Offshore windfarm construction elevates metabolic rate and increases predation vulnerability of a key marine invertebrate☆

Seth F. Cones [a,*], Youenn Jézéquel [b], Sierra Jarriel [b], Nadège Aoki [a], Hannah Brewer [c], John Collins [c], Laurent Chauvaud [d], T. Aran Mooney [b]

[a] Massachusetts Institute of Technology and Woods Hole Oceanographic Institution Joint Program in Oceanography/Applied Ocean Science & Engineering, Cambridge, MA, 02139, USA
[b] Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, 02543, USA
[c] Geology and Geophysics Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA
[d] Laboratoire des Sciences de l'Environnement Marin, UBO, CNRS, IRD, Ifremer, LIA BeBEST, UMR 6539, rue Dumont D'Urville, 29280, Plouzané, France

ARTICLE INFO

ABSTRACT

A global increase in offshore windfarm development is critical to our renewable energy future. Yet, widespread construction plans have generated substantial concern for impacts to co-occurring organisms and the communities they form. Pile driving construction, prominent in offshore windfarm development, produces among the highest amplitude sounds in the ocean creating widespread concern for a diverse array of taxa. However, studies addressing ecologically key species are generally lacking and most research is disparate, failing to integrate across response types (e.g., behavior, physiology, and ecological interactions), particularly *in situ*. The lack of integrative field studies presents major challenges to understand or mitigate actual impacts of offshore wind development. Here, we examined critical behavioral, physiological, and antipredator impacts of actual pile driving construction on the giant sea scallop (*Placopecten magellanicus*). Benthic taxa including bivalves are of particular concern because they are sound-sensitive, cannot move appreciable distances away from the stressor, and support livelihoods as one of the world's most economically and socially important fisheries. Overall, pile driving sound impacted scallops across a series of behavioral and physiological assays. Sound-exposed scallops consistently reduced their valve opening (22%), resulting in lowered mantle water oxygen levels available to the gills. Repeated and rapid valve adductions led to a 56% increase in metabolic rates relative to pre-exposure baselines. Consequently, in response to predator stimuli, sound-exposed scallops displayed a suite of significantly weaker antipredator behaviors including fewer swimming events and shorter time-to-exhaustion. These results show aquatic construction activities can induce metabolic and ecologically relevant changes in a key benthic animal. As offshore windfarm construction accelerates globally, our field-based study highlights that spatial overlap with benthic taxa may cause substantial metabolic changes, alter important fisheries resources, and ultimately could lead to increased predation.

1. Introduction

There is a global shift towards green energies as countries seek increased renewable resource use on a warming planet. Over 35 countries are investing in offshore wind to generate non-carbon-based energy, contributing to a predicted 400% increase in projects and 900% increase in power generation within the next decade (www.thewindpower.net). The installation of these turbines requires hammering massive piles into the seafloor, producing one of the highest amplitude man-made sounds ocean fauna have ever faced (Amaral et al., 2020; Sigray et al., 2022). Anthropogenic sound is widely recognized as a global stressor (Duarte et al., 2021) but the ecological consequences of these intense construction sounds remain largely uncertain (Popper et al., 2022). Animal responses to anthropogenic sound often manifest in behavioral changes that, in turn, impact physiological states and inter-specific interactions. Yet, sound-impact studies largely only focus on a particular response type (e.g., behavior) in isolation limiting our understanding of how impacts may be intertwined. There is thus a clear

need for integrative studies that address key taxa, their interdependent behavioral responses, physiological consequences, and how such impacts influence community interactions.

The effect of human generated sounds on marine species is multimodal and includes behavioral changes (Cones et al., 2022; Jones et al., 2021; Simpson et al., 2015), altered vital rates (Williams et al., 2022), and displacement from preferred habitats (Hawkins et al., 2014; Hemery et al., 2024; Tyack et al., 2011). These effects are likely interrelated, as changes in behaviors are underpinned by physiological adjustments. For example, seismic air-gun surveys have altered narwhal dive patterns (i. e., behavior), heart rate, and respiration (i.e., physiology), but also certainly disrupt natural foraging and access to food (Williams et al., 2022). Often, studies examine the impacts of sound under the scope of one or a few behavioral or physiological assays, forcing data amalgamation across multiple studies to determine sound-exposure guidelines (Popper et al., 2014). However, comparisons across individual experimental methodologies are difficult due to unique acoustic spectral characteristics, environmental conditions, and intra-taxa response variability (Harding et al., 2019). Such extrapolated comparisons can put managers and stakeholders, and our predictions of interdependent impacts at risk because it can be inherently challenging to combine studies across species to gain unifying principles of impacts. A study designed to track numerous parameters from behavior to community interactions will support comprehensive understanding of sound-induced impacts on marine animals.

Acoustic disturbance research has historically focused on large pelagic vertebrates, while abundant benthic invertebrate species are substantially less studied (Popper et al., 2022; Sole et al., 2023). Offshore windfarm areas have traditionally been selected as shallow (<100 m depth) substrates on continental shelves (Mooney et al., 2020), which boast highly productive benthic communities that contribute to many ecological functions (Stokesbury et al., 2004; Stokesbury & Bethoney, 2020). Within these communities, bivalves are abundant, ecologically important, and economically vital marine fauna who show a sensitivity to low-frequency sounds in the same range as pile driving [i. e., <1 kHz (Cones et al., 2023; Jézéquel et al., 2023a)]. The only field-based study examining the impacts of pile driving on a marine bivalve, the giant sea scallop (*Placopecten magellanicus*), found significant decreases (30–40%) in valve angle and heightened rates of valve adductions during sound exposure (Jézéquel et al., 2022). These rapid valve adductions were noted across multiple life stages and observed concomitantly with every sound impulse throughout the duration of exposure. These consistent behavioral responses, without habituation, suggest potential disruptions to vital ecological and physiological processes.

Scallops modulate their valve angles to facilitate vital ecophysiological functions such as gill venting, respiration, feeding, antipredator strategies, and excretion (Robson et al., 2010; Trueman, 1983). Many of these processes rely on valve adductions that are energetically costly for scallops and can alter their metabolic rates for extended durations (Livingstone et al., 1981; Robson et al., 2012; Thompson et al., 1980). Valve adductions are largely anaerobically powered (Livingstone et al., 1981), and repeated rapid valve adductions measured in response to pile driving sound (Jézéquel et al., 2022) may significantly affect scallops' metabolic rates throughout the entirety of pile driving exposure and post-recovery as oxygen debts are repaid. In addition, elevated metabolic rates force animals to reallocate energy to metabolically recover from oxygen debts obtained during anaerobic exercise. However, it remains unclear if rapid valve adductions during pile driving could disrupt scallop metabolic rate or energetically costly movement behaviors. Metabolic stress induced from pile driving may reduce swimming performance capacity and overall predator evasion performance. Thus, there is a crucial need to measure sound-induced metabolic costs and assess if changes increase scallop susceptibility to predation.

