



Respiratory and behavioral alterations in summer flounder (*Paralichthys dentatus*) exposed to pile driving sound

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Abstract

Understanding the interaction of human activities in the ocean and key resources is vital for the coexistence of offshore energy development and sustainable fisheries. Pile driving, commonly used in offshore construction, produces high-intensity sounds that propagate over long distances through the seafloor and water column. These sounds can affect marine animals living in the water column; however, far less is known about the impacts on the numerous benthic species occupying the sediment–water interface. The summer flounder (*Paralichthys dentatus*) is a benthic flatfish that comprises an important fishery overlapping with offshore energy development along the US Eastern seaboard. In this field-based study, we employed novel operculum-mounted acceleration tags on flounder exposed to repeated pile driving activity to assess respiration changes and body movements associated with acoustic exposures. Flounders exposed to pile-driving sound increased respiration rates during both impact (high intensity, impulsive) and vibratory (lower intensity, continuous) hammering, compared to pre-exposure baseline and nonexposed counterparts. The heightened operculum pumping was not driven by swimming rates, but rather an apparent sound-induced stress response, primarily driven by the impact hammer technique. All fish but one showed at least one short-duration reaction to the impact hammering, although it was largely divergent whether each fish demonstrated an escape response (fight–flight) or breath-holding (freeze-hide). Both types of short-duration responses were most common during initial impact hammer sequences, declining in prevalence as sound treatments were repeated. Despite potential behavioral habituation, prolonged increases in respiration rate suggest that physiological impacts persisted. Such sound-mediated physiological impacts have not been previously reported for a benthic, swim bladder-less fish, such as flounder, underscoring the need for consideration of this taxon in offshore construction management.

Keywords offshore wind, animal behavior, anthropogenic noise, environmental impacts, stress, personality

Introduction

The ocean environment is increasingly industrialized for resource extraction, marine infrastructure, and offshore energy (Paolo et al. 2024). These activities contribute substantial noise to the marine environment, particularly during construction (Slabbekoorn et al. 2010, Mooney et al. 2020). Understanding the potential impacts of these high-amplitude sounds on a diversity of marine animals is key to better evaluating trade-offs between construction needs and fishery impacts, mitigation strategies, and spatial planning.

The construction of fixed foundation piles—such as those used for docks, offshore wind turbines, and oil and gas platforms—most commonly requires a technique known as impact hammer (IH) pile driving, which produces intense impulses that can propagate for hundreds of meters, up to kilometers, through the water column and substrate (De Jong and Ainslie 2008, Bruns et al. 2016). Although broadband, IH pile driving produces particularly high amplitudes in the lower frequencies (<1 kHz) where many fishes are sound-sensitive (Wahlberg and Westerberg 2005, Reinhall and Dahl 2011). In several fish species, exposure to impact pile driving can cause behavioral changes—such as increased shel-

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tering (Jarriel et al. 2025) and lowered anti-predator avoidance (Spiga et al. 2017), and temporary hearing loss and physical tissue damage in fish with swim bladders (Halvorsen et al. 2012, Casper et al. 2013). An alternative technique, vibratory hammer (VH) pile driving, is becoming increasingly popular and sometimes used in combination with IH, as it produces a continuous, lower amplitude sound, although it is still of regulatory and biological concern (Dahl et al. 2015, Koschinski and Lüdemann 2020). Given increasing concerns of noise pollution on species, populations, and communities, there is a need to understand how water- and substrate-borne sounds influence marine life, with a growing concern for species associated with the benthos (Hawkins et al. 2021).

Sound propagation through and adjacent to the benthic habitat is complex. In addition to relatively well-studied water-borne sound, acoustic signals at the benthos produced by pile driving include fast-traveling compression waves, shear waves, and seismic interface waves along the sediment–water interface, which also create effervescent waves in the bottom 1 m of the water column (Hawkins et al. 2021). These seismic interface waves have the potential to travel kilometers through the substrate, influencing the acoustic particle motion near the benthos at far ranges from the sound source (Jensen et al. 2011, Hazelwood et al. 2018). Particle motion, or the back-and-forth vibratory component of sound waves, is the most common acoustic sensory modality for fish, although is underreported in sound impact studies (Popper et al. 2022). These phenomena and the production of substrate-borne waves generated by pile driving likely incur additional exposure conditions that benthic animals must face. Yet there is limited empirical data addressing how these stressors impact animals (Hawkins et al. 2021, Guan et al. 2025), leaving potential gaps in the management of such stressors and putting key fisheries taxa at risk.

Benthic communities and the species therein are key to marine ecosystems in a myriad of ways (Crespo and Pardal 2022), including supporting important fisheries. Summer flounder (*Paralichthys dentatus*) are benthic fish, with adult morphology adapted for high surface-area contact with the sediment, making them potentially sensitive to pile driving acoustic vibrations traveling through both the water column and the substrate. The summer flounder fishery is one of the largest commercial and recreational fisheries along the east coast of the United States, responsible for \$24 million in economic output along New England and the Mid-Atlantic in 2023 alone ((NOAA Fisheries Office of Science and Technology, n.d.). Their habitat overlaps with areas potentially subject to offshore energy and mineral development in the United States, underscoring the need to understand how summer flounder may be impacted by offshore construction.

As with most flatfish, adult flounder lack a swim bladder, a gas-filled organ that enhances sensitivity to sound pressure in many fishes, confining their hearing abilities to just acoustic particle acceleration (Chapman and Sand 1974, Radford et al. 2012). Flatfish hearing, measured in the European plaice (*Pleuronectes platessa*) and common dab (*Limanda limanda*) spans from 30 to 250 Hz (Chapman and Sand 1974). Despite having perhaps less hearing sensitivity than fish with auditory specializations, this hearing range directly overlaps with the highest amplitude frequencies produced by pile driving (Reinhall and Dahl 2011, Sigraay and Andersson 2011). Only a few studies to date have evaluated impacts of pile driving on flatfish physiology (Bruintjes et al. 2017) and be-

havior (Mueller-Blenkle et al. 2010, Kim et al. 2024), highlighting substantial knowledge gaps regarding reactions in other flatfish species and other types of behavioral or physiological responses.

Stress can be detrimental to the growth and reproduction of animals when extended over long periods of time (Pankhurst and Van Der Kraak 1997). In addition to physiological stress markers, such as heightened cortisol or rapid breathing, behavioral reactions can also offer insight into how or if a stressor is perceived. Several types of startle responses to a stressor are well-documented for fish, including head retraction, freezing, and escape responses (Domenici and Hale 2019). For example, zebrafish (*Danio rerio*) exhibit both erratic darting and freezing when exposed to a chemical stressor (Speedie and Gerlai 2008). It is critical to understand whether summer flounder react to impact and vibratory pile driving and if they alter their metabolic state for prolonged periods of time.

Operculum pumping rate in flatfish is directly related to respiration rates and oxygen uptake and can be used as an energetics proxy in free-swimming fish (Dalla Valle et al. 2003). However, traditional methods of visual counts of operculum movement are insufficient for *in situ* conditions and long durations of observations. Small, neutrally buoyant accelerometers attached to the operculum allow insight into respiration patterns in a minimally invasive way (Cones et al. 2025a). A similar method has been applied to determine respiration and activity in gilthead sea bream (*Sparus aurata*) and European sea bass (*Dicentrarchus labrax*) (Martos-Sitcha et al. 2019, Ferrer et al. 2020). This method lends itself well to the summer flounder, given their morphology and benthic, stationary nature.

