Characterizing behavioral responses of Pacific cod to bottom trawl vessels and gear using archival tag accelerometer data

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Abstract

Fish behavior during the capture process affects the overall efficiency of survey vessels and gear, influencing selectivity and catchability, which in turn influences stock assessments. The effects of behavior on capture are typically investigated through experiments that use video or acoustic technologies to observe behavioral responses of fish to vessels and gear directly. While these approaches provide valuable information about fish behavior, their use is limited to observing the movement of fish inside a small observed area. In this proof-of-concept study, we demonstrate a novel application of bio-logging Pop-up Satellite Archival Tags (PSATs) equipped with accelerometer sensors to observe behavioral responses of free-swimming demersal fish to approaching bottom trawl fishing vessels and gear. By combining PSAT and fishing vessel geolocation data from the Vessel Monitoring System, we characterized diving and herding responses of three individual Pacific cod (*Gadus macrocephalus*) at-liberty for 21–106 days to trawling fishing vessels. We found that fish descended as trawlers approached, presumably in response to noise generated by the fishing vessel and gear, which supports the previously untested hypothesis that Pacific cod dive in response to approaching fishing vessels and gear, similar to closely related gadids. Additionally, one 88 cm fish swam ahead of a trawl towed at 1.25 $m \cdot s^{-1}$ (i.e., 1.42 body lengths per second) for 55.6 minutes, covering a distance of 4.17 km before capture, which challenges previous assertions that Pacific cod are unlikely to outswim bottom trawl gear towed at typical towing speeds. This study demonstrates that opportunistically collected archival tag data can be used to improve knowledge of behavioral interactions between fish and fishing gear.

Keywords: biotelemetry, vessel avoidance, herding behavior, diving behavior, Pacific cod, *Gadus macrocephalus*

Introduction

Accelerometer data from biologging archival tags are useful for observing animal behavior at spatial and temporal scales that are not possible through direct (e.g., visual) observation (Brown et al., 2013). In fisheries research, accelerometers have been used extensively to monitor the physiological and behavioral effects of capture. For example, archival tags equipped with accelerometers have been used to quantify energy expenditure and stress caused by capture (Bouyoucos et al., 2017) and estimate post-release mortality (Doukakis et al., 2020; Nielsen et al., 2018; Rose et al., 2019; Whitney et al., 2016). Accelerometer data have also been used to distinguish pre-and-post-capture periods in longline experiments (Gallagher et al., 2017), but they have not been used to characterize behavioral responses of fish to fishing vessels and mobile fishing gear (e.g., trawls) in the period leading up to capture. However, tagged fish are occasionally captured by mobile fishing gear (Bryan et al., 2021) and opportunistically using accelerometer data from these events may provide information about fish behavior during the capture process with few restrictions on the spatial and temporal scale of observation (Brown et al., 2013).

Fishing vessels and gears produce stimuli that can trigger behavioral reactions in fish that affect the catchability and selectivity of fisheries and fisheries-independent surveys (Table 1). Observing and predicting these reactions is challenging because they result from a complex chain of events influenced by the stimuli from specific vessels and trawl gear, distance of the fish to the vessel and fishing gear, environmental conditions affecting the propagation of stimuli, sensory capabilities of the fish, and the degree to which fish respond to perceptible sensory signals (De Robertis and Handegard, 2013; Hawkins and Popper, 2017). Inferences about the stimuli that elucidate behavioral reactions are often based on the distance between the fish and vessel and gear. At long distances (> 100 m), fish can detect and react to high levels of low-frequency noise from vessel machinery and trawl gear (Daly and White, 2021) that overlap with the frequency range (< ~500 Hz) where fish hearing is most sensitive (Mitson, 1995). At these ranges, fish often dive toward the sea floor and/or move horizontally out of the path of the approaching vessel (De Robertis and Handegard, 2013; Handegard and Tjøstheim, 2005), which can affect survey estimates of abundance (Aglen, 1996; Godø, 1994; Kotwicki et al., 2013; Ona and Godø, 1990). At shorter distances, visual cues such as mud clouds caused by bottom trawl gear and visual detection of the gear itself influence behavior (Kim and Wardle, 2003). At very close range, fish respond to vibrations and physical contact with the gear (Winger et al., 2010; Ryer and Barnett, 2006).

Many fish species exhibit herding behavior where they swim directly away from approaching trawl gear components such as bridles/sweeps, meshes, and doors (Main and Sangster, 1981; Winger et al., 2010). Herding relies on detection of directional cues from approaching gear using senses such as vision or hearing (Winger et al., 2010), and is often more pronounced under bright conditions (e.g., day) because of the importance of visual cues (Glass and Wardle, 1989; Ryer and Barnett, 2006). Fish herded into the mouth of the trawl are captured when the trawl moves faster than the fish can swim, often when the fish reaches exhaustion and falls back into the trawl. The speed and duration of swimming vary with species, fish size, temperature, and physiological state, and larger fish can typically swim faster, farther, and longer than small fish (He et al. 1993; Martínez et al., 2003; Winger et al., 2004, 2000).

Archival and acoustic tags without accelerometers have been used to characterize behavioral reactions of fish to fishing gear and elucidate habitat use patterns with the aim of improving understanding of fisheries selectivity and catchability (e.g., Carvalho et al. (2015), Nichol et al. (2007)).

Acoustic tags have proven effective in observing behavioral responses of fish to vessels and gear, but only when they remain within range of acoustic receivers (Engås et al., 1998). Archival tag data have been used to predict availability to trawl gear by quantifying the proportion of time free-swimming fish spend in areas and at depths that overlap with sampling by fisheries or fishery-independent surveys (Carvalho et al., 2015; Nichol et al., 2007). However, habitat use patterns of free-swimming fish do not account for reactions to vessels and gear, such as diving in response to an approaching vessel. Video technologies, such as trawl mounted cameras and remotely operated vehicles, are effective for observing underwater behavior but are constrained to small sampling volumes (Glass and Wardle, 1989; Winger et al., 2010; Williams et al., 2013). These examples highlight that technologies for observing behavior have limitations for monitoring complex behavioral interactions with fishing vessels and gear. Consequently, it is useful to explore new methods that may improve understanding of behavioral interactions between fish and fishing vessels/gear, especially for species where existing methods may be inadequate.

Several studies have sought to determine how vertical migration or trawl avoidance behaviors (e.g., herding) affect the catchability and selectivity of Pacific cod (*Gadus macrocephalus*) by bottom trawl surveys (Somerton et al., 2004; Nichol et al., 2007; von Szalay et al. 2007; Weinberg et al., 2016; Lauffenburger et al., 2017). Some of these studies have reached tentative conclusions about selectivity or catchability (Somerton et al., 2004; Nichol et al., 2007; Weinberg et al., 2016), but the mechanisms hypothesized to be driving selectivity and catchability patterns remain unclear because of challenges observing vessel and gear interactions. In Alaska, Pacific cod are highly demersal and often overlap with a more abundant congener, walleye pollock (*Gadus chalcogrammus*), meaning it is challenging to observe vessel and gear interactions using acoustic methods (Weinberg et al., 2016). Pacific cod are also highly mobile and undertake long-distance migration (Nielsen et al., 2023), posing a barrier to observation using acoustic tags requiring receiver arrays.

Evidence from past tagging and catchability experiments suggest that Pacific cod dive in response to approaching bottom trawl vessels. Based on a small sample size (n = 11) of tagged fish in the eastern Bering Sea, Nichol et al. (2007) found that free-ranging Pacific cod spent 53% of daylight hours >2.5 m above the seafloor. However, fishing experiments have found only 4% of acoustic backscatter above the headrope of a ~2.5 m high trawl was attributed to Pacific cod (Weinberg et al., 2016) because most are concentrated in the near-bottom acoustic dead zone (within ~1-m of the seafloor) when vessels pass overhead (Lauffenburger et al., 2017). Combined, these studies are consistent with the expectation that Pacific cod dive as trawl vessels approach, as has been observed in two closely-related gadids, walleye pollock (De Robertis and Wilson, 2010; De Robertis et al., 2020) and Atlantic cod (*Gadus morhua*; Rosen et al., 2012). These diving responses to approaching trawlers can begin well before (>500 m) the vessel arrives overhead (Engås et al., 1998; Handegard et al., 2003; Handegard and Tjøstheim, 2005). Evidence of diving behavior would suggest that habitat use patterns in free-swimming Pacific cod (e.g. Nichol et al., 2007) are not a reliable indicator of availability to bottom-trawl gear.

Video of Pacific cod near the mouth of the trawl suggests they herd in response to approaching trawl gear (Weinberg et al., 2016), although it is unclear how far they can swim before exhaustion (i.e., swimming endurance) and what maximum swimming speed they can sustain without reaching exhaustion. Based on fishing experiments, Weinberg et al. (2016) concluded that Pacific cod do not outrun bottom trawl survey gear towed at 1.5 $m \cdot s^{-1}$ because there was no difference in catch per unit effort ($kg \cdot ha^{-1}$) between tows conducted at 1.5 $m \cdot s^{-1}$ and 2.1 $m \cdot s^{-1}$. However, only a small fraction (1.3%) of the fish captured in the experiment were large adults (>80 cm fork length), which are more likely to evade capture because maximum sustained swimming speed increases with body size (He, 1993; Winger et al., 2010).

