearly perpendicular to the path of the camera vehicle. In addition, vertical swimming switched from slightly upward to strongly downward. We interpret these behavioral changes as responses to the tow cable, which, by midway in the transit interval, would appear to the fish as a silhouetted object, approximately 10 m above the school (assuming no hysteresis in the tow cable), and approaching the fish at a downward velocity of ~0.9 m/s. Presumably, the tow cable also would produce vibrational stimuli along with the visual stimuli, but we were unable to distinguish the relative importance of the 2 stimuli in eliciting the observed response. Such downward and lateral avoidance behavior has been described previously for cod in response to the towing warps of bottom trawlers (Handegard and Tjøstheim, 2005).

During the third phase (flight), from 20 s to 22 s, individual fish direction on the horizontal plane abruptly changed from perpendicular to about 45° away from the line of vehicle travel and swimming speed began to increase at an accelerating rate. During this period, nearest neighbor distance rapidly declined and polarity increased. Group speed rapidly increased, primarily because the individual rate of swimming increased in addition to the polarity (group speed equals mean individual speed when polarity equals 1.0). We suspect that the these changes were reactions to the sight or sound of the camera vehicle, which was approximately 8 m from the center of the field of view of the benthic camera when the strong change in direction occurred 19 s after vessel passage. Although not silhouetted against the sky, the camera vehicle must have been conspicuous to the fish at this distance because it has 4 continuously illuminated lights and has a looming movement that has been shown to elicit reactions in some Pacific groundfishes (Ryer et al., 2009).

These behavioral changes in response to the passage of the vessel, tow cable, and camera vehicle are consistent with the notion of threat-sensitive predator avoidance (Helfman, 1989; Domenici, 2010; Rieucau et al., 2014) where, because of energetic costs (Ydenberg and Dill, 1986), fish balance timing and strength of escape behaviors against the risk of predation. This tradeoff often results in a graded response, starting with an increase in awareness of the threat and progressing to flight when the predatory attack is initiated. Therefore, for example, in the first phase, fish displayed indications of increased awareness but no obvious avoidance. In the second phase, fish initiated avoidance behavior; however, they did not greatly increase their individual swimming speed, presumably because the perceived threat was relatively small and approaching slowly. In the third phase, fish encountered the camera vehicle, changed their swimming direction so that it was directly away from the threat, and rapidly accelerated their individual swimming speed, presumably because the camera vehicle was large and moving rapidly and, therefore, presented a more serious threat.