This study uses operculum accelerometer tags on summer flounder to track respiration rates and short-duration reactions—freezing and escape responses—of summer flounder when exposed to alternating sequences of actual impact and vibratory pile driving. Responses were measured in a field-based experiment before, during, and after multiple pile driving sequences and compared to control fish (identical experiments but without pile-driving sound). The influence of both pile driving types was assessed, as well as potential changes in response during the exposure and with repeated exposures.

Methods

Fish acquisition and husbandry

A total of 48 summer flounder were caught via line fishing in the Vineyard Sound and Buzzards Bay (Massachusetts, USA) from July to September 2024 under MA Scientific Collecting Permit #175150. Additionally, several fish were acquired via trawling by the R/V Gemma of the Marine Biological Laboratory (Woods Hole, MA, USA). Fish were then transported to the Woods Hole Oceanographic Institution's (WHOI) Environmental Systems Lab (Woods Hole, MA, USA) and maintained in 8.0 × 2.0 m (45 cm water depth) flume tank supplied with circulating local seawater at ambient temperature (20.0–22.5°C). Live, locally caught mummichogs (*Fundulus heteroclitus*) and juvenile menhaden (*Brevoortia tyrannus*) were provided in the holding tank each week for feeding.

After capture, flounders were maintained in tanks for a minimum of 24 h before being used in the study. Any fish that

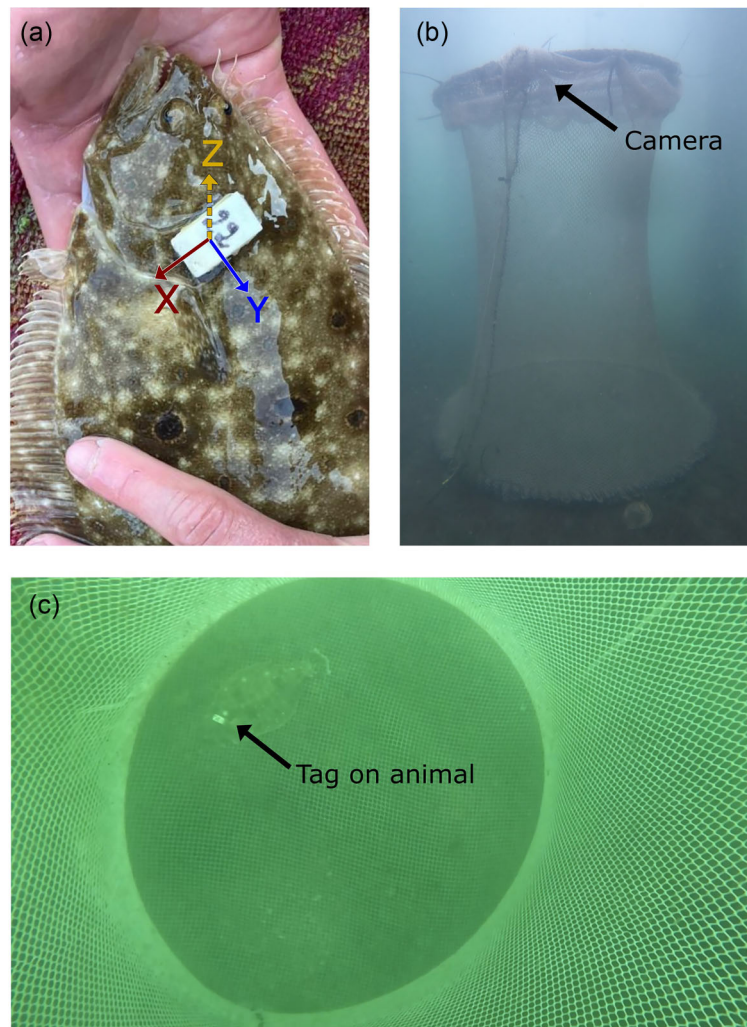


Figure 1 (a) Accelerometer tag affixed to the operculum of a flounder during the tagging process. Arrows show the positive orientation of the three accelerometer axes (x , y , and z). Note that “ z ” is the upward direction, perpendicular from the tag. (b) *In situ* cage setup. A camera was attached inside the top of cage, facing down. (c) View of tagged fish in the cage, resting on the bottom.

was deemed unhealthy was not used for experiments. Flounder ranged from 252 to 1007 g (mean: 482.2 g) in weight and 31–48 cm (mean: 35.8 cm) in length. Each fish was used only once in this experiment.

This study was carried out in accordance with the principles of the Basel Declaration and recommendations and approval of the WHOI Institutional Animal Care and Use Committee scientific protocol.

Field experimental procedure

Tagging procedure

To investigate pile driving sound impacts on summer flounder respiration and behavior, one TechnoSmart Axy 5 XS (22 × 13 × 8 mm, 3.7 g in air) biologging tag, containing an accelerometer and magnetometer, was attached to the operculum of each fish (Fig. 1a). The tag was placed on the dorsal third of the operculum, the widest section, with the positive x -axis oriented at an angle toward the pectoral fin (Fig. 1a). This precise attachment orientation and location was repeated for all fish. The tag measured triaxial ac-

celeration at 100 Hz, capturing both the movement of the flounder body and the beating of the operculum while the animal was resting on the bottom.

The tag was secured to the fish operculum with Reef Glue (Seachem Laboratories, GA, USA), while the fish was held still out of the water. Seawater was replenished over the head and gills of the fish while the glue was curing, and the procedure only lasted ~5–6 min total before the animal was returned to the water. Despite the relatively quick process, preliminary tests showed that flounder required several hours to acclimate after tagging and return to a resting respiration rate (~0.5 Hz, [Supplementary Fig. S1](#)). Flounders that had their tags fall off overnight and re-attached within a few hours of pile driving the next day had elevated respiration rates throughout the experiment (~0.8 Hz) and were thus excluded from analyses ($n = 13$, [Supplementary Fig. S1](#)). Longevity of the tag attachment was dramatically improved by first gluing a fake plastic tag to the same location on the operculum an hour prior to the final tagging procedure.

Tagged fish were placed in cylindrical mesh cages (top diameter: 0.75 m; bottom diameter: 1 m; height: 1.5 m) ~19 h before pile

driving and allowed to acclimate to the cage overnight (Fig. 1b). Cages were slowly lowered into the water until resting on the bottom (depth: 4–6 m). Each cage contained only one fish per experiment (Fig. 1c).

Pile driving methods

A total of 11 days of pile driving were conducted between 16 September and 3 October 2024 off of a dock at WHOI. During this time, daytime water temperatures ranged from 18.7°C to 21.0°C (retrieved from NOAA Station BZBM3 Woods Hole, MA, USA).

An independent construction company alternated two techniques to repeatedly drive a cylindrical steel pile (length: 10 m; diameter: 0.3 m; wall thickness: 0.02 m) into the substrate. First, a steel IH (weight: 1500 kg) was dropped onto the pile at a rate of ~10 strikes/min from a height of 1.2 m, producing high-intensity, impulsive sounds. IH sequences lasted 15 min, resulting in the steel pile penetrating 3–5 m into the seabed. Next, a VH (weight: 212 kg, H&M model 135, 1150 blows per minute) was used to remove the pile from the substrate and reposition it in an adjacent location for another round of the IH pile driving. VH sequences are characterized by continuous, lower amplitude sounds. This process was repeated five times per experiment day, with pile-driving activity commencing at 12:30 and lasting for 3–4 h. In total, each summer flounder was exposed to five IH and five VH sequences per day, always starting with the IH exposure. The high-intensity impulsive sound of the IH was the primary focus of this study; thus, this was selected to be the first treatment each day. Construction methods were identical to previous experiments, and additional details on construction and sound levels can be found in Jarriel et al. (2025) and Jézéquel et al. (2022).