Scallops contribute significantly to fisheries and the ecological function of marine systems. Ecologically, they play an important role in

benthopelagic coupling, acting as biofilters to mitigate anthropogenic eutrophication, and they transport nutrients into sediments (Newell, 2004). Commercially, numerous scallop species are exploited and serve as a vital protein and revenue source for communities worldwide (scallop fishery: 1.7 billion USD, [FAO, 2016]). This confluence of ecological contributions and commercial value have led to substantial investments in bivalve aquaculture, valued at 6.47 billion USD, to address food security for growing human populations, combat eutrophication, sequester carbon, enhance biodiversity, and capitalize on their role as environmental sentinels (Chauvaud et al., 1998; Garcia-March et al., 2016; Heilmayer et al., 2004; van der Schatte Olivier et al., 2020). Given their notable behavioral responses to pile driving and the ecological and economic value of this taxon, there is substantial concern and many unknowns regarding how offshore windfarm construction will impact the fishery and its inherent ecosystem services near construction areas.

Here, we used a novel, field-based approach to measure pile driving impacts on *P. magellanicus* behavior, metabolic physiology, and predator interactions. We sought to answer three fundamental questions: 1) Do decreases in valve angle arising from pile driving sound exposure alter the mantle water oxygen levels? 2) Do repeated valve adductions alter metabolic rates? 3) Do potential changes in physiology lead to weakened swimming and antipredator performance? To address these questions, we integrated multiple approaches including fiber optic oxygen probes, benthic respirometers systems, and biologging sensors to precisely measure valve angles. We exposed scallops to repeated pile driving at known distances and sound levels, and we monitored oxygen levels near the gills as well as oxygen consumption following a before, during, and after gradient. After pile driving, we elicited innate antipredator responses by exposing scallops to sea star chemical cues and measured a suite of predator escape performance metrics. By combining these various metrics of physiological state and performance, we were able to provide the first insights into pile driving effects on bivalve physiology in response to real pile driving.

2. Methods

2.1. Study animals

Scallops used in this study were healthy, hatchery-raised in waters off Cape Elizabeth, ME (provided by Pine Point Oyster Co.). Individuals were 2–3 years old (shell height: [mean ± standard deviation] 60.0 ± 5.0 mm; wet weight: 9.9 ± 2.3 g), and no experimental animals had visible shell damage. Scallops were relocated on August 30th, 2022 to the Environmental Systems Laboratory at the Woods Hole Oceanographic Institution where they were acclimatized for at least 20 days before experiments started in an outdoor transparent tent with tanks filled with flowing, ambient, unfiltered seawater.

2.2. Experimental procedure

Pile driving was conducted for 11 days between September 20th and October 12th, 2022, off the Woods Hole Oceanographic Institution's dock. A cylindrical steel pile (length: 10 m, diameter: 0.3 m, wall thickness: 0.02 m) was used and construction methods were identical to previous experiments (see Cones et al., 2022; Jézéquel et al., 2022). Exposures began as (1) a steel impact hammer (weight: 1500 kg) was dropped onto the pile from a height of 1.2 m at a rate of 10 strikes/min for 15 min, which resulted in the steel pile penetrating a minimum of 3 m into the seabed. (2) Next, a vibratory hammer (weight: 212 kg, H&M model 135, 1150 blows per minute) was used to pull the pile out of the substrate and to reposition it in an adjacent location for another round of the impact hammer pile driving. This process was repeated five times per experiment day, with pile driving activity occurring for 3 h (Fig. 1). In total, each scallop was exposed to five, 15 min pile driving sequences. Data were only analyzed in response to the impact hammer since our
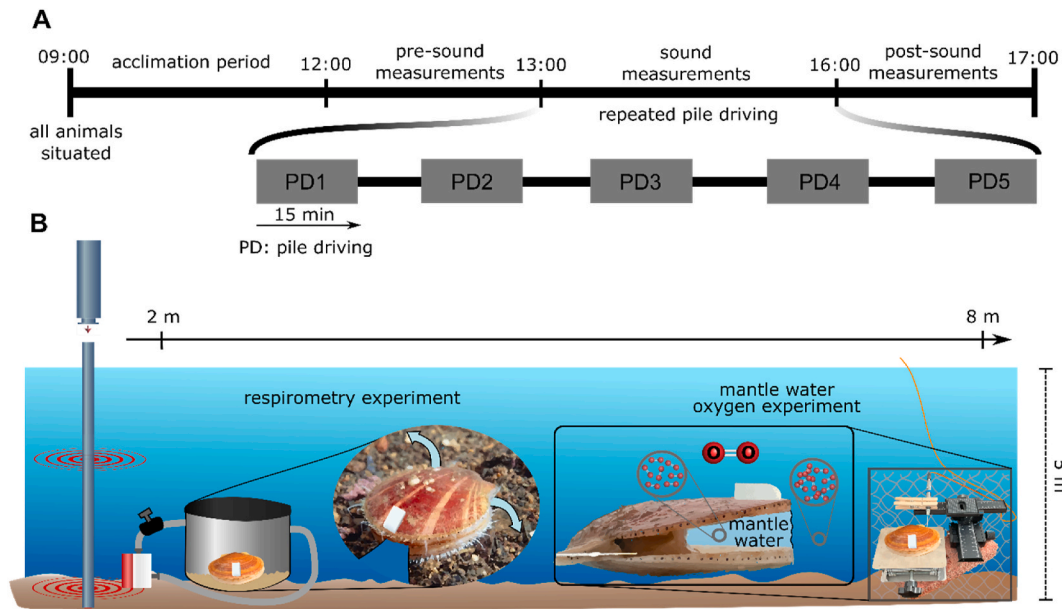
Fig. 1. (A) Experimental procedure during respirometry and mantle-oxygen experiments. Animals were positioned in the respective settings 3 h before data collection for acclimation. Data collection began at 12:00 (noon) when 60 min of pre-sound exposure baseline measurements were recorded. Next, there was 3 h of repeated pile driving. Pile driving construction consisted of five 15-min pile driving sequences interspersed with consistent breaks as piles were repositioned. After 3 h of sounds exposure, post exposure data were collected for an additional hour. (B) A schematic of the respirometry (left) and mantle water oxygen (right) experiments. Animals were positioned 2-8 m from the pile and were at a depth of 5 m.

previous study showed that high-intensity transient impulses from impact hammer (hereafter referred to as pile driving) strikes were significantly more impactful to scallop behaviors compared to low intensity continuous sounds from the vibratory hammer (Jézéquel et al., 2022). Piles could not be driven in the exact same locations, resulting in each pile varying in distance (mean = 4.3 m, min = 1.7 m, max = 7.2 m) to the experiment animals. Although there were slight variations in the animal-pile distance between pile driving sequences, this did not impact our ability to address the study goals since our aim was to assess if pile driving exposure induced physiological responses rather than examining dose dependent relationships within this small spatial range.