between individuals within the school). The responses, especially swimming direction, changed abruptly twice, separating the period into 3 phases that can be considered sequentially increasing states: arousal, awareness, and flight.
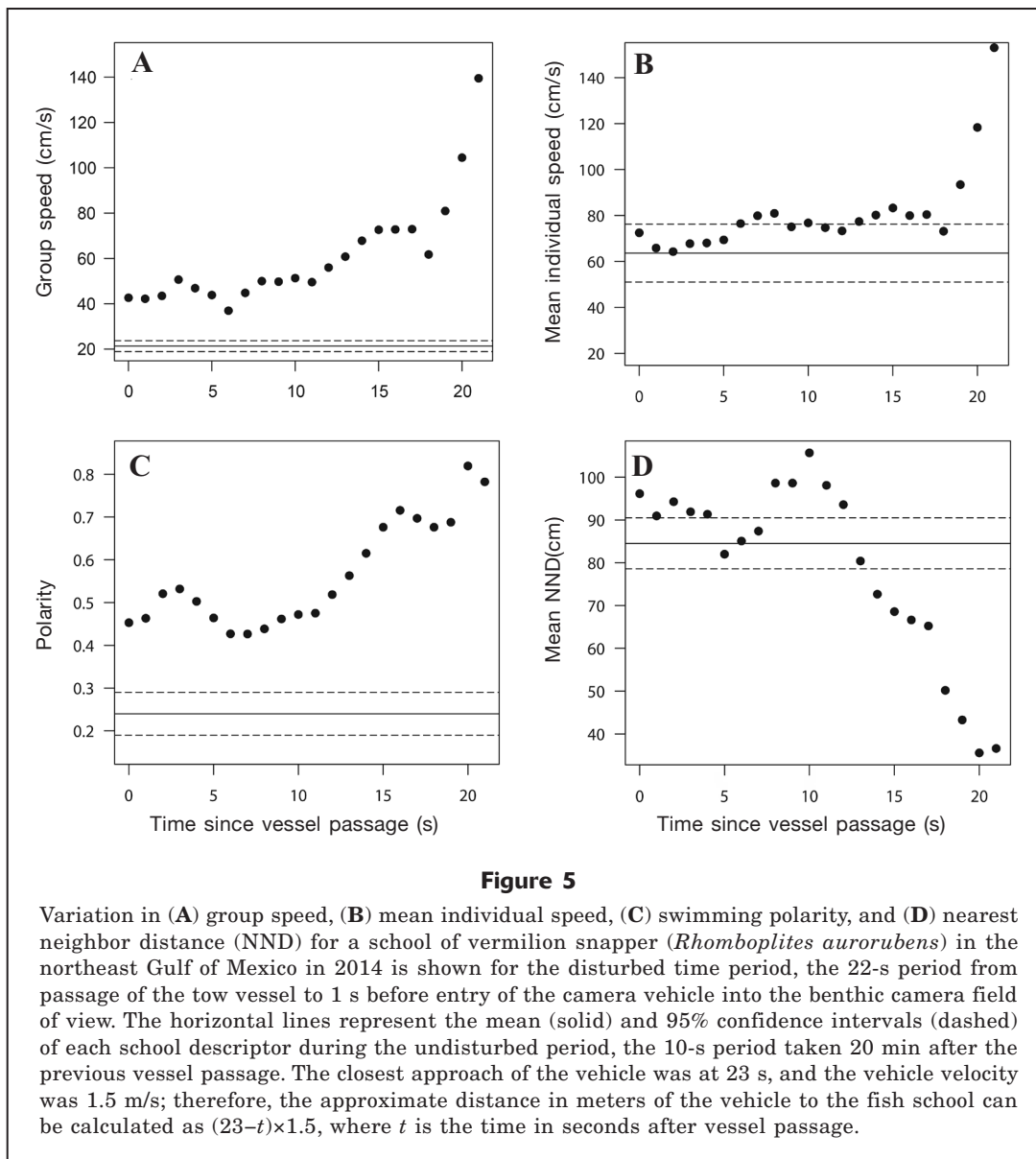
During the first phase (arousal), up to 11 s after vessel passage, the fish were in a heightened state of arousal, presumably in response to the sound or sight of the passing tow vessel, because their group swimming speed and polarity were distinctly greater than the levels observed during the undisturbed period. Although this behavior was clearly a response, it had not progressed to active avoidance of the vessel because the individual swimming direction was still aligned with the path of the vessel and had a slight upward component of movement. Previously documented fish reactions to an overhead or recently passed vessel usually involved lateral motion or diving (Handegard and Tjøstheim, 2005; De Robertis and Handegard, 2013).

In the second phase (awareness), from about 12 s to 19 s after vessel passage, the fish displayed increasing signs of arousal, including an increase in group speed and polarity and a steady decline in nearest neighbor distance, all of which both theoretical and laboratory studies typically have shown are correlated and change with the arousal state of the school (Magurran and Pitcher, 1987; Parrish et al., 2002). During this phase, the fish started to display distinct avoidance behavior

Figure 5

Variation in (**A**) group speed, (**B**) mean individual speed, (**C**) swimming polarity, and (**D**) nearest neighbor distance (NND) for a school of vermilion snapper (*Rhomboplites aurorubens*) in the northeast Gulf of Mexico in 2014 is shown for the disturbed time period, the 22-s period from passage of the tow vessel to 1 s before entry of the camera vehicle into the benthic camera field of view. The horizontal lines represent the mean (solid) and 95% confidence intervals (dashed) of each school descriptor during the undisturbed period, the 10-s period taken 20 min after the previous vessel passage. The closest approach of the vehicle was at 23 s, and the vehicle velocity was 1.5 m/s; therefore, the approximate distance in meters of the vehicle to the fish school can be calculated as $(23-t)\times1.5$, where t is the time in seconds after vessel passage.