Flounder behavior and respiration rates were assessed throughout an entire day of pile driving, including 60 min of pre-exposure to serve as a “normal” baseline for each fish, five alternating IH and VH sequences, and a post-exposure period of 15 min. Sound-exposed fish ($n = 12$) were placed in cages within 3.5–9.6 m from the pile (average: 5.5 m). Precise distances of each cage from the pile were re-measured before each IH. An underwater camera (GoPro 12, San Mateo, CA, USA) was carefully mounted inside the top of each cage, facing down, 30 min before pile driving each day to compare with tag data and confirm tag-detected behaviors (Fig. 1b). Cameras were attached via free-diving, with minimal disturbance to the cage or fish. Following the post-exposure period, cages were extricated from the water and the flounder removed. We then measured total length, from nose to tip of the tail, and weighed each fish.

Identical experiments were conducted on three days without pile driving within the same period to serve as controls (11 and 12 September 2024 and 1 October 2024). Control fish ($n = 7$) experienced matching experimental procedures, including tagging, overnight acclimation, and video recording, with the absence of pile-driving sound exposure. Again, only fish with tags that stayed on overnight and through the experiment were included. Further, time constraints to ensure water temperature was comparable for control fish limited the numbers of control experiments conducted. Average IH start and end times were used to delineate the “treatments” on control days. Same as sound-exposed fish, control fish were released to the wild after being used.

Acoustic measurements

The acoustic field was recorded and quantified for sound pressure, water-borne, and substrate-borne particle motion.

Sound pressure levels were measured at multiple distances from the sound source using Snap autonomous recorders (Logger-head Instruments, FL, USA). Six recorders were secured to rebar stakes embedded in the substrate, with hydrophones positioned ~1 m above the seabed at an array of distances from the pile. A full day of pile driving was analyzed from the recorder closest to the flounder cages (mean distance from pile: 4.3 m), including five impact and five vibratory driving sequences (sensitivity = -209.6 dB re $1 \text{ V } \mu\text{Pa}^{-1}$).

Given the sensitivity of flatfish to particle motion (Chapman and Sand 1974) and their benthic nature, it was important to also quantify the water- and substrate-borne vibrations. A calibrated PCB triaxial accelerometer suspended in the water, 1 m below surface, measured the water-borne vibrations near the flounder cages at a sampling rate of 20 kHz (model W356B11/030CA; sensitivity: $x = 1.028 \text{ mV m s}^{-2}$, $y = 1.040 \text{ mV m s}^{-2}$, $z = 1.032 \text{ mV m s}^{-2}$). The accelerometer was connected to a signal conditioner (Model 480B21, Piezotronics), which was then wired to two analog filters (Model 3362/3382, Krohn-Hite Corporation). Outputs of the filters were then inputted into a data acquisition board (USB 6251, National Instruments), which was in turn connected to a laptop that ran a custom MATLAB (Mathworks, MA, USA) script to record the audio files. Additionally, a calibrated three-component geophone (model GS-11D from Geospace®) with a 1000 Hz frequency sampling recorded substrate-borne vibrations at several distances around the flounder cages. All data were recorded on a Quanterra Q8 24-bit data logger after $\times 8$ pre-amplification.

All acoustic processing was done in MATLAB 2023b, with custom scripts. Sound pressure and in-water acceleration data were filtered between 60 and 3000 Hz, with an eight-pole Butterworth filter, to focus on frequencies that flounders are most receptive to (Chapman and Sand 1974). The geophone used had a frequency response extending to very low frequencies, so substrate acceleration was filtered between 0 and 1000 Hz. The amplitude of each IH strike was quantified in 0-peak sound pressure level (SPL_{pk} ; dB re $1 \mu\text{Pa}$) and 0-peak acceleration level (PAL_{pk} ; dB re $1 \mu\text{m s}^{-2}$). Next, root-mean-squared sound pressure (SPL_{rms} ; dB re $1 \mu\text{Pa}$) and acceleration levels (PAL_{rms} ; dB re $1 \mu\text{m s}^{-2}$) were calculated over the pulse length containing 90% of the signal energy. To assess the cumulative effect of multiple IH strikes on the flounder, single strike exposure levels in pressure (SEL_{ss} ; dB re $(1 \mu\text{Pa})^2 \text{ s}$) and acceleration (SEL_{ss} ; dB re $(1 \mu\text{m s}^{-2})^2 \text{ s}$) were calculated by integrating the time series over the pulse length containing 90% of the signal energy. Finally, we computed cumulative sound exposure levels (SEL_{cum} ; dB re $(1 \mu\text{Pa})^2 \times s$; dB re $(1 \mu\text{m s}^{-2})^2 \text{ s}$) for each IH sequence and full day with the following equation:

$$\text{SEL}_{\text{cum}} = 10 \log_{10} \left[\sum_{n=1}^n (\text{SEL}_{\text{ss}}) dt \right], \quad (1)$$

where n is the n th impulse [following BOEM (2023)].

For the in-between vibratory sequences, SPL_{rms} and PAL_{rms} were calculated over 1-s intervals for sound pressure and water-borne acceleration, respectively. The full, 60-min “pre” sound exposure similarly calculated for SPL_{rms} in this way. However, neither substrate nor in-water PAL was available for this full period.

A full day of sound pressure, water-borne acceleration, and substrate particle acceleration at slightly variable distances is summarized in the “Results” section to demonstrate the sound levels experienced by flounders.

Data analysis

Video analysis

To validate behaviors inferred from tag data, animal movements were also video recorded with GoPro 12 s mounted inside the top of each cage facing down. Five-minute video sections were viewed in Windows Media Player and manually annotated. Video sections were randomly chosen and continuously annotated at a 1-s resolution. Video and tag timestamps were synced using IH strikes (precise timing visible in tag data and audible in video). Annotated sections were then compared to corresponding tag-predicted behaviors when at least one behavioral change occurred, resulting in 11 sections of 5 min each, spanning eight different tagged fish. Visual behaviors were classified as “active” when the fish was moving, including repositioning or swimming, “resting” when the fish was still on the bottom, or “fast start” when the fish suddenly changed speed and direction, often colliding into the soft net of the cage. Following the definitions outlined in Domenici and Hale (2019), “fast start” describes the accelerative motion of the fish, regardless of context. Fast starts can be an escape response, but also occur during nonthreatening situations such as prey capture or social interactions (Domenici and Hale 2019). However, in the context of sound treatments and when occurring in high numbers, fast starts were assumed to be escape responses, a flight response to a perceived threat (Domenici and Hale 2019). Thus, both “fast start” and “escape response” will be used here to describe the same behavior, with the latter term having an implied context of occurrence.

Fast starts were far rarer than the other two behaviors (Fig. 2), so these were additionally verified by seeking out tag-detected fast starts and verifying with video. In total, 11 fast starts were visually confirmed across 6 individual fish.