New individuals were used for each experiment day. At least 12 h prior to the start of experiments, scallops were tagged with TechnoSmart AxyS (22 × 13 × 8 mm, 6 g) biologging tags by gluing the sensor to the upper valve periphery, and a small magnet (11 mm diameter, 1.7 mm thickness) on the opposite valve. The tag measured tri-axial acceleration at 100 Hz and magnetic field strength between a magnetometer and the magnet at 2 Hz. Acceleration data measured scallop valve movements and body vibrations from substrate-borne sounds during pile driving, and the magnetometer was used to precisely measure the angle between the upper and lower valves. After the experiments, tagged scallops were sacrificed and magnetometers were calibrated by establishing the relationship between the magnetic field strength (through the magnetometer-magnet coupling) and the gap opening distance of the valves. Opening distances were then converted to valve angles using the equation:

$$VA = 2 \times arcsin\left(\frac{0.5W}{L}\right) \times 100$$

where VA is valve angle, W is the valve gap (in mm), and L (in mm) is shell height of the scallop (described in detail in Jézéquel et al., 2023a).

Data were analyzed in a before-during-after scheme (Methratta, 2020). In this way, pre-pile driving periods served as controls to collect baseline data which were compared to the exposure treatments. Such an experimental design is widely employed (Deruiter et al., 2013; Fewtrell & McCauley, 2012; Jézéquel et al., 2022; Miller et al., 2022; Tyack et al., 2011; van der Knaap et al., 2022) and particularly vital for field-based

stressor studies because it accounts for the spatiotemporal dynamics that naturally occur in the ocean which influence more traditional pairings. Otherwise, these spatiotemporal disconnects increase error and reduce statistical power (Methratta, 2020). Thus, numerous field studies (e.g., noted above) track individual responses before, during, and after sound exposures to determine consequences of disturbances.

Each morning between 08:00 and 09:00, animals were placed on the seafloor for mantle water oxygen and respirometry experiments (Fig. 1). Each animal was given at least a 3 h acclimation period, and then pre-exposure measurements began 1 h prior to sound exposure. Post-exposure measurements were taken for 1 h immediately after the last pile driving sequence. 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 to TAM.

2.3. Mantle water oxygen experiment

We used fiber-optic oxygen probes (Pyroscience OXR430-CL5, 430 μm sensor diameter) to non-invasively monitor the dissolved oxygen levels in the scallop mantle water. Each morning, one to three scallops were glued onto separate stainless-steel platforms and sensors were mounted on a sliding bracket, which together allowed movements in three orthogonal axes. Sensors were carefully positioned and inserted 7–10 mm posteriorly into the mantle cavity adjacent to the shell wing (Fig. 1). Then, the components were locked in position and the systems were transferred on the seafloor. Cages lined with 1 mm mesh were placed over the setups to exclude visual interactions with potential fish predators. Mantle water oxygen levels were monitored continuously at 0.7 Hz before, during, and after pile driving.

For each experiment day, a control experiment setup was placed on the seafloor with a cleaned scallop valves. This served to measure ambient oxygen levels in the water and calculate mantle water oxygen differential, or the difference between ambient oxygen levels and mantle water oxygen levels.

2.4. Respirometry

To monitor metabolic rates before, during, and after pile driving, on each experiment day one to three scallops were isolated in individual custom-built closed respirometer systems (Fig. 1). Each system consisted of a cylindrical (diameter: 10.16 cm; height: 17.15 cm) opaque chamber and a water pump that were connected via non-toxic tubing (V = 1.58 L). A flow-through oxygen sensor (Pyroscience OXFLOW) was integrated into the tubing downstream from the scallop chamber. A thin (2 cm) layer of sterilized sand was placed on the bottom of each chamber to provide a natural substrate for each scallop. The water pump circulated the water at a flow rate of 2.25 L min^{-1} to prevent oxygen gradients within the chamber and consistently move seawater over the oxygen sensor. Oxygen sensors were calibrated daily using Pyroscience two-step calibration method.

Chambers with animals were carefully positioned and buried 5–10 cm into the substrate each morning at set locations. All chambers and tubing were visually inspected for air bubbles prior to sealing. The systems remained 'open' to the ambient seawater to ensure high oxygen levels during acclimatization and were subsequently 'closed' at 11:00. The oxygen probes were connected to a computer at the surface, which provided real-time dissolved oxygen levels within each chamber. Dissolved oxygen levels were continuously monitored from 11:00 to 18:00 at 1.0 Hz, and systems were manually flushed by a freediver that temporarily disconnected a tubing connection at the water pump. This served to restore high oxygen levels inside the chamber. Flushing only occurred during quiet periods between pile driving sequences and served to prevent dissolved oxygen levels from decreasing below 75 % air saturation (MacDonald & Thompson, 1986).

Each experiment day had a control respirometer which measured the microbial respiration in the water. These systems were set up identically to the experiment chambers, but instead of a live scallop, a pair of dead and cleaned scallop valves were placed in the chambers. Metabolic rate (mg O$_2$ hr^{-1}) was calculated by $M = \Delta$ VO$_2$/time. Then, to normalize to mass-specific metabolic rates (mg O$_2$ g^{-1} hr^{-1}), we divided M by the scallop wet mass in grams.

2.5. Predator attack simulations

To assess if potential physiological changes impacted scallop anti-predator behaviors, we simulated sea star (*Asterias forbesi*) predator interactions and quantified swimming performance and behaviors on pile driving-exposed scallops. Immediately after the last pile driving sequence of the day, one to two scallops from the mantle water oxygen experiment were quickly transferred to individual rectangular holding tanks (0.6 m × 0.4 m x 0.5 m; 0.12 m^3) filled with circulating seawater from the experiment site. Escape swimming behaviors were induced by injecting 1 mL of homogenized sea star (1 g of sea star per 5 mL seawater [Thompson et al., 1980]) into the scallop mantle near the shell wing. Injections were made posteriorly to limit any visual effects. Sea star chemical cues elicited an innate escape swimming response where the scallops snapped their valves together in a series of adductions and abductions (Thompson et al., 1980). However, because the scallops were glued to the platform, we systematically repeated sea star interactions every 15 s for 10 min. Control experiments were conducted with identical methods and at the same experimental site but occurred on days without pile driving. The same batch of homogenized sea stars was used for both controls and experiments.