We emphasize that the fish response to a camera vehicle during a single pass should not necessarily be considered typical because there are a variety of factors that could have been influential. First, stimulus detection by individual fish or the school may vary with environmental conditions. For example, detection of visual stimuli will be diminished in turbid or low-light conditions. Second, the behavioral response to a given level of stimulus may vary with previous experience of such stimuli. A response to vessel noise, for example, may be less in areas with high vessel traffic because of acclimatization to stimuli. Third, the behavioral response to a given level of stimulus may vary with the perceived level of predatory threat. For example, an avoidance response may be inhibited in complex habitats that provide nearby refuge. Conse-

quently, we expect behavioral responses to be varied and recognize that considerable additional field studies will be needed to provide realistic predictions of behavioral responses to stimuli produced by moving camera vehicles.

We deemed the 10-s interval that occurred 5 min before passage of the tow vessel to be indicative of the values of the school and individual fish descriptors during an undisturbed state. However, the school had previously experienced the disturbance created by the setting of the benthic cameras and 2 prior passes of the towed camera system; therefore, an *undisturbed* state should be considered in a relative sense. Our qualitative observations of the behavior of vermilion snapper toward the benthic cameras indicate that the school returned to fairly calm behavior within a few minutes
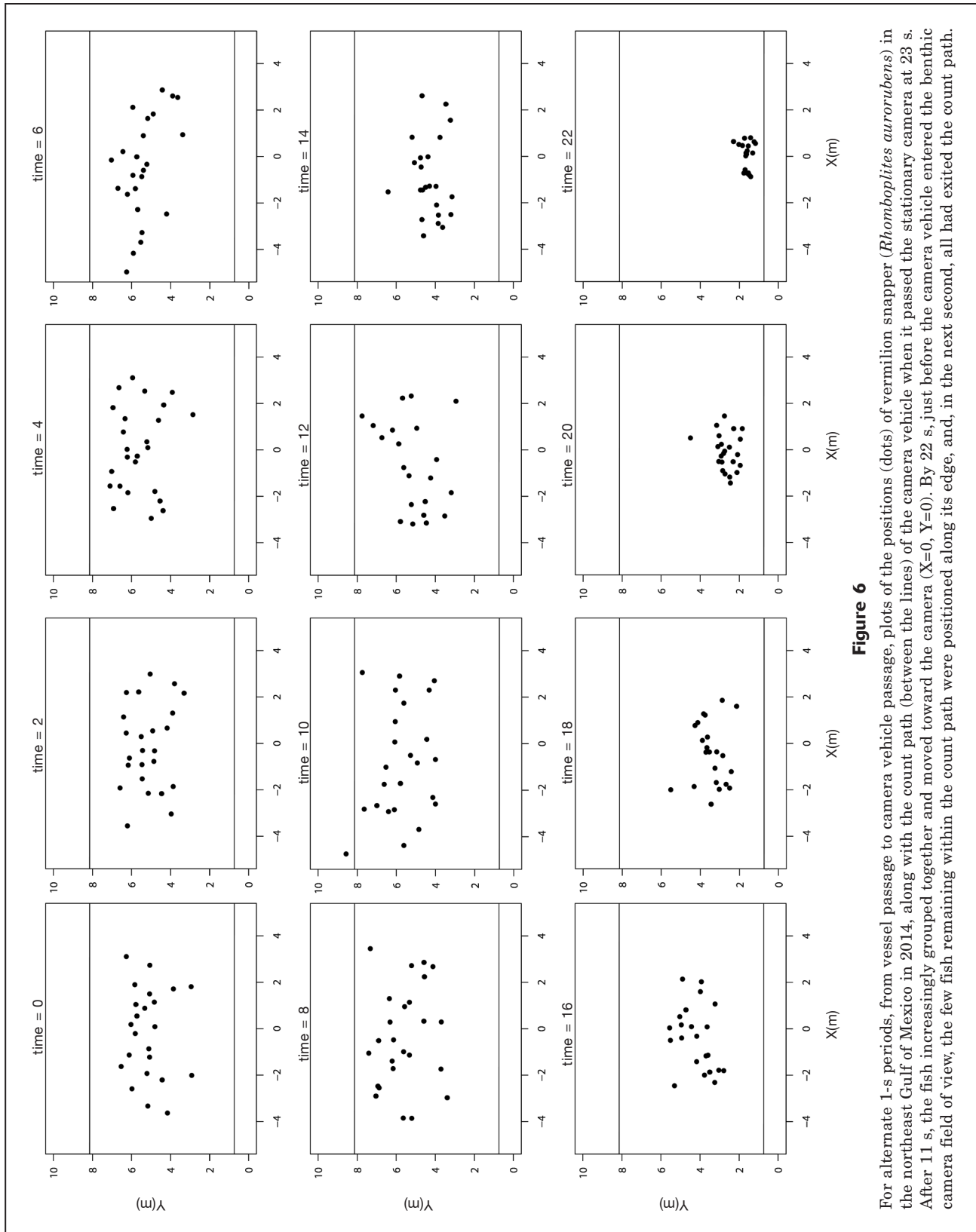
Figure 6