In this proof-of-concept study, we combine accelerometer, light, and depth data from Pop-Up Satellite Archival Tags (PSATs) with fishing vessel GPS data to characterize behavioral interactions between Pacific cod and the bottom-trawl vessels and gear that captured them. This study aims to address five questions about behavior that are likely to affect the catchability and selectivity of bottom-trawl gear: (1) Do Pacific cod dive in response to approaching trawl vessels or gear?; (2) Do Pacific cod attempt to outswim approaching trawl gear?; (3) How long and how far do Pacific cod swim before reaching exhaustion?; (4) Do individuals exhibit consistent reactions to trawl vessels?; (5) Do the accelerometer data show evidence of behavioral reactions to vessels or trawl gear besides diving or herding? Although the study is based on small sample size of three tagged and re-captured fish, we demonstrate how accelerometer data can be combined with fishing vessel GPS data to characterize behavioral responses to vessels and gear with relatively few constraints on the spatial and temporal scales of observation.

Methods

Archival tag data collection

PSATs were deployed on adult Pacific cod as part of an on-going multi-year project to understand seasonal movement patterns and behavior of Pacific cod in Alaska. Wildlife Computers (Redmond, Washington, USA) miniPATs were deployed on Pacific cod in the Aleutian Islands, Bering Sea, and Gulf of Alaska. MiniPATS collected depth (0 – 1700 m, 0.5 m resolution), temperature (-40 °C – 60 °C, 0.05 C resolution), tri-axial acceleration (-2 – 2 g, 0.05 g resolution), and light level (5 × 10-12 W·cm^{-2} – 5 × 10^{-2} W·cm^{-2}) data at intervals ranging from 1 – 5 seconds, depending on programmed deployment duration. When the tag reaches the water surface, onboard data are summarized and transmitted to the Argos satellite network. Transmitted data can be used to reconstruct movement pathways of tagged fish (Nielsen et al., 2023). If the tags are physically recovered, the full dataset can be recovered. Archival tag integer light levels were converted to irradiance in W·m^{-2} using a conversion equation reported by the manufacturer (Rohan et al., 2021).

The three fish (Fish #1, #2, and #3) described in this manuscript were tagged and released in the Aleutian Islands in February 2019 (Fish #1 and #2) and Gulf of Alaska in March 2021 (Fish #3), and subsequently captured by bottom trawl vessels during commercial fishing operations (Table 2; Figure 1). In the Aleutian Islands, 21 fish captured by trawl or pot at 88–118 m bottom depth in Nazan Bay (Atka Island, Alaska) or near Adak Island, Alaska, then tagged and released (Bryan et al., 2021). In the Gulf of Alaska, 25 fish captured by pot at 55–102 m bottom depth near the Shumagin Islands, Alaska, were tagged and released. Pacific cod tagged with non-satellite tags take 1.6 to 16.7 days to recover from barotrauma from capture depths between 30 m and 100 m, respectively (Nichol and Chilton, 2006). PSAT-tagged fish exhibit normal free-ranging behaviors within a few days to a couple of weeks of capture (Nielsen et al., 2023).

The PSATs (124 mm long, 38 mm wide, weighing 60 g in air) were attached to Pacific cod using a harness and a tether design (Courtney et al., 2016) so that PSATs floated above the fish when stationary but were pulled horizontally while swimming, which allows the use of vertical and horizontal accelerometer data to characterize activity patterns (Nielsen et al., 2018). The harness consisted of padded plates on both sides of the fish connected by wires running through the dorsal musculature at two locations and a 150-lb monofilament tether connecting the PSAT to the plates (Bryan et al., 2021). A hidden Markov model was used to reconstruct movement pathways (estimated daily locations and corresponding uncertainty) from depth and light data for all three fish. Pathways for Fish #1 and #2 are available in Nielsen et al. (2023).

Animal ethics statement

Tagging was conducted in accordance with National Marine Fisheries Service's (NMFS) Animal Care and Use Policy (04–112), which is currently limited to research on free-living marine mammals, seabirds, and sea turtles and does not cover research on captive or wild fish. However, every effort was made to follow accepted standards and ensure the ethical treatment of captured fish, including guidelines from the U.S. Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research and Training[1] and Chapter V of the American Fisheries Society Guidelines for the Use of Fishes in Research[2].

Classifying behavioral phases, pre-herding behavior, and herding distance

We sought to identify behavioral phases in accelerometer time series by dividing the time series into discrete segments corresponding with distinct trends in the accelerometer data in order to evaluate whether specific behaviors were reactions to fishing vessels and trawl gear. In addition, we aimed to estimate how long each fish maintained high-intensity swimming before falling back into the trawl. To classify behavioral phases, we used a segmentation and clustering algorithm for bivariate time series (Patin et al., 2020) to identify clusters and segments in centered and scaled (mean zero, standard deviation one) time series of vertical and horizontal accelerometer axes during the 5 hours leading up to capture (see Segmenting and clustering accelerometer data). The capture time for each tag was assigned as the time when light levels began decreasing monotonically towards a minimum. We considered monotonically decreasing light levels to indicate capture because the top panel of the trawl and sediment plumes created by contact between the bottom trawl gear and bottom obstruct downwelling light.

We opted to only segment and cluster a truncated portion of the full time series because our analysis focused on small-scale behaviors and the algorithm is memory-intensive and cannot handle time series with >~10,000 values. We selected a 5-hour window because preliminary inspection of the vessel time series revealed the longest period between trawl gear deployment and capture was approximately 4.5 hours, and a 5 hour time series appeared to include free-swimming behavior prior to vessel encounter for all fish. The vertical axis, A_z, corresponds with the vertical direction and records a value of -1.0 g (g-force; 9.80665 $m \cdot s^{-2}$) when the archival tag is oriented vertically and not moving because the tag experiences upward acceleration with a magnitude nearly equal to the acceleration due to gravity but in the opposite direction (Rose et al., 2019). The vertical axis, or tilt, is used to infer fish swimming activity. The tag is vertical when the fish is not swimming but changes to a more horizontal orientation as the free-floating tag is pulled behind the fish as it swims (Nielsen et al., 2018). Therefore, A_z values of -1.0 g correspond to stationary behavior, and sustained A_z values near 0 correspond to high

[1] https://olaw.nih.gov/policies-laws/gov-principles.htm
[2] https://fisheries.org/docs/policy_useoffishes.pdf

swimming activity. The combined horizontal axes, A_{xy}, represent the total magnitude of horizontal acceleration, defined as:

$$A_{xy} = \sqrt{A_x^2 + A_y^2}.$$

We estimated herding distance as the product of tow speed (speed over ground; m·s^{-1}) and the duration of the herding phase, i.e., the phase of high amplitude accelerometer measurements immediately before capture (s). We assumed swimming speed during herding (m·s^{-1}) for each fish was the same as the vessel trawling speed, although the vessel has to travel faster than the fish for the fish to be captured. This approach also assumes that fish swim in a straight line in the same direction the vessel is moving, which would not be the case if fish move from side to side or change depths. We also calculated relative swimming speed for each fish terms of body lengths per second (BL·s^{-1}) because swimming capabilities vary with fish size (Winger et al., 2010).

We evaluated the behavioral responses of Pacific cod to fishing vessels prior to the onset of herding, including potential diving responses as the vessel approached. To do so, we qualitatively compared time series of behavioral clusters and depth to time series of vessel speed, vessel distance from capture and herding locations, and vessel activities (slowing down while approaching the trawl location, deploying gear). Although we were unable to directly determine whether patterns in accelerometer and depth time series were responses to auditory, visual, or tactile cues from trawl vessels and gear, we evaluated whether behaviors could plausibly be responses to vessel/gear based on the distance between the vessel and herding or capture locations (informed by literature values from other species). The Fishing vessel activity time series section describes how we constructed these time series.

Segmenting and clustering accelerometer data

We used a segmentation and clustering algorithm for bivariate time series (Patin et al., 2020) to identify behavior types (clusters) and phases (segments) in accelerometer time series for each fish. The segmentation and clustering algorithm was implemented using the R package *segclust2d* version 0.3.1 (Patin et al., 2020). We briefly describe the segmentation and clustering algorithm here but refer the reader to Lavielle (2005), Picard et al. (2007), and Patin et al. (2020) for a detailed description of the method and foundational basis. Given a specified number of clusters, M, and segments, K, the algorithm divides a bivariate time series into K optimal stationary phases with duration ≥ L_{min}, the minimum length of a segment. Each segment represents a sequence of random variables drawn from a Gaussian distribution with mean μ_m and variance σ_m^2 that is common to all segments belonging to cluster m. Each segment has an additional vector of multinomial distribution parameters, $\pi_{m,k}$, of length M that indicates the probability that segment k belongs to clusters $\{1, \ldots, M\}$. Optimal μ_m, σ_m^2, and segment breaks are estimated using a mixed dynamic programming and expectation-maximization algorithm that maximizes the likelihood of a penalized contrast function based on Gaussian likelihood (Lavielle, 2005; Picard et al., 2007). In segmented and clustered accelerometer time series, μ_m and σ_m^2 correspond with the mean and variance of accelerometer values for behavioral cluster m, i.e., $\mu_{xy,m}$ and $\sigma_{xy,m}^2$ for A_{xy} and $\mu_{z,m}\sigma_{z,m}^2$ for A_z.