Tag analysis

All tag analyses were performed in MATLAB 2023b. The animal-borne accelerometer was used to identify three behaviors: fast starts, active movements (excluding high-acceleration fast starts), and resting. These three behavioral modes were distinguished using acceleration magnitude thresholds from the axis having the most variance for each state. First, the acceleration data were processed for fast starts by running a peak detector (findpeaks.m, MATLAB) over the Z-axis (threshold: 1.43 g; green stars in Fig. 2b). This peak threshold, over which we considered a fast start, was determined and validated from the video annotations. Second, “active” states were identified, also using a peak detector. Due to the diversity of “active” behaviors, all three acceleration axes were summed into the animal’s overall dynamic body acceleration (ODBA). ODBA filters out acceleration due to gravity and is an effective proxy to measure animal activity level (Gleiss et al. 2011). Active sections were detected automatically, with a ODBA (using all three axes of acceleration) threshold of 0.09 g at a 1 s resolution (window size: 180; red stars in Fig. 2). Lastly, during resting, the tag movement resulted only from the movements of the oper-

culum, which produced clear operculum pumping signals on the Y-axis acceleration (blue diamonds in Fig. 2a).

With fast starts and active data removed, respiration rates were calculated from the remaining resting data. Y-axis acceleration was converted to a frequency domain using a fast Fourier transform (FFT) over continuous 5-s intervals, with a Hanning window and zero padding applied to limit spectral leakage and increase frequency resolution (following Cones et al. 2025b). The dominant frequency, in hertz (Hz), for each 5-s segment was extracted as the respiration rate for that time point. Any time periods that were classified as resting but were <5 s long (i.e. interrupted by active events) were ignored for respiration analyses. Next, a period equal to the duration of each active event was removed immediately after the activity ended. This was a conservative approach to remove heightened respiration rates during recovery from swimming (see Fig. 2a) and avoid conflating effects of changes in swimming activity with pile driving.

Immediate changes in respiration with the onset of impact pile driving were assessed separately from the automated processing. Only fish that were resting on the bottom when IH started were used for this specific analysis. The first strike of each IH sequence was manually selected, and then an FFT was run on the 5 s immediately prior and the 5 s following the strike. If there was a visible change in the animal’s respiration, which occurred when the difference between these values was >0.1 Hz, the end of the visibly disrupted breathing was manually selected. This was done manually because it often occurred on a finer scale than 5-s increments, which was our minimum resolution for an accurate FFT.

Statistical analysis

All plots and statistical analysis were done in MATLAB 2023b. Control fish underwent identical analyses, with average IH onset times used to segment the data. Respiration change through the experimental periods was assessed in two ways. First, respiration rates for each fish across different sound treatments (pre, IH, VH, and post) were compared with repeated-measures ANOVA, followed by a Tukey–Kramer multiple comparisons test. Second, to evaluate how these changes in respiration compared with the control, no-sound fish, we used the difference between the average respiration rate for each fish’s “pre” 60-min period and each successive sound treatment period. Using each fish’s own “baseline” to determine change, rather than a grouped average, aimed to limit individual variation in breathing rate, daily temperature fluctuations, and imbalanced treatment and control sample sizes. A Mann-Whitney rank-sum test was used to compare the change from pre between sound-exposed and control fish for each period. This same analysis was then applied to activity levels, using the percentage of time spent swimming for each period for each fish.

For a finer resolution of respiration patterns (minutely), the average respiration rates each minute were calculated across all sound-exposed fish. For VH sequences, which were of variable durations between days, a minimum of three fish were required for each time point to be used. The end of VH sections was removed if they did not meet this requirement. To show the change occurring at IH onset, minute averages were plotted for the 5 min just before each IH sequence (including pre and VH) through the end of IH (all five bouts plotted together). A four-parameter logistic sigmoidal model was fitted to the data using MATLAB’s curve fit-

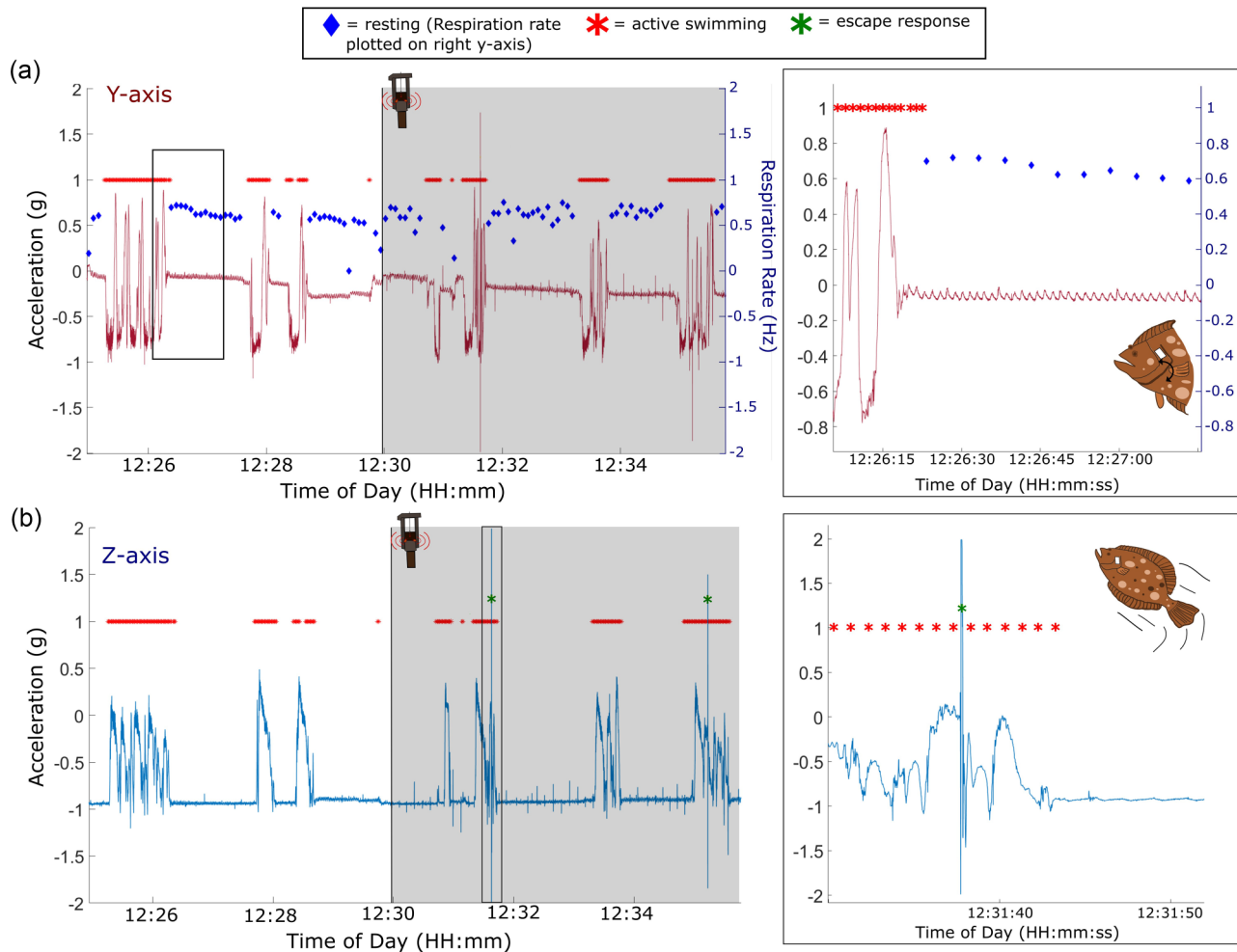


Figure 2 Raw acceleration data and behavioral designations of a single animal before and during pile driving (onset at vertical line). Active events, designated by red stars every second, were automatically detected as perturbations in all three axes (x -axis not shown). (a) In between active sections (red stars at $y=1$), respiration rate was extracted from the y -axis acceleration while the animal was at rest. Blue diamonds indicate 5-s intervals of resting, with their position on the right y -axis being the corresponding respiration rate in Hz. Left panel: IH pile driving starts around 12:30 local time, as denoted by a vertical black line and shading. Right panel: A zoomed-in section is shown (black box in left panel). After the active swimming (red stars at $y=1$), respiration rates are heightened and then begin to decrease as the animal recovers (blue diamonds). (b) Z-axis acceleration was used to detect fast starts (green stars at $y=1.25$, peaks above 1.43 g) and contributed to detection of active sequences (red stars at $y=1$). Left panel: This animal had two fast starts after IH pile driving began (black vertical line and shading). Right panel: Close-up view of one individual's fast start (black box in left panel).