We quantified antipredator performance through tag and video data. Video data were annotated in BORIS (v7.12.2) (Friard & Gamba, 2016) for the total number of valve adductions, the number of swimming events, the duration spent fully closed, the number of simulated predator interactions in which scallops did not behaviorally respond, and the exhaustion time. The exhaustion time was defined as the duration, in seconds, in which scallop valves remained open and did not respond to three subsequent simulated predator interactions. Exhaustion time was

referenced back to the time of the first of three no response scores. Swimming events were defined as sequences of at least three strong (>1 g) valve adductions repeated with less than 1 s inter-clap-interval. Valve adduction rate was normalized and measured as the number of valve adductions per second scallop valves were open.

2.6. Acoustics

We quantified the pile driving sound field in three ways: particle acceleration of experimental setups, water-borne particle acceleration, and substrate-borne acceleration levels. Considering *P. magellanicus* and other marine bivalves are sensitive to low frequency (<1 kHz) underwater particle motion (Jézéquel et al., 2023a; Cones et al., 2023), the sound field during pile driving exposure was quantified in particle acceleration levels (PALs) using a calibrated triaxial accelerometer (PCB model W356B11; sensitivity: x = 10.26 mV ms^{-2}, y = 10.38 mV ms^{-2}, z = 10.62 mV ms^{-2}) with a sampling frequency of 2 kHz (for a detailed description, see Cones et al., 2022). Recordings were taken when the accelerometer was glued to the respirometer chamber and mantle water oxygen experimental platform to directly measure sound levels received by the animals.

For acoustic measurements, triaxial data were combined as the 3-D vector quantity. The received sound levels were assessed by computing 0-peak accelerations (PAL$_{zpk}$ dB re 1 μm s^{-2}). Next single strike particle acceleration exposure levels [PAEL$_{ss}$ dB re (1 μm s^{-2})^2 x s] were calculated by integrating PAL$_{zpk}$ over the pulse length containing 90% of the signal energy, and cumulative particle acceleration exposure levels [PAEL$_{cum}$ dB re (1 μm s^{-2})^2 x s] were measured over the course of one pile driving sequence and for all five pile driving sequences.

We also recorded substrate-borne sounds using an ocean bottom seismometer. A calibrated geophone (model GS-11D from Geospace®) with a 1000 Hz sampling frequency was buried in the seafloor by divers adjacent to the experimental setups. Geophone installation occurred before the start of the three-week experimental period and remained fixed. It recorded ground-motion along three-orthogonal axes (one vertical and two horizontal). All data were recorded on a Quanterra Q8 24-bit data-logger after × 8–32 pre-amplification. The vertical axis of the ocean bottom seismometer was clipped at 5 m s^{-2} during pile driving, so only the magnitude of horizontal substrate acceleration data are reported as [sqrt ($x^2 + y^2$)].

2.7. Statistics

A one-way ANOVA was used to test for differences in both mantle water oxygen deficit and mass specific metabolic rates across sound treatments. If a one-way ANOVA resulted in significant result, a post-hoc Tukey-Kramer pairwise comparison was performed to identify the groups that had significantly different means. A one-sample *t*-test was used to test for differences in metabolic rates across individual sound exposure treatments. Lastly, two-sample t-tests were used to test for differences in all anti-predator performance metrics in control and experimental groups. Data within the text are presented as the mean and standard deviation. For each boxplot, the central red mark indicates the median, and the lower and upper box edges (IQR) indicate the 25th and 75th percentiles, respectively. The whiskers denote the limits of the data that are not considered outliers, which were values 1.5 * IQR above the third quartile or below the first quartile. The outliers, if present, are plotted in red. The barplots show the mean and the error bars depict the standard deviations.

3. Results

3.1. Acoustic levels

A full synopsis of the experimental acoustic field is shown in Table 1. Accelerometer-based received sound levels were similar at the mantle

Table 1

Received water and substrate-borne sound levels for the mantle water oxygen and respirometry experiments. Rise time is the time, in milliseconds, for pile driving impulses to increase from 5% to peak amplitude. Particle acceleration levels were measured directly on experiment setups and are expressed as zero to peak (PAL$_{zpk}$). Particle acceleration exposure levels were measured for one hammer strike (PAEL$_{ss}$), one pile driving sequence (PAEL$_{cum}$/sequence), and over the entire experiment day (PAEL$_{cum}$/day). Lastly, substrate-borne sounds were measured by an ocean bottom seismometer within 1 m from both experiments, and only horizontal magnitudes were calculated since the vertical axis was clipped.

Experiment	Rise Time (ms)	PAL$_{zpk}$ dB re 1 (µ ms^{-2})	PAELss dB re 1 (µ ms^{-2})^2 × s	PAEL$_{cum}$/sequence dB re 1 (µ ms^{-2})^2 × s	PAEL$_{cum}$/day dB re 1 (µ ms^{-2})^2 × s	Horizontal substrate sound dB re 1 (µ ms^{-2})
Mantle water oxygen	14.5 ± 93	122.13 ± 4.9	81.68 ± 3.8	102.15 ± 3.1	109	125.5 ± 2.7
Respirometer	13.3 ± 93	122.88 ± 5.04	82.4 ± 2.7	103.74 ± 3.09	109.8	

water oxygen and respirometry experiments (PAL$_{zpk}$ of 122.1 ± 4.9 and 122.9 ± 5.0 dB re 1 (µ ms^{-2}), respectively). Horizontal substrate sound levels in zero to peak adjacent to the experiment setups were 125.5 ± 2.7 dB re 1 (µ ms^{-2}). Sound exposure levels were calculated on three different time scales: one pile driving strike, 15 min pile driving sequence, all five pile driving sequences over an experiment day. Single