Ideally, the choice of K, M, and L_{min} parameters is based on prior knowledge about animal behavior (Patin et al., 2020), but we had little prior information to guide parameterization. At minimum, we expected two behavior clusters: free-ranging swimming and herding. Pacific cod undertake vertical migration behavior (Nichol et al., 2013) that would presumably appear in depth data, but it was unclear if vertical movements would comprise distinct patterns in accelerometer data. Given the lack of prior knowledge, we evaluated a range of K and M, and constrained L_{min} based on our expectations of behavior and visual inspection of accelerometer data. Individual tags appeared to have up to seven different accelerometer modes in the 5 hours before capture so we evaluated M ranging from 2 (minimum expected) to 7 (maximum based on visual inspection), which matches the typical range of distinct acceleration waveforms in accelerometer tag studies (two to seven with an average of four; Brown et al., 2013). Based on visual inspection of the accelerometer time series, we inferred there were likely fewer than 20 distinct segments in each 5-hour time series, so we set K_{max} to 25 to provide a buffer. Immediately before capture, each time series had high amplitude fluctuations in accelerometer measurements that appeared to last for a minimum of ~120 seconds, which we assumed to be an indication of herding as fish attempted to outswim the approaching trawl. The minimum duration of individual segments was set to 60 seconds (L_{min} = 60/sampling interval) to ensure the herding phase could form a discrete segment.

For each fish, we classified behaviors using the minimum number of clusters necessary to ensure the period of high-intensity accelerometer measurements immediately before capture formed a distinct phase. We selected the number of segments after selecting the number of clusters by visually inspecting profiles of K versus pseudo-Bayesian Information Criterion (a penalized likelihood function based on Bayesian information criterion BIC) to find the K at the 'elbow' of the curve, as suggested by Lavelle (2005), Picard et al. (2007), and Patin et al. (2020).

Fishing vessel activity time series

We constructed fishing activity time series for each capture vessel using Vessel Monitoring System (VMS) geolocation data from NOAA's Alaska Regional Office's Catch-In-Areas (CIA) database (Alaska Regional Office, 2023) and logbook data. Commercial fishing vessels in Alaska are required to log their position every 6 minutes (Aleutian Islands) or 30 minutes (Bering Sea) through VMS. Although public Automated Identification System (AIS) data can be logged more frequently than VMS, fishing vessels often turn off their AIS while fishing to avoid sharing information with potential competitors (Welch et al., 2022). We calculated vessel speed and distances between vessel positions and fish herding and capture locations using time-referenced archival tag and VMS data. One fish was captured in the Bering Sea by a vessel with 30-minute-interval VMS data, which we supplemented with haul time and location records from the vessel's logbook. To maintain confidentiality, we do not provide capture vessel names and only report capture locations at the level of NMFS statistical areas (Fig. 1).

We estimated herding and capture locations by linearly interpolating between the VMS positions immediately before and after the onset of herding and capture. Distance traveled between positions was calculated as:

$$D_{1,e} = S_{1,2}T_{1,e},$$

where $D_{1,e}$ is the distance traveled between the VMS fixes immediately before (*1*) the herding/capture event (*e*), $S_{2,1}$ is vessel speed between VMS fixes immediately before and after (*2*) *e*, and $T_{1,e}$ is the time elapsed between the VMS fix immediately before herding/capture and the time of herding/capture. This approach assumes that vessels traveled in a straight line at constant speed between recorded positions.

Results

Behavioral clusters and segments

Accelerometer patterns differed among fish so we selected different numbers of clusters (4–5) and segments (9–15) to classify behavioral phases for individual fish during the 5 hours leading up to capture (Table 3). Fish #1 had four clusters and nine behavioral segments, while Fish #2 and #3 had five clusters with 15 and 13 segments, respectively. Herding duration and distance differed considerably among individuals, ranging from 120 seconds and 0.07 km (Fish #1) to 3335 seconds and 4.17 km (Fish #2). Herding behavior clusters were associated with increased swimming activity, as they exhibited the highest mean vertical accelerometer values, μ_z, for all three fish and the highest horizontal axis value, μ_{xy}, for Fish #1 and #2 (Table 4). For each fish, the herding behavior cluster had the highest standard deviation among clusters for both vertical, σ_z, and horizontal, σ_{xy}, axes, likely due to rapid movement during high-intensity swimming. Fish #3 exhibited a 'freezing' behavior (Behavior Cluster 1) that was characterized by horizontal acceleration near zero, vertical acceleration near -1.0 (tag oriented vertically), and low values of σ_z (0.01) and σ_{xy} (0.05). Visual inspection of the full 22-day time series indicated that freezing behavior only occurred during the 5-hour period before Fish #3 was captured.

Time series for individual fish

Fish #1 (69 cm fork length [FL]) was tagged in the Aleutian Islands in winter spawning grounds during the spawning season. This fish was at liberty for 21 days before being captured near the tagging location in a 1.7-hour bottom trawl tow during daylight hours on March 13, 2019 in NMFS Area 541 (Fig. 1; overview in Fig. 2; see Fig. S1 for events surrounding capture). During the 5 hours preceding capture, the vessel completed a tow ~25 km away from the capture location on March 12 at 22:02 UTC, then transited to the deployment location of the capture tow at 4 m s^{-1}. The vessel slowed down (March 13 at 23:41) and deployed trawl gear at approximately 23:47 on March 13. During the haul, the vessel towed at an average speed of 0.39 m·s^{-1} (0.55 BL·s^{-1} [body lengths per second]) with approximately the same bearing for the entire tow. At the beginning of the tow, the vessel was 1.1 km away from the herding location and 1.2 km from the capture location. From 00:05 to 00:18 on March 13, Fish #1 descended from 116 to 129 m while the vessel was 0.86 to 0.76 km from its position at the onset of herding (Fig 2; Fig. S1). Fish #1 then ascended to 117 m by 00:36 when the vessel was 0.36 km from the herding location. The diving and ascent behavior may not indicate a vessel response because the fish also dove and ascended on two other occasions during the 5 hours before capture (March 12 at 20:30–21:15 and 21:35–22:15). Fish #1 began herding at 00:50:45 on March 13 and herding ended 120 seconds later at 00:52:45 (based on the duration of high-intensity swimming immediately before capture [Behavior Cluster 5]). During the herding period, the vessel covered a distance of 0.07 km at 0.58 m s^{-1} (0.84 BL·s^{-1}), and Fish #1 ascended from 117 m to 113.5 m (Fig. S1).

Fish #2 (90 cm FL) was tagged in the Aleutian Islands during the winter spawning season and was recaptured after migrating to summer foraging grounds in NMFS Area 541 (Fig. 1). Fish #2 was at liberty for 106 days before capture in a 4.8-hour tow during daylight hours on June 8, 2019 (overview in Fig. 3, see Fig. S2 for events surrounding capture). The capture vessel was operating in the capture area prior to the capture event and was within 1 km of the capture location twelve times during the week before capture. Five hours prior to capture (17:02 UTC), the vessel was within 0.1 km of the capture location and 4 km from the initial herding location, then transited at ~4 m·s^{-1} to a location 1.4 km and 5.5 km from the herding and capture locations, respectively. The vessel slowed down at 17:46 and deployed trawl gear at approximately 17:50 to tow near a bank at ~150 m bottom depth. The vessel traversed back and forth at an average speed of 1.51 m s^{-1} during the tow, traveling a cumulative distance of 25.4 km. At the beginning of the tow, Fish #2 was at 260 m, deeper than the bottom depth for the tow, which suggests the fish was off the bank. Between 17:02 and 20:00, Fish #2 ascended to ~160 m. The fish descended slightly from 160 m to 162.5 m at 21:00 when the vessel was 0.49 km away from the initial herding location (Fig. S2). This depth change coincided with a slight increase in acceleration, as shown by the transition from Behavior Cluster 2 to Behavior Cluster 5 at 21:00. Herding (Behavior Cluster 5) began at 21:06:10, approximately 3.25 hours after haul deployment. The fish was captured at 22:01:50 after 55.6 minutes of herding (Fig. 3). Based on vessel speed and location, herding covered 4.17 km at an average speed of 1.25 m s^{-1} (1.39 BL·s^{-1}). While herding, Fish #2 ascended from 162.5 m to 151 m from 21:10 to 21:14, and depth varied from 145 to 162.5 m between the onset of herding and capture. During the final 8 minutes of herding, starting at 21:54, Fish #2 exhibited three depth decreases and increases with magnitudes of 10 m, 6 m, and 3 m (in chronological order; Fig. S2). Notably, a 10-m ascent is larger than the typical 9.1 m maximum headrope height for Alaska bottom trawl gear (Witherell, 2012).