ter tool to see where the inflection point lay. Changes in respiration throughout each IH and VH were assessed by plotting minute averages of each sound exposure type and fitted with linear regressions.

Fast start escape responses were converted to a per-minute rate to account for different lengths of time in the different periods. Due to the relatively low rates of fast starts, the data was non-normal, so a Kruskal–Wallis nonparametric test was performed to compare rates of fast starts between pre, IH, VH, and post. If significance was found, a Tukey–Kramer multiple comparisons test was applied as well.

Linear regressions were performed between a number of predictor variables—such as fish size, resting respiration rate, and received level at the cage—to try and understand variability in swimming, propensity to fast start, and propensity to breath hold. However, no significant correlations were found; thus, they are not shown in the “Results” section.

Results

Acoustic measurements

Flounder experienced average peak amplitudes up to 202 dB re 1 μPa (SPL_{pk}), 114 dB re 1 $\mu\text{m s}^{-2}$ (in-water PAL_{pk}), and 133 dB re 1 $\mu\text{m s}^{-2}$ (substrate PAL_{pk}) at their closest distance from the pile driving (3.5 m). After a full day, corresponding to five repeated IH sequences, cumulative sound exposure levels were 187.1 dB re (1 μPa)² $\times$ s (pressure, Table 1), 106.5 dB re (1 $\mu\text{m s}^{-2}$)² s (in-water acceleration, Table 2), and 131.0 dB re (1 $\mu\text{m s}^{-2}$)² s (substrate acceleration, Table 3). VH levels at these distances were ~ 145 dB re 1 μPa for SPL_{rms} and 70 dB re 1 $\mu\text{m s}^{-2}$ for in-water PAL_{rms} , ~ 40 dB and ~ 20 dB lower than root-mean-squared levels of impact pile driving, respectively (Tables 1 and 2).

Even at the farthest distances from the pile (9.6 m), flounder were exposed to peak sound levels of 196.2 ± 2.31 dB re 1 $\mu\text{m s}^{-2}$

Table 1. Sound pressure levels of five impact and five vibratory sequences through the course of an experimental day.

Distance (m)	Impact hammer				Vibratory hammer
	SPL _{pk} (dB re 1 μ Pa)	SPL _{rms} (dB re 1 μ Pa)	SEL _{ss} (dB re (1 μ Pa) ² × s)	SEL _{cum} (dB re (1 μ Pa) ² × s)	SPL _{rms} (dB re 1 μ Pa)
3.35	202.5 ± 2.00	183.2 ± 1.15	162.2 ± 1.73	183.5 (125 strikes)	145.8 ± 5.22
3.41	202.0 ± 2.47	180.6 ± 1.87	158.6 ± 0.91	179.1 (108 strikes)	145.1 ± 3.36
4.71	199.8 ± 1.84	180.6 ± 1.67	158.5 ± 1.07	179.6 (126 strikes)	139.8 ± 1.92
5.04	197.8 ± 2.36	178.8 ± 2.32	157.2 ± 1.32	177.8 (110 strikes)	138.6 ± 3.55
5.65	199.2 ± 2.22	177.9 ± 2.10	156.6 ± 1.54	178.0 (129 strikes)	133.7 ± 2.26

SEL_{cum} for the entire day (just IH) was 187.1 dB re (1 μ Pa)² × s (2 October 2024). The ambient sound level during “pre” was 118.3 ± 1.49 dB re 1 μ Pa (2 October 2024).

Table 2. In-water particle acceleration levels of five impact and five vibratory sequences through the course of an experimental day.

Distance (m)	Impact hammer				Vibratory hammer
	PAL _{pk} (dB re 1 μ m s ⁻²)	PAL _{rms} (dB re 1 μ m s ⁻²)	SEL _{ss} (dB re (1 μ m s ⁻²) ² s)	SEL _{cum} (dB re (1 μ m s ⁻²) ² s)	PAL _{rms} (dB re 1 μ m s ⁻²)
2.73	117.7 ± 3.57	90.5 ± 2.01	79.3 ± 1.01	100.2 (119 strikes)	70.0 ± 0.05
2.83	119.1 ± 5.22	89.6 ± 2.45	78.9 ± 1.17	100.0 (126 strikes)	71.9 ± 2.96
2.88	118.2 ± 3.01	91.2 ± 1.41	79.2 ± 0.64	100.1 (122 strikes)	70.7 ± 1.50
3.75	114.3 ± 2.92	88.4 ± 1.82	77.9 ± 0.94	98.8 (118 strikes)	69.9 ± 0.29
3.76	114.1 ± 4.39	86.6 ± 3.04	77.2 ± 1.62	98.1 (118 strikes)	70.4 ± 1.60

SEL_{cum} for the entire day (just IH) was 106.5 dB re (1 μ m s⁻²)² s (3 October 2024).

Table 3. Substrate-borne particle acceleration levels of five impact sequences through the course of an experimental day.

Distance (m)	Impact hammer			
	PAL _{pk} (dB re 1 μ m s ⁻²)	PAL _{rms} (dB re 1 μ m s ⁻²)	SEL _{ss} (dB re (1 μ m s ⁻²) ² s)	SEL _{cum} (dB re (1 μ m s ⁻²) ² s)
3.35	136.4 ± 2.30	116.4 ± 1.89	104.8 ± 1.72	126.1 (129 strikes)
3.41	133.1 ± 1.16	115.8 ± 1.65	105.0 ± 1.61	126.3 (129 strikes)
4.71	130.9 ± 0.95	122.5 ± 0.80	101.8 ± 0.89	123.0 (129 strikes)
5.04	128.0 ± 1.85	109.8 ± 1.31	100.3 ± 0.93	120.8 (110 strikes)
5.65	128.9 ± 1.51	109.5 ± 0.96	99.2 ± 0.89	120.4 (129 strikes)

SEL_{cum} for the entire day (just IH) was 131.0 dB re (1 μ m s⁻²)² s (2 October 2024).

(SPL_{pk}, mean ± SD), 106.5 ± 2.52 dB re 1 μ m s⁻² (in-water PAL_{pk}), 121.7 ± 2.12 1 μ m s⁻² (substrate PAL_{pk}).

resting and 42.2% were active. It was more important that resting false positives were minimized, as this could lead to inaccurate breathing rates.