strike exposure levels were 81.7 ± 3.8 and 82.4 ± 2.7 dB re 1 (µ ms^{-2})^2 × s for the mantle water oxygen and respirometer systems, respectively. For a single 15 min pile driving sequence, PAEL increased to 102.2 ± 3.1 and 103.7 ± 3.1 dB re 1 (µ ms^{-2})^2 × s. Over an entire experiment day, PAEL was greatest at 109 and 110 dB re 1 (µ ms^{-2})^2 × s.
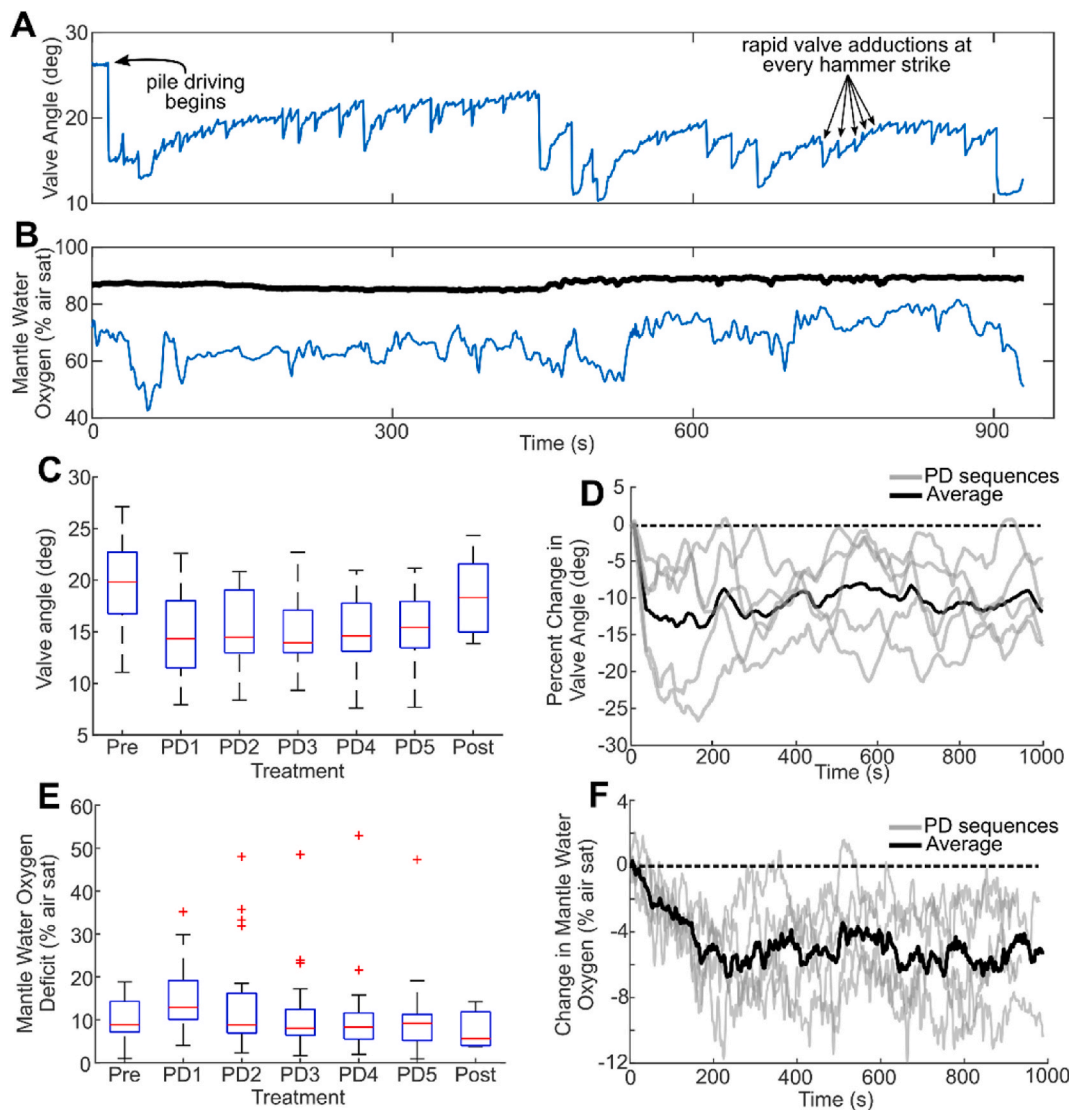
Fig. 2. Pile driving reduces scallop valve angle and mantle water oxygen levels. Concurrent valve angle (A) and mantle water oxygen (B) from an experimental animal during a pile driving sequence. Pile driving onset is indicated by the black arrow shortly after t = 0. Black time series is the air saturation in the control setup measuring ambient oxygen levels in the water column. (C) Average valve angles for all 25 experiments during pre and post sound treatments and average valve angles during pile driving sequences. (D) Mean valve angles for all experiments over individual pile driving sequences (grey) and averaged across of five bouts (black) beginning at sound onset (t = 0). (E) Average oxygen deficit (ambient DO minus mantle DO) for 25 experiments before sound onset, each pile driving sequence, and post pile driving. (F) Percent change in mantle water oxygen differential from the onset of sound (t = 0) throughout each pile driving sequence (grey: mean value over five pile driving sequences per day and per individual, black: average value across all individuals).

3.2. Mantle water oxygen experiments

Over 11 sound exposure days, we conducted 25 mantle water oxygen experiments. Scallops showed reduced valve angles in response to pile driving sound exposure, with the strongest valve angle reductions occurring at the onset of each pile driving sequence (Fig. 2A). The average valve angles observed before (19.44°) and after pile driving (18.49°) were higher than those recorded during any of the pile driving sequences [14.82–15.71° (Fig. 2D)]. This signifies an average valve angle reduction of 22.5% from the pre-exposure conditions. Similarly, scallops had reduced valves angles throughout the course of individual pile driving sequence relative to just prior to pile driving onset (Fig. 2D). In addition, repeated valve adductions of varying magnitude were seen throughout in response to each pile driving strike (Fig. 2A).

Average mantle water oxygen deficit (ambient oxygen – mantle water oxygen) was greater during all pile driving sequences (15.65–10.02 % air sat) relative to pre- (9.85% air sat) and post-exposure (7.64 % air sat; Fig. 2E). The difference was most noticeable for the first pile driving sequence where mantle water oxygen deficit was 59% greater than pre-exposure conditions, however, these trends were statistically insignificant [One-way ANOVA, $F_{(6, 147)}$ = 1.72, p = 0.12].

A rapid decrease in mantle water oxygen level was observed when isolating data at the onset of individual pile driving sequences (Fig. 2F). For all experiments and pile driving sequences, average mantle water oxygen decreased 5.25% of air saturation relative to just prior to sound onset and reached a maximum deficit of 6.74%.

3.3. Respirometry experiments

Across six pile driving days, we conducted 14 respirometry experiments. In line with the mantle water oxygen experiments, scallops exhibited higher average valve angles both before (18.22°) and after (18.52°) sound exposure compared to all pile driving [15.17–16.04° (Fig. 3A)] sequences. This signified a reduction in average valve angles of 14.6% from pre-exposure conditions for all pile driving sequences. At a finer temporal scale, scallops had reduced valves angles over the duration of individual pile driving sequences relative to just prior to the first sound impulse (Fig. 3B).