Fish #3 (83 cm) was tagged in winter spawning grounds near the Shumagin Islands in the Gulf of Alaska and was at liberty for 22 days before being captured in NMFS Area 509 (Fig. 1) in the eastern Bering Sea in a 5.0-hour tow during daylight hours on April 15, 2021 (overview in Fig. 4, see Fig. S3 for events surrounding capture). Reconstructed movement pathways from PSAT data show the fish was migrating away from spawning grounds and traveled 24 km the day before capture. Precise vessel speeds during the tow could not be determined because VMS data were only available in 30-minute intervals. Several trawlers including the capture vessel, passed within 10 km of the capture location during the 24-hours before Fish #3 was captured. The tow in which Fish #3 was captured began approximately 17.8 km away from the capture location. Fish #3 descended 33 m from 68.5 m to 101.5 m from 21:02 to 21:10, although the vessel was approximately 15 km away from the capture location so it is unlikely that noise from the capture vessel elicited the diving response. On five occasions between 21:16 and 22:54, Fish #3 exhibited 'freezing' behavior characterized by A_z near -1.0 g, A_{xy} near zero, and low variability in A_z and A_{xy} (Behavior Cluster 1; Table 4). Freezing behavior began while the capture vessel was ~14.5 km away from the herding location, so it was unlikely to be a response to the capture vessel. Freezing behavior lasted for 2 to 6 minutes per occurrence (Fig. 4) but was not observed during the remainder of the 22-day time series. At 21.5 minutes before the onset of herding, Fish # 3 ascended from 97.5 m to 81.0 m while the vessel was 2.18 to 1.08 km away from the herding location. Shortly thereafter, the fish descended from 81.0 m to 101.5 then rose to 97 m over 8.5 minutes (23:24:00 to 23:32:30) while the vessel approached to within 0.10 km of the herding location. Fish #3 descended again at 23:32:55, 35 seconds before beginning to herd at 23:33:30 (Behavior Cluster 5; Fig. 4). Fish #3 continued descending while herding and reached a maximum depth of 102.5 m at 23:36:35. Herding speed was estimated to be 1.51 m ·s^{-1} (1.82 BL·s^{-1}), although the 30-minute interval between VMS fixes may make speed estimates less accurate than for the other fish. Fish #3 was captured at 23:36:55. Similar to Fish #1 and #2, Fish #3 ascended sharply around the capture time then descended.

Time series comparison among fish

Behaviors differed among fish, so Figure 5 shows a time series comparing fish depth and herding behavior while vessels approached within 1,512 m of the herding location (i.e., the maximum reported reaction distance of fish to approaching vessels [Table 1]). All three fish descended while vessels were within 1.5 km of the estimated vessel position at the onset of herding, although Fish #1 and Fish #3 ascended after their initial descent. Fish # 2 and Fish #3 began descending while vessels were 200–500 m from the herding location, but Fish #3 descended further (5.5 m) than Fish #2 (2.5 m). Fish #1 ascended while herding, whereas Fish # 3 descended then ascended. Fish #2 ascended at the onset of herding, then exhibited multiple ascents and descents while herding. Herding lasted for 120 s at 0.58 $m \cdot s^{-1}$ (Fish #1), 3335 s at 1.25 $m \cdot s^{-1}$ (Fish #2), and 205 s at 1.51 $m \cdot s^{-1}$ (Fish #3). All three fish ascended or began ascending just before capture.

Discussion

We combined accelerometer, light, and depth data from archival tags with vessel location data to characterize behavioral reactions of Pacific cod to bottom trawl vessels and gear. We were able to identify behavioral reactions to the vessel that likely occurred before close-range encounter with the trawl gear, during herding by the trawl gear, and during net entry and capture. Despite the limited sample size, our results provide insights into behavioral reactions of Pacific cod to bottom trawl vessels and gear that are difficult to gain by other means.

Behavior before the onset of herding

All three fish showed variation in depth occupied during the 5 hours leading up to capture. In some cases, depth changes occurred at distances greater than expected for an auditory response to the sound of the capture vessel (e.g. 17 km for Fish #3). However, diving behavior while vessels were closer to vessels may have been responses to vessel noise, as observed in acoustic-tagged Atlantic cod that react to trawl vessels at distances up to 1,470 m (Engås et al., 1998). We found evidence of diving behavior shortly before and during herding in two out of three fish (Fish #2, Fish #3), which suggests at least some Pacific cod dive in response to approaching/passing trawl vessels or approaching trawl gear.

The diving behavior in Pacific cod appears to be consistent with diving behavior in other gadids as trawl vessels approach and pass overhead (e.g., Handegard and Tjøstheim, 2005; Kotwicki et al., 2013; Ona and Godø, 1990). Diving occurred at distances greater than expected for visual detection of the vessels or gear (>70 m), suggesting they may be responses to auditory cues. Although all three fish showed net depth increases as capture vessels approached from within 1.5 km to the herding location, Fish #1 did not show a depth increase immediately before herding. Regardless, the fish was likely within 5.6 m of the seafloor at the onset of herding, based on its 3.5 m ascent while herding and the ~9.1 m (5 fathoms) typical maximum average vertical net opening height for Alaska bottom trawl fisheries (Witherell, 2012).

Herding behavior

The longest herding duration was 55.6 minutes for Fish #2, which suggests large Pacific cod are capable of keeping pace with or outrunning trawls gear towed at ‘typical’ speeds for prolonged periods. However, the shorter herding durations for Fish #1 and Fish #3 suggests there may be considerable variation in swimming endurance among individual fish, as observed in Atlantic cod (Winger et al., 2000). While we are unable to determine what factors affected swimming endurance, we hypothesize that physiological factors play a role. Swimming speed (Winger et al., 2000) and temperature (Winger et al., 2010) can affect swimming endurance but it is unlikely that temperature explained differences in swimming endurance in our study because temperatures were similar for all three recaptures (4.1–4.2°C). Interestingly, the fish with the shortest swimming endurance also swam slower (0.84 $BL\cdot s^{-1}$) than the fish with the longest endurance (1.39 $BL\cdot s^{-1}$), suggesting that factors other than speed influenced swimming endurance. Variation in metabolic capacity associated with spawning may have played a role since Fish #1 and #3 were caught during spawning season (March and April), whereas Fish #2 was caught outside of the known spawning season, in June (Neidetcher et al., 2014). Spawning is associated with reduced feeding in Pacific cod (Poltev et al., 2012) and, in Atlantic cod, starvation reduces swimming endurance because of decreased glycolytic and oxidative capacity of muscle tissue (Martínez et al., 2003).

The capacity of Pacific cod to outrun bottom trawl gear towed at typical speeds may have implications for selectivity assumptions made in stock assessment models. NOAA bottom trawl surveys are a critical source of fisheries-independent data for stock assessment and models have assumed the surveys are fully selective for large size classes of Pacific cod (Barbeaux et al., 2021; Barbeaux et al., 2022; Spies et al., 2022). Surveys tow at a target speed of 3 knots (1.54 $m\cdot s^{-1}$) for 15 (Gulf of Alaska and Aleutian Islands) or 30 minutes (eastern Bering Sea), covering distances of ~1.39 or ~2.77 km, respectively. Fish #2 was captured by a tow conducted at 1.25 $m\cdot s^{-1}$ (1.39 $BL\cdot s^{-1}$) after herding for 55.6 minutes. Similarly, whereas Winger et al. (2000) observed Atlantic cod were able to sustain swimming speeds up to 1.8 $BL\cdot s^{-1}$ for 200 minutes. Assuming that Winger et al.'s experiments apply to Pacific cod suggests that the 1.54 $m\cdot s^{-1}$ survey towing speed would be below the maximum sustained swimming speed for Pacific cod >86 cm FL (1.54 $m\cdot s^{-1}$/1.8 $BL\cdot s^{-1}$ = 0.86 m). Swimming speed and endurance experiments would help determine whether large Pacific cod can outrun bottom trawl survey gear towed at typical speeds.

Behavior during net entry and capture

All three fish ascended as light levels declined around the time of capture, although this may have occurred as fish entered the trawl mouth and moved through the trawl gear towards the codend. Typically, the footrope of a bottom trawl is in contact with the seafloor while fishing, but the bottom mesh panels of the trawl closest to the mouth are constructed with a positively buoyant mesh that floats off bottom to avoid snagging. It is possible that Pacific cod rise off bottom when passing over the foot rope and then descend while falling back towards the codend. Notably, Atlantic cod typically remain close to the bottom panel of the trawl as they fall back towards the codend (Rosen et al., 2012). However, it is also possible that fish ascended immediately before entering the trawl as a trawl avoidance response.

Limitations of using PSATs to characterize vessel and trawl interactions

The physical attachment of the PSATs to Pacific cod may have had physiological and behavioral effects that make tagged fish unrepresentative of the population as a whole. Archival tags cause drag that may increase the metabolic demands of swimming, although PSAT tags have minimal impact on the metabolic rate and swimming kinematics of 47 to 87 cm juvenile sandbar sharks (*Carcharhinus plumbeus*) with less than one-third the body mass of Pacific cod from this study (Lynch et al., 2017). However, PSAT tags may cause behavioral changes, such as in Atlantic salmon (*Salmo salar*; 45-116 cm FL; 0.8-11.5 kg), where individuals tagged with PSATs did not dive as deep or grow as fast as individuals tagged with smaller acoustic or data storage tags (Hedger et al., 2017).

A better understanding of Pacific cod hearing capabilities and vessel radiated noise would improve our ability to determine whether observed behaviors can be attributed to vessel responses. Although we inferred that certain behaviors could be auditory responses based on the literature (Table 1), variability in vessel acoustic signatures can affect the distance at which they are detectable to fish and the resulting behavioral response (De Robertis and Handegard, 2013). Information about vessel noise could be obtained opportunistically by monitoring noise from vessels of interest or by combining VMS data with passive acoustic mooring data to characterize the frequency and intensity of vessel noise (e.g., Daly and White, 2021).