Video-tag comparison

Behaviors predicted by the tag matched those observed in video 96.6% of the time, with most of the discrepancy being small offsets in the start and end times of swimming events. Of the 3.4% of seconds that were inaccurately predicted by the tag processing, 51.8% were misidentified as active when actually resting, with the remaining 48.3% were deemed resting when actually moving.

Of the seconds removed from the tag analysis, such as any resting that was <5 consecutive seconds, 57.8% were observed to be

Respiration rates

Once acclimated (requiring ~4 h), flounder respiration rates settled around 0.51 ± 0.09 Hz (mean ± SD), or 30 operculum beats per minute, as the baseline. However, individual variation in resting respiration rate was noted, as baseline rates ranged from 0.34 to 0.69 Hz. Fish exposed to pile driving significantly elevated their respiration rate by an average of 0.07 Hz during IH and by 0.05 Hz during VH, up to a maximum 0.18 Hz increase for both (repeated measures ANOVA, $F_{(3,30)} = 7.84$, pre-IH: $P = 0.0016$ pre-VH:

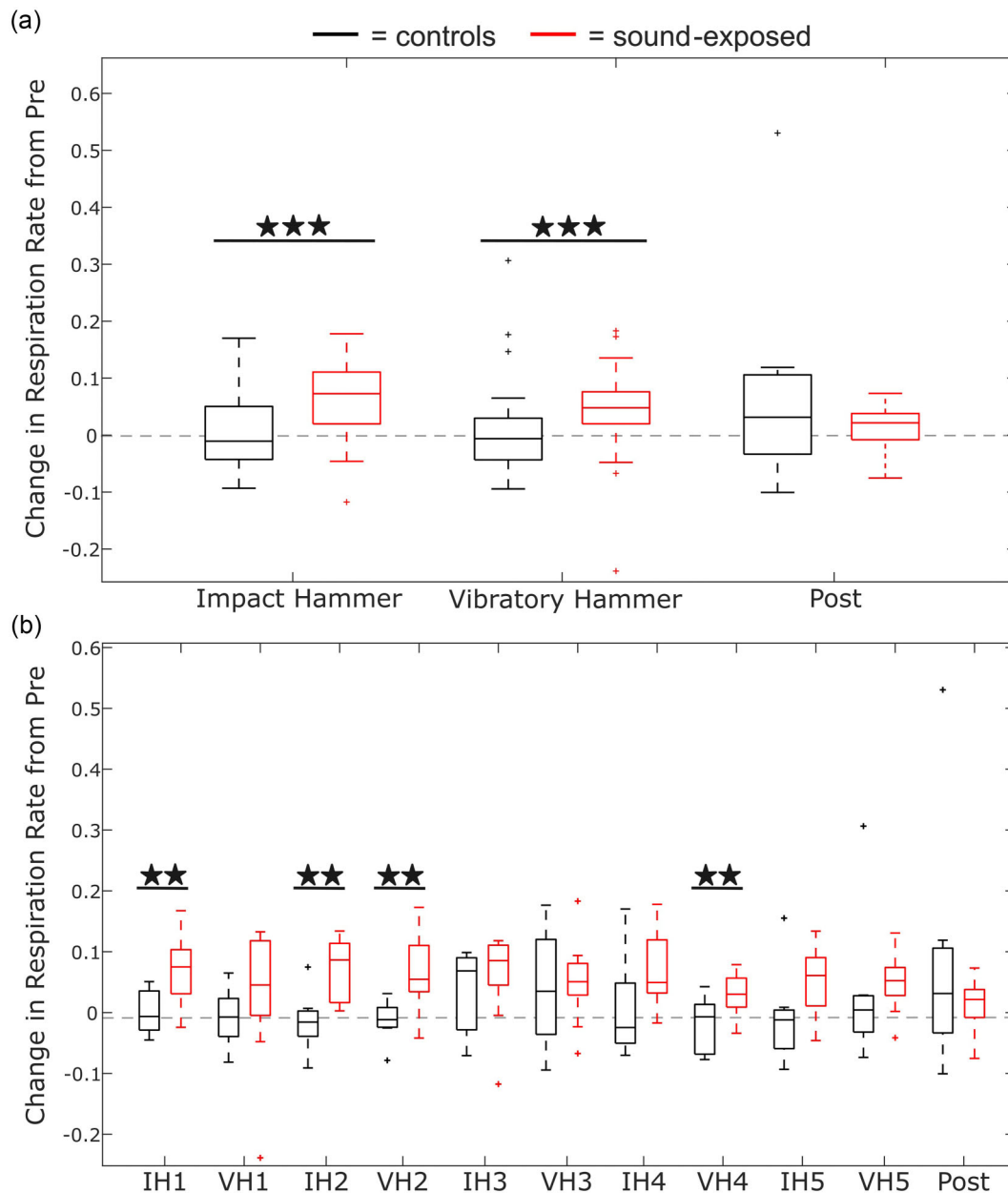


Figure 3 Change in respiration rate during sound treatments from pre-exposure, with the dashed line representing no change from baseline. Stars represent statistical significance between treatment and control groups ($P < 0.05$, $P < 0.01$, $P < 0.001$). (a) Sound-exposed fish (red, on right) had a significantly higher increase in their respiration rate during both IH ($P < 0.0001$) and VH ($P < 0.0001$) than control fish (black, on left). There was no difference between sound-exposed and control fish during the post-exposure period. (b) Respiration rates of sound-exposed remained heightened throughout the extent of sound exposure. This was a significant increase over control fish in the first and second IH (MW, IH1: $P = 0.0059$, IH2: $P = 0.0031$), and second and fourth VH (MW, VH2: $P = 0.0097$, VH4: $P = 0.0204$).

$P = 0.0060$). This increase in respiration rate was greater than any change seen in the control fish across the same time periods (MW, IH: $Z = 4.52$, $P < 0.0001$; VH: $Z = 4.07$, $P < 0.0001$, Fig. 3a). Further, respiration rates were more elevated in fish exposed to pile driving compared to nonexposed individuals during the first and second IH (MW, IH1: $P = 0.0054$, IH2: $P = 0.0031$), and during the second and fourth VH (MW, VH2: $P = 0.0097$, VH4: $P = 0.0204$; Fig. 3b). While there was no significant increase over the controls in the later IH sequences, the respiration of the sound-exposed fish re-

mained elevated above “pre” until the sound exposure concluded (Fig. 3b).

On closer inspection, changes in respiration rate through IH and VH were more nuanced (Fig. 4a). The shift to an elevated respiration rate appeared to occur almost concurrently with the onset of IH noise (Fig. 4b). While there was no significant increase or decrease in respiration rate during IH periods (Fig. 4c, $R^2 = 0.006$, slope = -0.005 , $P = 0.5$), there was a decline toward recovery during VH sequences (Fig. 4d, $R^2 = 0.194$, slope = -0.009 , $P < 0.0001$).