Average metabolic rates varied between the three treatments: before, during, and after pile driving construction (One-way ANOVA, $F_{(2, 33)}$ = 4.43, p = 0.0198). Post-hoc pairwise comparisons revealed that metabolic rates were significantly higher after pile driving relative to pre-exposure baselines (Tukey-Kramer, p = 0.015), while metabolic rates measured throughout the entire pile driving activity did not differ statistically from baseline (Tukey-Kramer, p = 0.17, Fig. 3C). Average metabolic rate before pile driving was 0.0733 mg O_2 g^{-1} hr^{-1} and increased 33.1 % to 0.0976 mg O_2 g^{-1} hr^{-1} during entirety of pile driving. After pile driving, metabolic rates were even greater at 0.114 mg O_2 g^{-1} hr^{-1}, representing a 56.0 % increase relative to before pile driving.

Metabolic rates were analyzed across individual pile driving sequences to test for potential changes in oxygen consumption across minute time scales. There were significant reductions in metabolic rate in the first 200 s of the first (t-test, t-stat = −4.6, df = 5, p = 0.0058, Fig. 3F) and third (t-test, t-stat = −2.55, df = 10, p = 0.029, Sup Fig. 1) pile driving sequences relative to the last 600 s. During these periods, metabolic rate distributions overlapped zero signifying oxygen
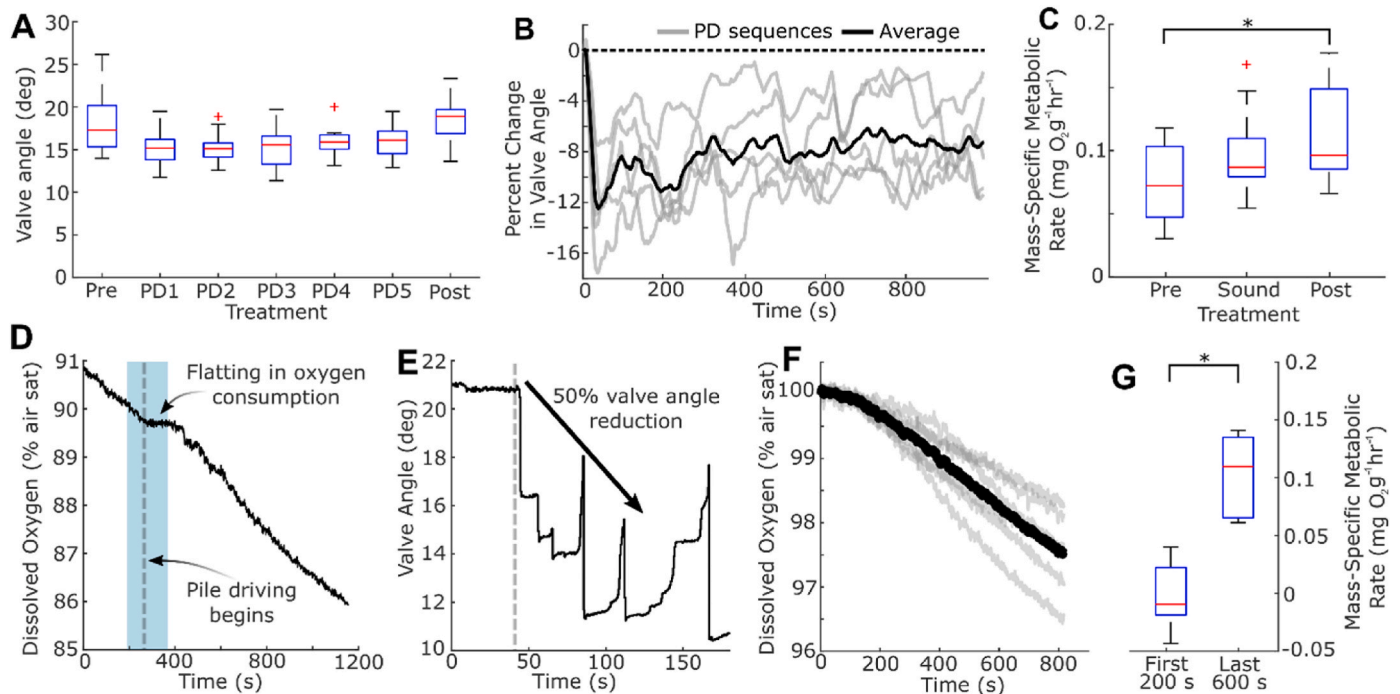
Fig. 3. Pile driving alters the metabolic rate and oxygen consumption patterns of *P. magellanicus*. (A) Average valve angles for all 14 exposure experiments before (Pre), during pile driving sequences, and after (Post) sound treatments. (B) Mean valve angles for all experiments over individual pile driving sequences beginning at sound onset (t = 0). (C) Metabolic rates before (Pre), during sound exposure (averaged over the entire 3-h pile driving exposure (Sound)), and 60 min after sound stopped (Post, One-way ANOVA, $F_{(2, 33)}$ = 4.43, p = 0.0198). (D) One example experiment showing a 'breath hold,' or a flattening in oxygen consumption during the first pile driving sequence. The dotted grey line denotes sound onset, and (E) co-occurring valve angle of the blue shaded area shows the flattening in oxygen consumption corresponded to a 50% valve angle reduction from baseline during sound onset. (F) Oxygen consumption rates reflected as the dissolved oxygen in all chambers (grey lines) during the first pile driving sequence beginning with sound onset at t = 0; the black line represents the mean. (G) The metabolic rates for the initial 200 s are significantly lower than those at last 600 s after sound exposure (t-test, t-stat = −4.6, df = 5, p = 0.0058). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

depletion rates similar to control chambers with no animal present (Fig. 3G). Concurrent tag data showed periods of flattened oxygen consumption rates were accompanied by drastic reductions in valve angles (Fig. 3D and E). Metabolic rates during the second (*t*-test, t-stat = 0.10, df = 10, p = 0.92), fourth (*t*-test, t-stat = 0.25, df = 6, p = 0.81), and fifth (*t*-test, t-stat = 0.66, df = 6, p = 0.53) pile driving sequences were statistically similar throughout.