Conclusions

We used PSAT data to address five questions about Pacific cod behavioral interactions with trawl vessels and gear, and we summarize our conclusions to these five questions here. First, we found evidence that Pacific cod dive in response to approaching trawl vessels and gear, although this behavior was not observed in Fish #1, which may indicate that this individual was on-bottom as the vessel approached. Second, all fish exhibited high-intensity swimming immediately before capture, suggesting they exhibit herding behavior that is consistent with an effort to outswim the approaching trawl gear. Third, although there was high individual variability in swimming endurance, accelerometer data suggest that one fish herded for 55.6 minutes and 4.17 km at a typical towing speed before capture, which is much longer and farther than suggested by previous studies on Pacific cod. Fourth, reactions to trawl vessels and gear were not consistent among fish, as shown by differences in diving and herding behavior among individuals. Fifth, we identified behavioral reactions other than diving and herding that may not have been reactions to trawl vessels and gear. During capture, Pacific cod showed a depth decrease that may have occurred as fish were navigating entry into the trawl and falling back towards the codend. We also identified a novel ‘freezing’ behavior in Fish #3 that began when the capture vessel was too far away to plausibly elicit a behavioral response. It is possible that freezing was a free-ranging behavior or a response to the other vessels operating in the area. These insights improve our understanding of behavioral interactions of Pacific cod to trawlers and suggest several avenues for future research to evaluate the impact of these behaviors on catchability and selectivity.

Overall, our study highlights how accelerometer data from archival tags can be used to characterize behavioral interactions between fish and trawl vessels/gear. Our study is the first to show that behavioral reactions of Pacific cod to trawl vessels and gear are likely to influence catchability and selectivity at typical trawling speeds. Although our sample size was insufficient to make inferences about population-level behaviors or the degree of variation in behaviors among individual fish, future tagging research will afford more opportunities to improve our understanding of how interactions with trawl gear influence catchability and selectivity of Pacific cod.

The increasing availability of vessel position information from vessel tracking systems such as VMS and AIS has fostered new opportunities for researchers to monitor spatial fishing patterns across the globe (Kroodsma et al., 2018; Welch et al., 2022). As more archival tags are deployed, tag technology improves, and vessel monitoring data become more readily available, new opportunities will arise that can improve our understanding of how behavioral reactions of fish to vessels and gear influence capture. This information can be leveraged to reduce bycatch (Kennelly and Broadhurst, 2021) and improve surveys (Fréon et al., 1993).

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Data availability statement

Non-confidential archival tag data are available upon reasonable request to the corresponding author. Confidential vessel geolocation and haul information data may be available for limited use cases, subject to legal restrictions on data sharing.

CRediT

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Tables

Table 1. Plausible reaction distances (RD) of fishes to auditory, visual, and tactile stimuli from trawl vessels and gear.

Stimuli	RD (m)	Source
Auditory	Up to 1,512	3
Visual	<40	4
Tactile	<1	1, 2

[1]-Ryer and Barnett (2006), [2]- Ryer (2008), [3]-Winger (2010), [4]-Zhang and Arimoto (1993)

Table 2. Release location and date, fork length (in centimeters), mass (in grams), bottom/ambient temperature (T °C) at tag release and capture, sampling interval for the archival tags (seconds), and days at liberty. Capture regions are Aleutian Islands (AI) or eastern Bering Sea (EBS).

	Release					Recapture						
Fish #	Lon./Lat.	Date	FL (cm)	Mass (g)	T (°C)	Area	Date	Fork Length (cm)	Mass (g)	T (°C)	Sampling Interval (s)	Days at Liberty
1	173.57 °W, 52.26 °N	Feb 20, 2019	70		4.5	541 (AI)	Mar 13, 2019	69	3680	4.1	3	22
2	176.43 °W, 51.92 °N	Feb 23, 2019	88		4.2	541 (AI)	Jun 8, 2019	90	9620	4.2	5	106
3	160.15 °W, 54.88 °N	Mar 26, 2021	83	4800	4.2	509 (EBS)	Apr 16, 2021			4.2	5	21

Table 3. Number of clusters and segments selected for accelerometer time series, estimated herding duration (s), estimated herding distance (km), and estimated vessel speed between the onset of herding and capture in absolute units (herding speed; $m \cdot s^{-1}$) and body lengths (vessel speed divided by fork length) per second ($FL \cdot s^{-1}$).

					Herding Speed	
Fish #	Behavioral Clusters, *m*	Behavioral Segments, *k*	Herding duration (s)	Herding distance (km)	Absolute ($m \cdot s^{-1}$)	Body lengths ($FL \cdot s^{-1}$)
1	4	9	120	0.07	0.58	0.84
2	5	15	3335	4.17	1.25	1.39
3	5	13	205	0.31	1.51	1.82

Table 4. Mean (μ) and standard deviation (σ) of archival tag accelerometer axes (g; g-force) for each behavior cluster (m) in the five-hour accelerometer time series for each fish, where xy is the combined horizontal axes and z is the vertical axis. For each fish, the behavioral cluster corresponding to high-intensity swimming immediately before capture (herding) is bolded. Asterisks (*) denote “freezing” behavior clusters in Fish #3.

		Horizontal Axes		Vertical Axis	
Fish #	Behavior Cluster, *m*	$\mu_{xy,m}$ (g)	$\sigma_{xy,m}$ (g)	$\mu_{z,m}$ (g)	$\sigma_{z,m}$ (g)
1	1	0.67	0.14	-0.67	0.13
	2	0.79	0.08	-0.53	0.08
	3	0.80	0.07	-0.50	0.06
	4	**0.86**	**0.29**	**-0.32**	**0.43**
2	1	0.60	0.19	-0.88	0.12
	2	0.73	0.21	-0.76	0.19
	3	0.90	0.12	-0.61	0.16
	4	0.84	0.10	-0.69	0.10
	5	**0.76**	**0.26**	**-0.60**	**0.33**
3	1*	0.08	0.05	-1.04	0.01
	2	0.56	0.05	-0.87	0.03
	3	0.58	0.13	-0.82	0.11
	4	0.71	0.11	-0.72	0.13
	5	**0.99**	**0.24**	**-0.28**	**0.30**

Figures

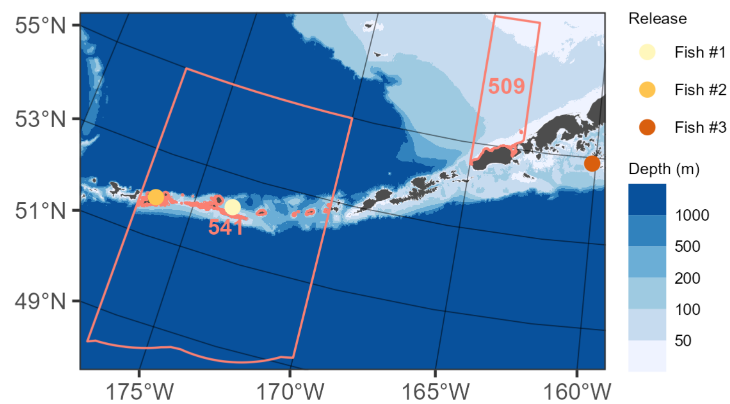

Figure 1. Map of release locations for tagged Pacific cod (circles) and approximate capture locations (NMFS Statistical Areas 509 and 541).