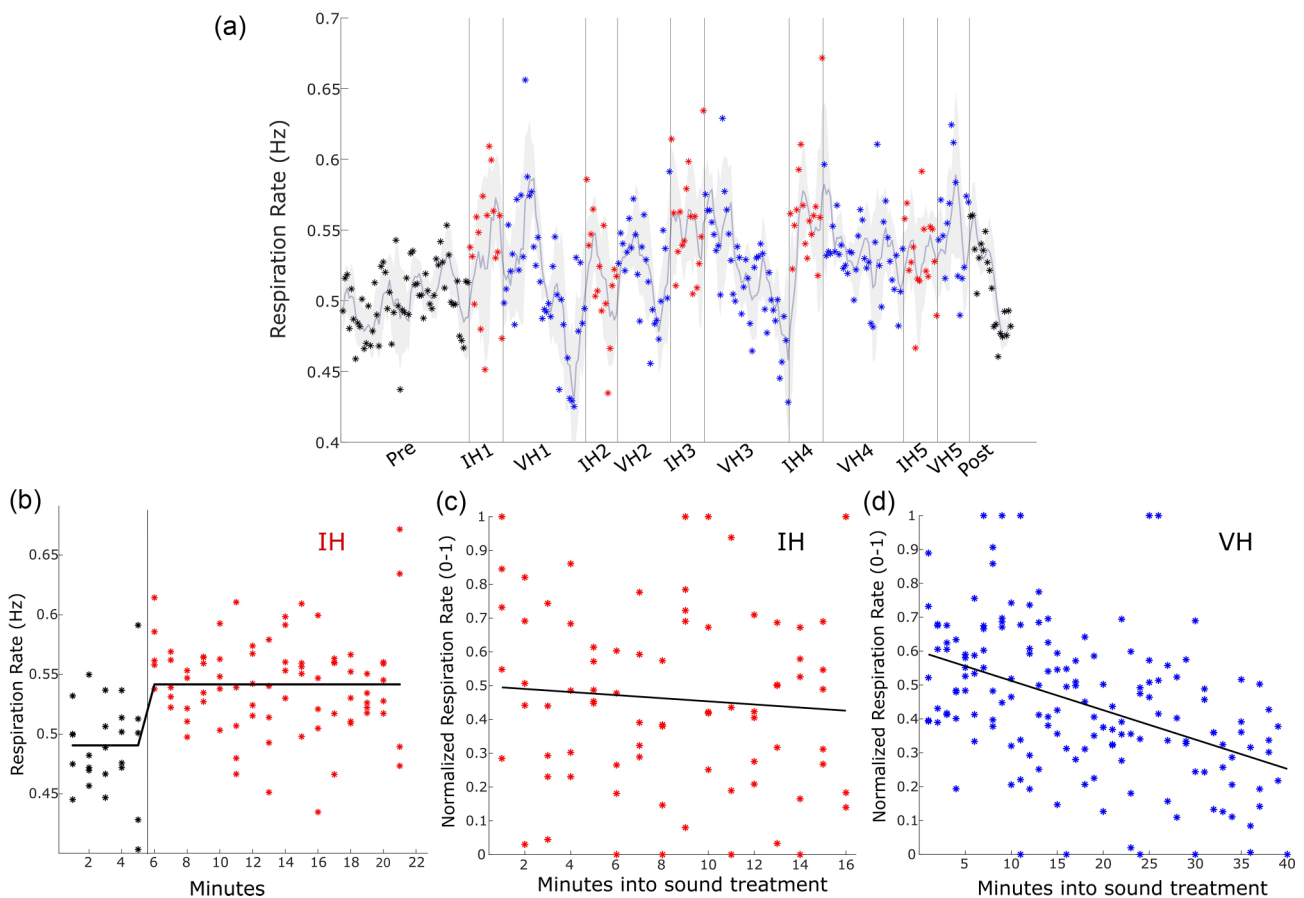


Figure 4 (a) Mean respiration rate of sound-exposed fish ($n = 12$) each minute through a 60-min pre-sound period (black points), five IH sequences (red points), five VH sequences (blue points), and a 15-min post-sound period (black points). (b) Averaged minutely respiration rate was elevated during IH sequences (red stars) compared to the 5-min just before sound onset (black dots at start, including pre and VH). When fitted with a four-parameter logistic sigmoidal model, the inflection point matched the transition point when IH started ($c = 5.33$ min, $R^2 = 0.23$). (c) When all IH sequences are normalized and plotted together, there is no discernible trend in respiration throughout the exposure ($R^2 = 0.006$, slope = -0.005 , $P = 0.5$). (d) However, a significant decline in respiration rate through time was found in VH sequences when normalized and plotted together ($R^2 = 0.194$, slope = -0.009 , $P < 0.0001$).

Short-duration responses—breath holds and escape responses

A temporary breath hold, characterized by a decrease in respiration >0.1 Hz before and after the first IH strike (Fig. 5a), was observed in 7 out of 12 noise-exposed fish (58.3%). Most fish that performed this “freezing” reaction only had a breath hold on the start of the first IH (Fig. 5b), although one fish reacted to three separate IH sequences in this way (first, second, and fourth IH sequences). One fish held its breath only on the second IH. Disrupted breathing lasted, on average, 9.5 s, with the longest disruption lasting 23.7 s.

Low rates of fast starts in the control fish showed that these were not common behaviors in flatfish, as only two out of seven (28.6%) control fish exhibited any fast starts during the experimental period. Fast starts of control fish were randomly distributed throughout the day (KW, $\chi^2_{(3,24)} = 2.24$, $P = 0.53$). Meanwhile, flounders exposed to pile-driving sound reported higher numbers of fast starts, with 7 out of 12 (58.3%) fish startling at least once during the sound exposure. Rates of escape responses among sound-exposed fish were significantly higher during the IH exposure sequences than pre-exposure (KW, $\chi^2_{(3,47)} = 533.1$, $P = 0.0074$), VH ($P = 0.0068$), or post-exposure ($P = 0.0013$, Fig. 6a). However, the

number of total escape responses in each IH decreased over time (Fig. 6b).

A sharp contrast was observed between the fish that showed freezing responses to pile-driving sound, with a breath hold, and those that exhibited escape responses (Fig. 7). Escape responses were reduced among fish that showed a breath hold, with the majority having no escape responses during IH and a maximum of two fast starts per fish (Fig. 7). Conversely, fish that did not have a breath hold upon IH onset were more likely to exhibit higher rates of fast start escape responses, up to nine per fish. Only one fish exhibited neither a freezing nor escape response to the sound.

Activity levels

Change in activity with the onset of pile-driving sound was highly variable among fish, including both increases and decreases in swimming (see Supplementary Fig. S2). Sound-exposed fish exhibited up to a 74% increase in swimming, but also as low as a 38% decrease in swimming during IH. During VH, this ranged from a 59% increase to a 38% decrease in swimming. However, control fish had much less variability and experienced little change in behavior (maximum 17% increase, 21% decrease in activity;

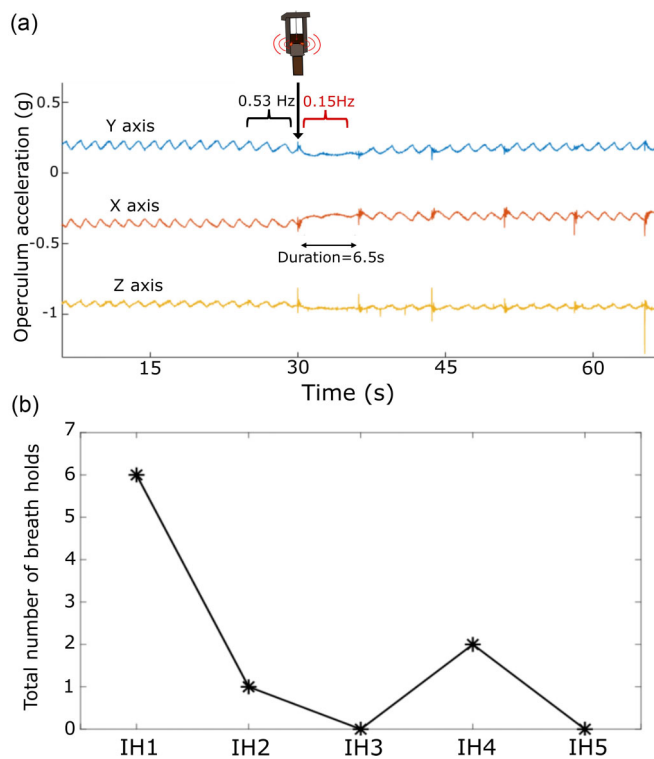


Figure 5 (a) Raw y-, x-, and z-axis acceleration of one tagged flounder, showing an abrupt decline in y-axis respiration from 0.53 Hz to 0.15 Hz upon the first IH strike (vertical spike in acceleration). The breath hold was short-lived, returning to a regular pattern after 6.5 s. (b) The total number of breath holds, across 12 fish, was highest during the first IH sequence, declining with subsequent IH sequences. Only the first strike of each IH sequence was examined for a breath hold.