3.4. Antipredator performance

In total, 15 antipredator experiments were conducted over 10 experimental days. Both experiments and controls (n = 8) were conducted over the same temperature (two-sample *t*-test, p = 0.31, experiment = 19.3 ± 1.8 deg C; control = 18.6 ± 1.2 deg C) and oxygen conditions (two-sample *t*-test, p = 0.35, experiment = 95.9 ± 7.9 % air sat; control = 91.6 ± 5.6 % air sat). Control scallops enacted significantly more swimming events than experimental animals exposed to pile driving (two-sample *t*-test, t-stat: 2.10, p = 0.0445, Fig. 4A). Control scallops also had a higher valve adduction rate when normalized for the duration valve were open (two-sample *t*-test, t-stat: 2.46, p = 0.021, Fig. 4B). Additionally, animals exposed to pile driving became exhausted significantly more rapidly (two-sample *t*-test, t-stat: 3.326, p = 0.0026, Fig. 4C). Lastly, experimental scallops spent less time fully closed (two-sample *t*-test, t-stat: 2.57, p = 0.0163, Fig. 4D) leading to an increased percentage of no responses to the predator stimuli (two-sample *t*-test, t-stat: 2.09, p = 0.0462, Fig. 4E).

4. Discussion

This integrative field-based study highlighted four key results. First, in support of our previous study (Jézéquel et al., 2022), pile driving repeatedly induced valve angle reductions and valve adductions across seconds to hourly time scales. Second, the altered valve behaviors resulted in decreased oxygen within the mantle cavity. Third, oxygen consumption rates and patterns were impacted by pile driving exposure. Metabolic rates were significantly greater after pile driving than during quieter preconstruction conditions while the animal was likely repaying oxygen debts from numerous valve adductions. Finally, the physiological changes resulted in weaker swimming behaviors and earlier exhaustion that could lead to increased predation in the wild, potentially increasing scallop mortality during and after exposure to pile driving.

4.1. Behavioral responses to pile driving exposure

The modulation of valve angles is an underlying mechanism for all scallop movement behaviors, and it governs many aspects of their biology [i.e., vision, gill venting, feeding (Robson et al., 2010), antipredator strategies (Trueman, 1983), and regulation of mantle volume]. Consequently, disruptions to natural, preferred valve positions could have cascading impacts to these essential ecophysiological functions. We found for both mantle water oxygen and respirometry experiments, scallops showed notably lower valve angles during pile driving and valve angle reductions were most severe at sound onset. Additionally, there was no evidence of behavioral habituation or desensitization to repeated pile driving sequences at seconds to hourly time scales. This result is in marked contrast to other sound-impact studies on other mollusks such as squid (Cones et al., 2022; Jézéquel et al., 2023b) and tank-based studies on other bivalve species (e.g., Hubert et al., 2022) that show the probability of behavioral response decreases with time. Lack of habituation indicates that impact severity may be positively correlated with pile driving duration or simply *in situ* pile driving may be a more impactful source than confined, tank, and speaker-based replications. Future work should continue such field-based exposures with actual pile driving at similar temporal scales as offshore windfarm construction.

4.2. Mantle water oxygen experiments

Reduced valve angles led to a reduction (4.75% air saturation) in the mantle water oxygen levels throughout pile driving sequences. Throughout sound exposure, mantle water oxygen levels mirrored valve angles and decreased rapidly at sound onset and persisted at lower values throughout exposure. Thompson et al. (1980) measured the physiological impacts of a 1-h duration valve closure in *P. magellanicus* and found closures led to several physiological changes including a decrease in mantle water oxygen, similar to our study. In addition, valve closures rapidly led to decreased blood oxygen and blood pH, and altered oxygen consumption (Thompson et al., 1980). Upon re-opening after the disturbance, oxygen consumption increased 700% and other physiological parameters took up to 3 h to return to baseline. These data suggest long recovery times are needed after valve angle reductions, and oxygen uptake will dramatically increase after a disturbance, a similar trend to our study (see section 4.3). Scallops have a much lower efficiency of oxygen uptake relative to other aquatic species such as fishes and thus need substantial recovery periods in which energy allocation is disrupted (Livingstone et al., 1981; Robson et al., 2012). In this context, our results suggest that mantle water oxygen levels will reduce during the entirety of sound exposure, and other physiological parameters such as blood oxygen (not measured here) may be altered for prolonged periods even after pile driving ends.
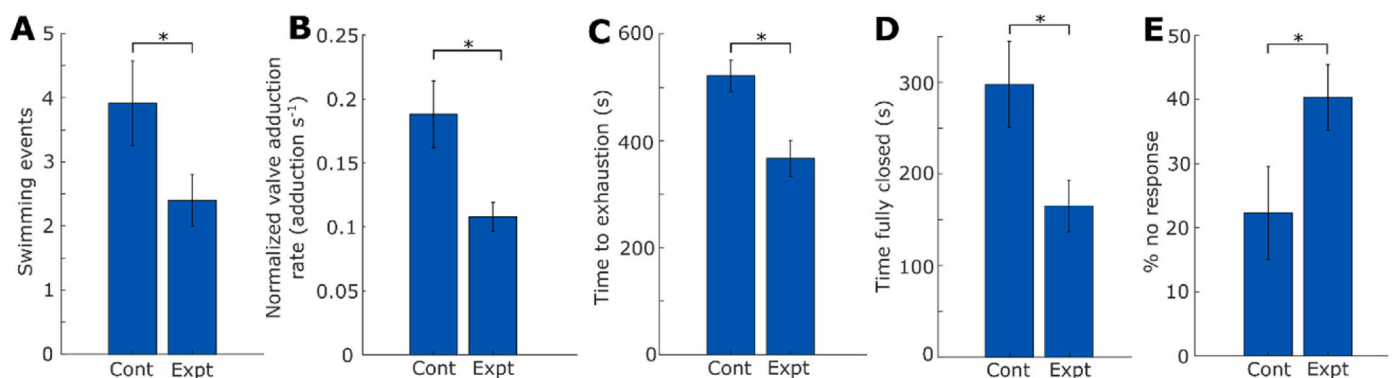
Fig. 4. Scallops exposed to pile driving performed worse during simulated sea star attacks. (A) Experimental sound-exposed scallops elicited significantly fewer swimming events (two-sample *t*-test, t-stat: 2.10, p = 0.0445) (B) and had a lower valve adduction rate (two-sample *t*-test, t-stat: 2.46, p = 0.021). (C) Experimental scallops became exhausted more rapidly (two-sample *t*-test, t-stat: 3.326, p = 0.0026). (D) Control animals spent more time with valves fully closed (two-sample *t*-test, t-stat: 2.57, p = 0.0163). (E) Sound-exposed scallops had a higher probability of not behaviorally responding to sea star stimuli (two-sample *t*-test, t-stat: 2.09, p = 0.0462).