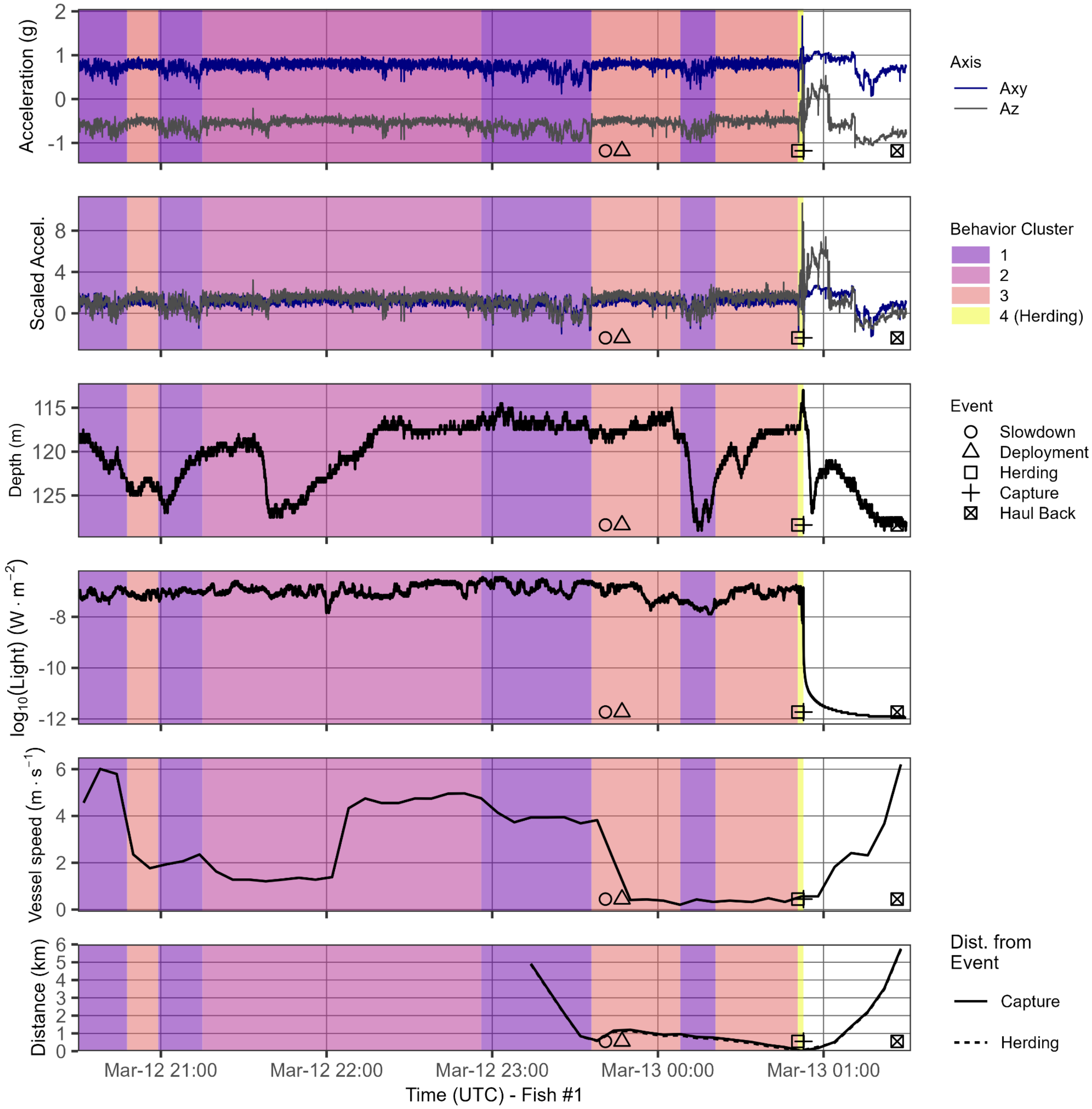

Figure 2. Archival tag and vessel time series for five hours leading up to capture of Fish #1. Panels show (from top to bottom): archival tag horizontal (A_{xy}) and vertical (A_z) accelerometer values (g-force), Z-score transformed (i.e., mean/standard deviation) accelerometer values, archival tag depth (meters), archival tag irradiance (W·m^{-2}), vessel speed (m·s^{-1}), and vessel distance from capture and herding locations. Fill color bands denote behavioral segments (i.e., phases) by behavioral clusters (i.e., behavior types). A behavioral cluster can occur multiple times in a time series. Symbols along the bottom of each panel show haul activity and fish behavior events (vessel slowdown, trawl gear deployment, onset of herding, capture, and haul back).

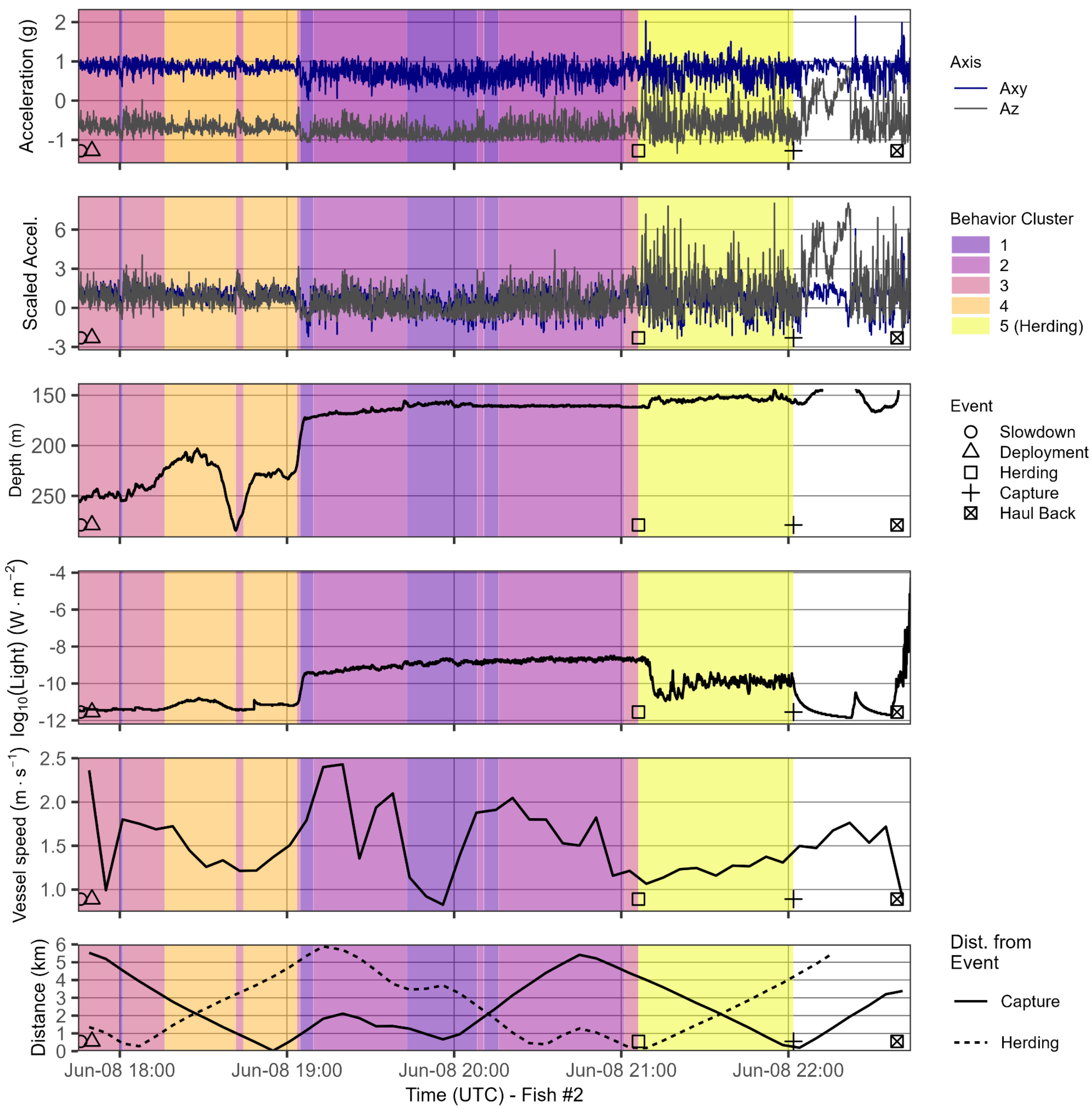

Figure 3. Archival tag and vessel time series for five hours leading up to capture of Fish #2. Panels show (from top to bottom): archival tag horizontal (A_{xy}) and vertical (A_z) accelerometer values (g-force), Z-score transformed (i.e., mean/standard deviation) accelerometer values, archival tag depth (meters), archival tag irradiance ($W{\cdot}m^{-2}$), vessel speed ($m{\cdot}s^{-1}$), and vessel distance from capture and herding locations. Fill color bands denote behavioral segments (i.e., phases) by behavioral clusters (i.e., behavior types). A behavioral cluster can occur multiple times in a time series. Symbols along the bottom of each panel show haul activity and fish behavior events (vessel slowdown, trawl gear deployment, onset of herding, capture, and haul back).