For alternate 1-s periods, from vessel passage to camera vehicle passage, plots of the positions (dots) of vermilion snapper (*Rhomboplites aurorubens*) in the northeast Gulf of Mexico in 2014, along with the count path (between the lines) of the camera vehicle when it passed the stationary camera at 23 s. After 11 s, the fish increasingly grouped together and moved toward the camera (X=0, Y=0). By 22 s, just before the camera vehicle entered the benthic camera field of view, the few fish remaining within the count path were positioned along its edge, and, in the next second, all had exited the count path.

after passage of the towed vehicle. Consequently, we felt that the passage of ~20 min after the last disturbance would approximate undisturbed conditions. Unfortunately, schools of vermilion snapper were not observed before the first passage of the camera vehicle to confirm this notion.

The design of our experiment (i.e., placing fixed cameras on the bottom to observe fish behavior in response to moving camera systems) provided a unique perspective on how these systems actually sample the fish community. During the one pass of the camera vehicle, for example, no vermilion snapper were counted by the moving camera vehicle, but the alternate view provided by a benthic camera (Fig. 6) showed that vermilion snapper were indeed within the tow path of the camera vehicle but had vacated it immediately before they would have been imaged by the forward directed cameras on the vehicle.

Besides confirming that fish avoidance had occurred during the pass of the camera vehicle, the use of the fixed cameras, especially the use of stereo and optical target tracking, allowed quantification of the timing and strength of the avoidance behaviors, which in turn, provided an indication of the possible stimuli that may have elicited these behaviors. For example, vessel noise has been implicated repeatedly as a stimulus sufficient to trigger fish avoidance behavior (De Robertis and Handegard, 2013), but, in this particular pass of the camera vehicle, vessel noise did not trigger any overt avoidance behavior. The sight or sound of the tow cable likely triggered the initial overt avoidance behaviors but was insufficient to drive the fish out of the path of the camera vehicle. However, the sight or sound of the camera vehicle seemed to increase the avoidance behavior sufficiently to cause the fish to vacate the count path before they could be seen and counted by the camera vehicle. These metrics of the timing and strength of the fish response could be used to help redesign the camera vehicle so that it could be stealthier and produce stimuli below the thresholds required to trigger avoidance behaviors.

The purpose for this article is to demonstrate the utility of fixed benthic cameras and stereo photography to measure the positions of a moving camera system, the target fish species, and the bottom topography, as well as how these measurements can be used to better understand how moving camera vehicles sample fish communities. The example we provide was based on one fortuitous pass of the camera vehicle in view of a single benthic camera while a school of vermilion snapper were present; consequently, our observations could be quite different had the sampling been at greater depths or in more turbid water (Abrahams and Kattenfeld, 1997) and certainly would have been different for other target species. However, when the use of stereo photography from fixed benthic cameras is appropriate, it can allow quantification of fish behaviors and help define the effect of this behavior on density estimates derived from images obtained with moving camera vehicles.

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