Supplementary Fig. S2). No significance was found between the two treatments.

Discussion

This field-based study examined the impacts of pile-driving sound on a particle motion-sensitive, commercially important benthic fish. Summer flounders in this study experienced sound conditions comparable to 1 km away from actual wind farm construction (Lippert et al. 2015: modeled SPL_{pk} at 1 km ~ 200 dB re 1 μ Pa; Sigray et al. 2022: measured PAL_{pk} at 880 m without mitigation = 129 dB re 1 μ m s $^{-2}$). Respiration rates and behavioral responses to sound exposure were measured with a novel technique using small, lightweight operculum accelerometers. We found prolonged, sound-induced increases in respiration rates (up to 0.18 Hz higher), suggesting potential physiological impacts. Short-duration behavioral reactions upon IH onset—freezing and escape responses—further support that pile driving sound was perceived as a stressor for flatfish. These behavioral and physiological changes in a hearing nonspecialist emphasize the contribution of particle motion and substrate vibrations to the sensory perception of benthic fish.

We recorded a baseline operculum beating rate of 0.5 Hz, or ~ 30 breaths per minute (bpm), for summer flounder, which is consistent with another flounder species, the European flounder (*Platichthys flesus*; Steffensen et al. 1982). We observed lasting in-

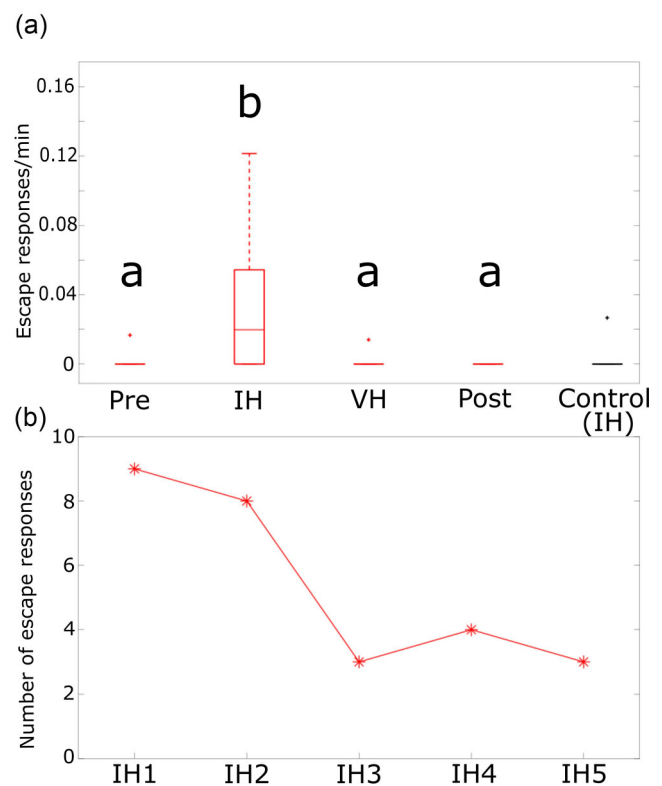


Figure 6 (a) Sound-exposed fish had significantly higher rates of startles during IH than pre-exposure ($P = 0.0074$), VH ($P = 0.0068$), or post-exposure ($P = 0.0013$). Control fish had lower rates of startles. (b) The number of total startles was highest among sound-exposed fish during the first IH sequence, declining in subsequent IH sequences.

creases in respiration rates coinciding with both impact and VH pile driving. The increase in respiration rate upon IH onset (Fig. 4b) suggests that the impulsive sound was the primary driver of the altered metabolic state. In addition to having post-swimming respiration rates removed prior to analysis, the variability in swimming changes over these periods (Supplementary Fig. S2) further supports that heightened respiration was not from increased activity, but rather a stress response to the sound exposure. Despite VH having overall heightened respiration rates (Fig. 3a), flounders were often able to recover and return to a lower respiration rate by the end of the period (Fig. 4d). In addition to experiencing reduced sound levels during VH (~ 40 dB lower for SPL_{rms} , ~ 20 dB lower for PAL_{rms}), this period included intervals without pile-driving sound as the hammers were switched. These quiet times likely contributed to the recovery observed (Fig. 4d), further evidenced by rapid recovery once all sound treatments concluded (during “post”; Figs 3 and 4a).

The long-term effects of such physiological changes remain challenging to determine within this study framework, particularly due to the variability in species and respiration metrics here and compared with the literature (i.e. ventilation frequency vs. oxygen uptake). For physiological context, an increase in respiration rate (9 bpm increase) in response to a sudden 12°C spike in temperature was matched with a significant increase in plasma glucose, a stress indicator, in olive flounder (*Paralichthys olivaceus*; Hokin et al. 2024). Given that the resting respiration rate of summer flounder (30 bpm) is about half that of olive flounder (60–65

in catching summer flounder. We thank Edward O'Brien and Kimberly Malkowski for facilitating SCUBA operations, Rick Galat and Kerry Strom for coordinating dock space, as well as many other members of WHOI Facilities. We thank the W.S. Shultz Co. for their pile driving support and flexibility. Finally, we appreciate the support and suggestions of Shane Guan and Michael Rasser, of Bureau of Ocean Energy Management's Division of Environmental Sciences.

Author contributions

Sierra Jarriel (Conceptualization [equal], Data curation [lead], Formal Analysis [lead], Investigation [lead], Methodology [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), Youenn Jezequel (Conceptualization [supporting], Investigation [supporting], Methodology [supporting], Writing—review & editing [equal]), Amelia Macapia (Data curation [supporting], Formal Analysis [equal], Investigation [supporting], Writing—review & editing [equal]), Nathan Formel (Conceptualization [supporting], Investigation [supporting], Methodology [supporting], Writing—review & editing [equal]), Seth F. Cones (Formal Analysis [supporting], Methodology [supporting], Writing—review & editing [equal]), Hannah Brewer (Investigation [supporting], Resources [supporting], Writing—review & editing [equal]), John Collins (Investigation [supporting], Resources [supporting], Writing—review & editing [equal]), and T. Aran Mooney (Conceptualization [equal], Funding acquisition [lead], Methodology [supporting], Project administration [lead], Resources [equal], Supervision [lead], Writing—review & editing [equal])

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Data availability

The raw data supporting the conclusions of this study are available upon reasonable request to the corresponding author.

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