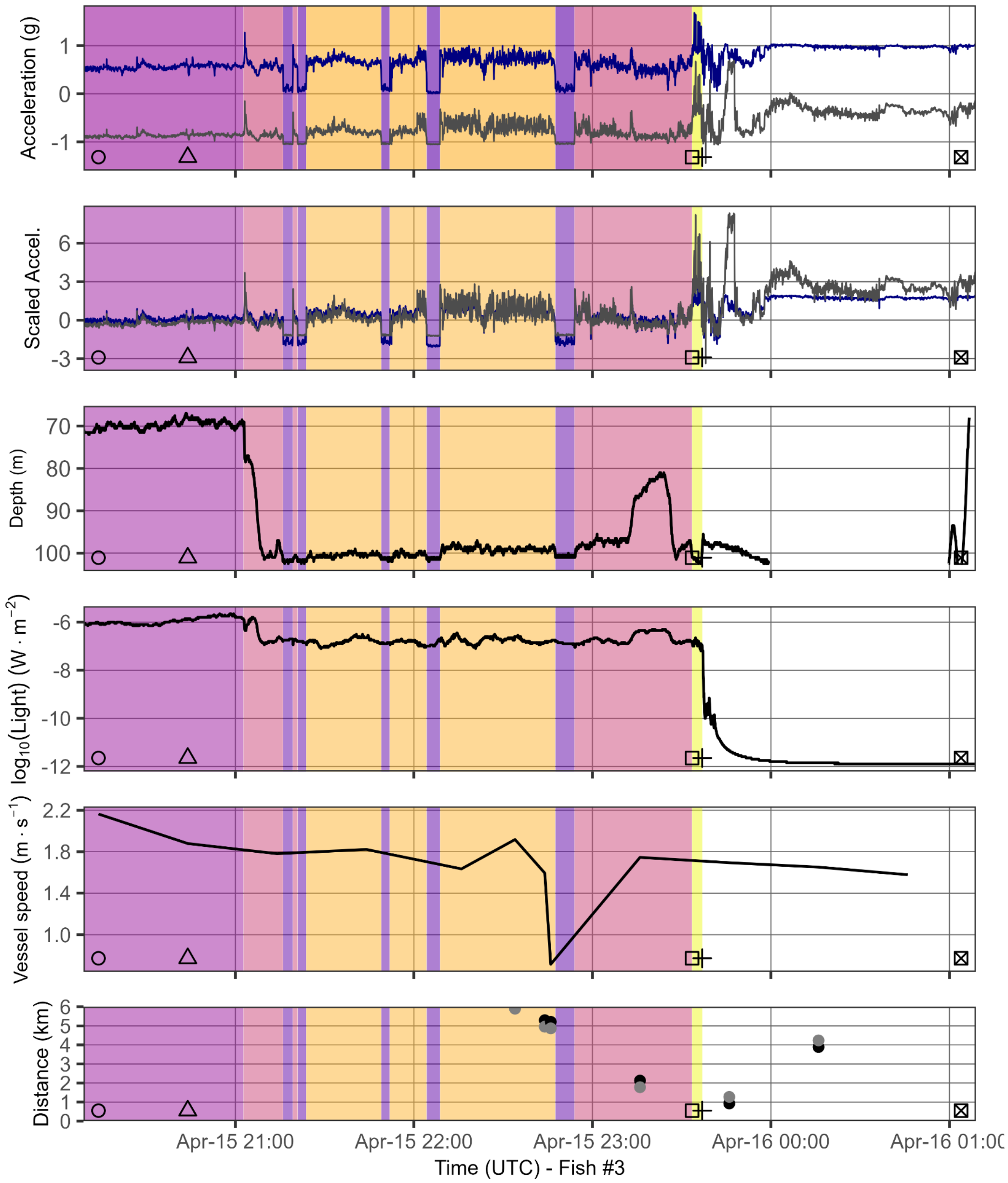

Figure 4. Archival tag and vessel time series for five hours before capture of Fish #3. Panels show (from top to bottom): archival tag horizontal (A_{xy}) and vertical (A_z) accelerometer values (g-force), Z-score transformed (i.e., mean/standard deviation) accelerometer values, archival tag depth (meters), archival tag irradiance ($W{\cdot}m^{-2}$), vessel speed ($m{\cdot}s^{-1}$), and vessel distance from capture and herding locations. Fill color bands denote behavioral segments (i.e., phases) by behavioral clusters (i.e., behavior types). A behavioral cluster can occur multiple times in a time series. Symbols along the bottom of each panel show haul activity and fish behavior events (vessel slowdown, trawl gear deployment, onset of herding, capture, and haul back).

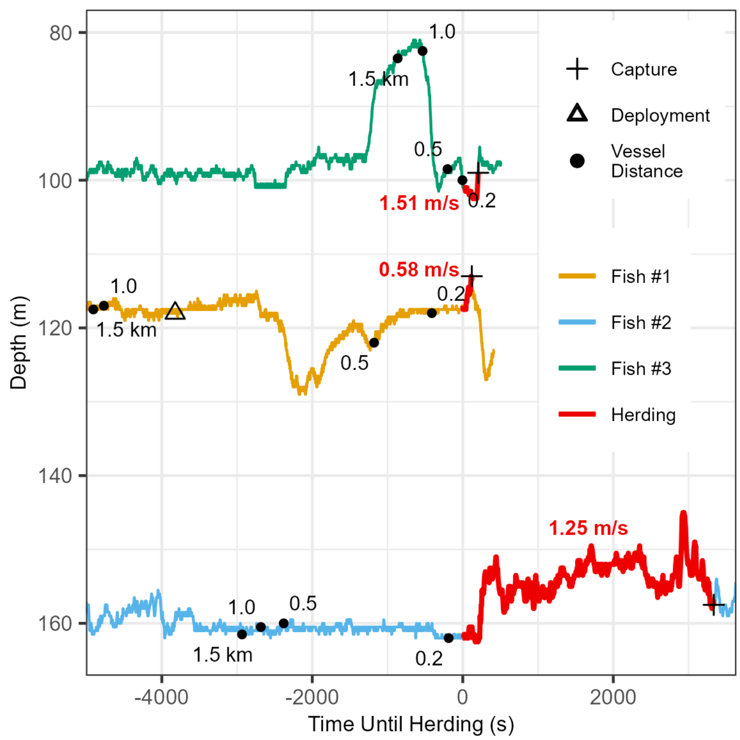

Figure 5. Time series of depth (m), distance of vessels to their position at the onset of herding (km), and herding speed ($m \cdot s^{-1}$) for all three fishes during the period leading up to capture and five minutes after capture. For each fish, thick red lines denote the segment of the time series classified as herding. Symbols denote the distance to the herding location, trawl deployment time, and capture time.

Supplement:

Characterizing behavioral responses of fishes to bottom trawl vessels and gear using archival tag accelerometer data (Supplementary Information)

Sean K. Rohan, Julie K. Nielsen, Bianca K. Prohaska, Alex De Robertis, Steve G. Lewis, Susanne F. McDermott

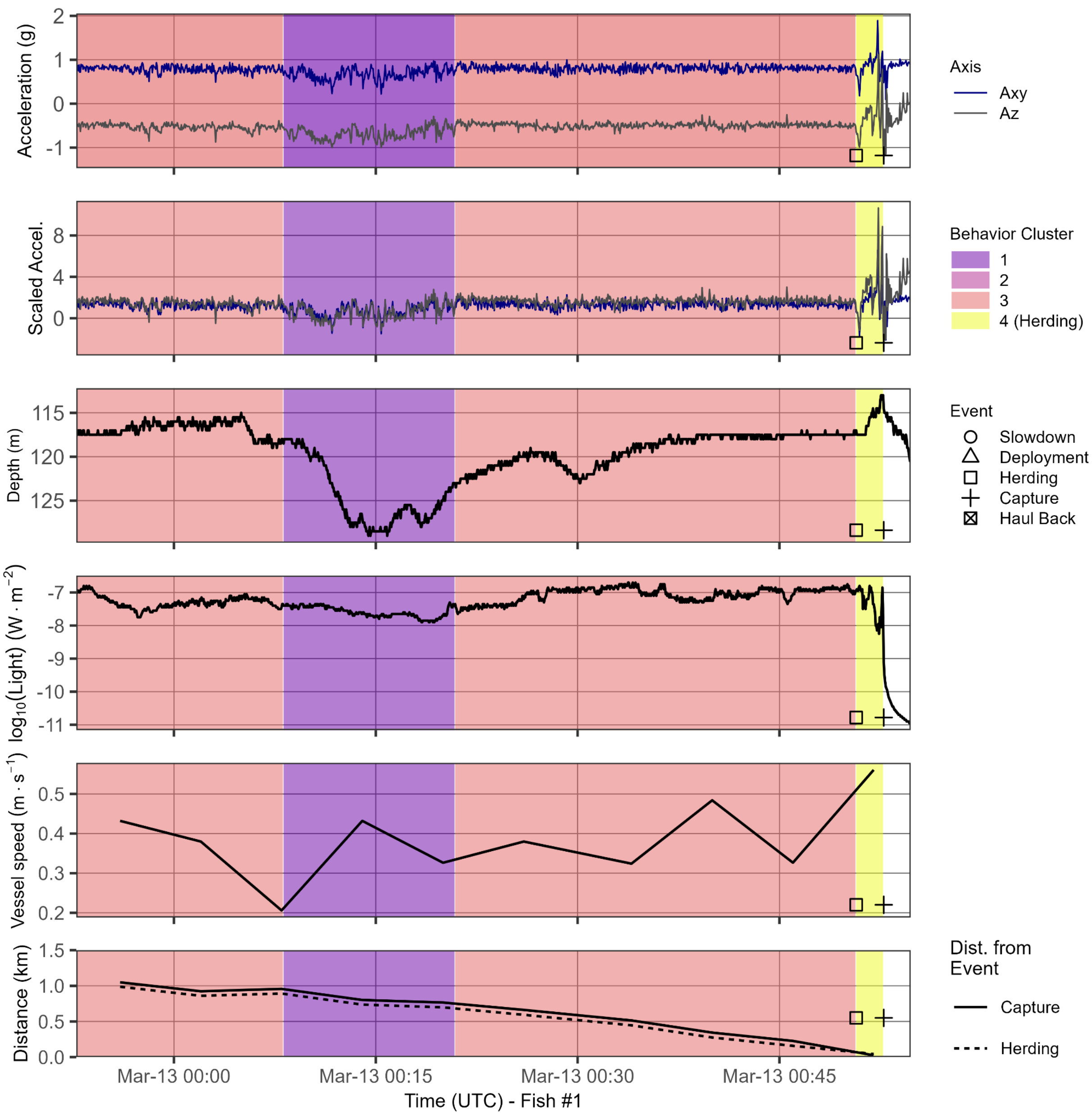

Figure S1. Archival tag and vessel time series for 60 minutes leading up to capture of Fish #1. Panels show (from top to bottom): archival tag horizontal (A_{xy}) and vertical (A_z) accelerometer measurements ($m \cdot s^{-2}$), Z-score transformed (i.e., mean/standard deviation) accelerometer measurements, archival tag depth (meters), archival tag irradiance ($W \cdot m^{-2}$), vessel speed ($m \cdot s^{-1}$), and vessel distance from capture and herding locations. Fill color bands denote behavioral segments (i.e., phases) by behavioral clusters (i.e., behavior types). A behavioral cluster can occur multiple times in a time series. Symbols along the bottom of each panel show haul activity and fish behavior events (vessel slowdown, trawl gear deployment, onset of herding, capture, and haul back).

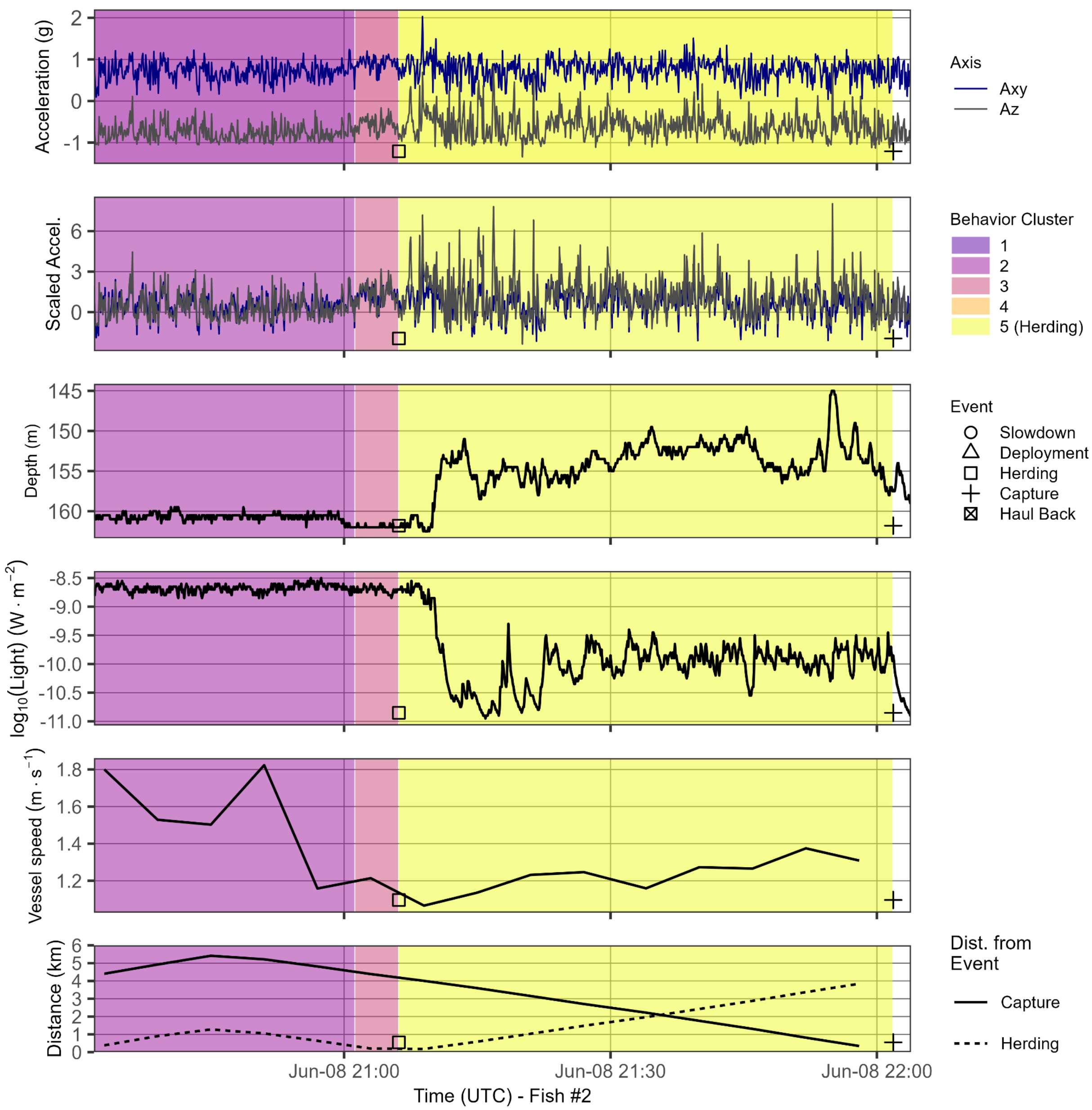

Figure S2. Archival tag and vessel time series for 90 minutes leading up to capture of Fish #2. Panels show (from top to bottom): archival tag horizontal (A_{xy}) and vertical (A_z) accelerometer measurements ($m \cdot s^{-2}$), Z-score transformed (i.e., mean/standard deviation) accelerometer measurements, archival tag depth (meters), archival tag irradiance ($W \cdot m^{-2}$), vessel speed ($m \cdot s^{-1}$), and vessel distance from capture and herding locations. Fill color bands denote behavioral segments (i.e., phases) by behavioral clusters (i.e., behavior types). A behavioral cluster can occur multiple times in a time series. Symbols along the bottom of each panel show haul activity and fish behavior events (vessel slowdown, trawl gear deployment, onset of herding, capture, and haul back).

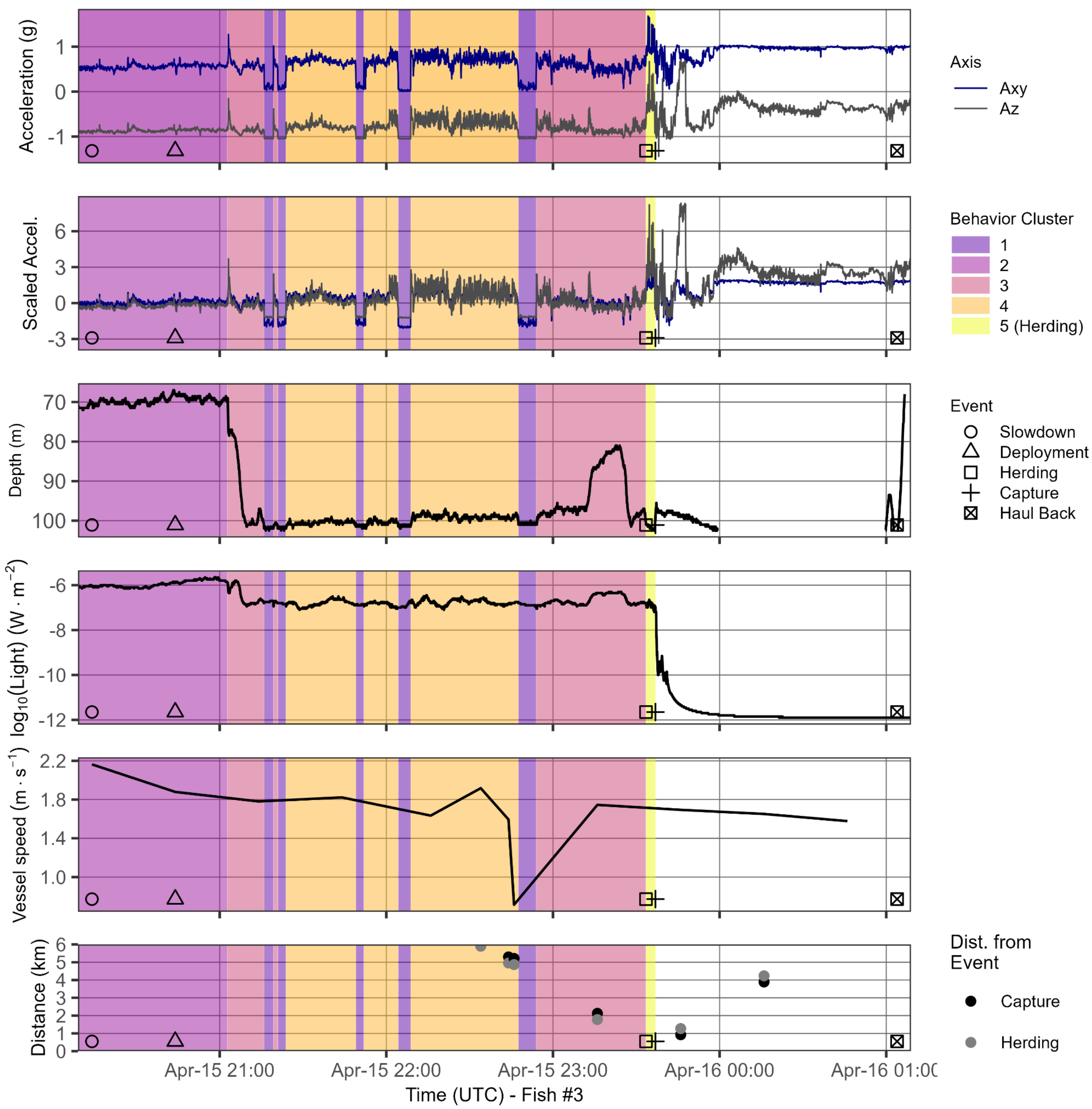

Figure S3. Archival tag and vessel time series for 60 minutes leading up to capture of Fish #3. Panels show (from top to bottom): archival tag horizontal (A_{xy}) and vertical (A_z) accelerometer measurements ($m{\cdot}s^{-2}$), Z-score transformed (i.e., mean/standard deviation) accelerometer measurements, archival tag depth (meters), archival tag irradiance ($W{\cdot}m^{-2}$), vessel speed ($m{\cdot}s^{-1}$), and vessel distance from capture and herding locations. Fill color bands denote behavioral segments (i.e., phases) by behavioral clusters (i.e., behavior types). A behavioral cluster can occur multiple times in a time series. Symbols along the bottom of each panel show haul activity and fish behavior events (vessel slowdown, trawl gear deployment, onset of herding, capture, and haul back).