4.3. Respirometry experiments

Scallop metabolic rates exhibited marked elevations both during and after pile driving exposure, surging by 33% and 56%, respectively, compared to baseline conditions. This notable increase underscores the great energetic toll exacted by the rapid valve adductions endured during pile driving exposure. The heightened metabolic rates are likely attributed to the contractions of the larger phasic portion of the adductor muscle that largely relies on phosphagen (anaerobic) energy pathways to power their valve movements (Livingstone et al., 1981; Thompson et al., 1980). Phasic muscle contractions enable fast valve adductions but have limited energetic scope. Consequently, repeated valve adductions resulted in oxygen debts that persisted for at least 1 h after the cessation of pile driving. Total recovery time is particularly important for scallops since they often select to fully recover metabolically before enacting other movement behaviors such as swimming to escape from predators (Robson et al., 2012). Therefore, a critical avenue for future research lies in determining the total duration required for metabolic recovery from pile driving exposure. Such insight will shed light on the extent to which scallops are compelled to divert energy to recover and remain susceptible to predation during this protracted recuperation period.

4.4. Antipredator performance

The heightened metabolic rates after the pile driving sound exposure led to weaker performance of antipredator behaviors. When oxygen debts are incurred, scallops are limited in the rate of energy expenditure, which narrows their metabolic scope and swimming performance (Robson et al., 2012). A lower number of swimming events, more rapid exhaustion, and less time fully closed all indicate that pile driving-exposed scallops had a lower probability of escaping a sea star predation attempt. Sea stars, in addition to crabs and lobsters, are well known scallop predators (Barbeau & Scheibling, 1994; Elner & Jamieson, 1979). Sea stars can be more abundant than scallops by over a 2:1 ratio in key scallop habitats (Stokesbury et al., 2004). High densities of sea stars suggest predation attempts may not occur in isolation and scallops may need repeated swimming events and/or full valve closures to evade capture. Thus, the earlier time to exhaustion may be detrimental and ultimately lead to higher mortality.

Successful predation requires a series of behaviors from location, attack, capture, and ingestion (Barbeau & Scheibling, 1994). Scallops are an excellent model to assess escape performance during capture attempts because valve adductions and angle regulate all antipredator behaviors, and therefore can be controlled and measured easily. While our results indicate a significant decrease in scallop's ability to evade a sea star, it is important to note that our antipredator tests did not concurrently measure pile driving sound effects on sea stars. Sea stars search for their food via chemoreception (Sloan & Campbell, 1982), and it is unknown whether pile driving sound would interfere with their ability to locate or attack prey. Our experiment methodology used homogenized sea stars rather than living animals, thus the hypothesis was tested in isolation and future assessments of pile driving sound impacts to sea stars are needed to fully clarify this predator-prey relationship.

4.5. Broader implications

Although our experiments represent a significant step forward in replicating offshore windfarm constructions in a controlled field setting, the pile diameter of our experimental setup was 1/30th of the diameter of the current piles being used in commercial installations (Kallehave et al., 2015). Thus, the physiological and anti-predator impacts found in this study will likely extend to a much greater spatial extent. Additionally, our setup only allowed for 15-min sound exposures. Because scallops failed to habituate to the impact pile driving, we would expect longer exposure durations would demonstrate even greater severity

impact. Previous studies measuring pile driving of a larger monopile offshore lasted 310 min at a more rapid hammering rate (60 strikes min^{-1} versus 10 strikes min^{-1} used in this study), resulting in over 6300 strikes for a single pile (Sigray et al., 2022). The PAL_{zpk} were 7 dB greater at 880 m from the pile without mitigation methods than what the experimental animals received in our study. Given the propagation efficiency of this low frequency sound, impacts such as those observed here could occur more than 1 km away from each pile installation (Sigray et al., 2022). This impact distance is greater than the spacing of turbines, suggesting that animals would be impacted throughout the entire windfarm area.

In context, the giant scallop, *P. magellanicus,* is abundant in the Mid-Atlantic Bight, USA, where multiple future offshore windfarms are planned. Stokesbury and Bethoney (2020) calculated *in situ* population density (277,090 scallops/km^2; 9 billion total) in locations within and near the proposed windfarm lease areas. Considering these numbers and a conservative impact radius of 1 km based on sound level data from Sigray et al. (2022), our data suggests that the potential impacts discussed herein could affect anywhere from 672,440 to 1,068,500 scallops (within a 95% confidence interval) or roughly 6.7–10.7 metric tons of scallop meat per wind turbine (Sup Mat 1). Notably, this estimate is only 0.00012% percent of the regional population in the Mid-Atlantic Bight and the total number of impacted scallops will likely be a function of the number of turbines. However, it is important to emphasize that the actual impact on these scallops may be more severe than noted here because there will be generally higher sound levels within the defined impact radius, and offshore windfarm pile driving construction typically occurs at a rate 2–3x faster than what we can replicate here. To gain a clearer understanding of the severity of these impacts within the affected area, it is essential to assess the relationship between received sound amplitude and the behavioral and physiological impact severity.

Our tests focused specifically on the impacts of offshore windfarm construction sounds on scallops. Sound impacts during non-construction windfarm phases (i.e., survey, operation, decommission) will likely differ from the impacts shown in the present study since response severity has been shown to vary with frequency spectra and temporal characteristics (Jézéquel et al., 2022; Mooney et al., 2020). Indeed, seismic airgun explosions, which are a common windfarm survey method, have been shown to alter blood biochemistry of *Pecten fumatus* (Day et al., 2017), but long term impacts on productivity and survivorship postexposure of other bivalves (*Pinctada maxima*) are less evident (Parsons et al., 2023). Field data from operational and decommission stages are lacking, but it is likely operational windfarm areas will act as a refuge from fishing pressure as commercial fleets will likely experience disrupted access to areas within windfarms.

5. Conclusion

Offshore wind energy development is rapidly proliferating worldwide in habitats with high bivalve abundance. This is the first field-based study to assess how pile driving sounds impact the behavior, metabolic physiology, and community interactions for a marine invertebrate. Our results demonstrate the ongoing and imminent construction may have cascading ecophysiological impacts spanning reduced oxygen availability to the gills, altered oxygen consumption rates and patterns, to weakened anti-predator behaviors. Our field-based study is a substantial step forward in moving sound-impact studies of marine bivalves into field conditions. Considering the clear physiological and antipredator impacts to scallops reported here, as well as previous field studies noting behavioral impacts across three life stages (Jézéquel et al., 2022), we stress the importance of selecting location of both wind farms and pile foundations in context of natural scallop density data. By combining acoustic measurements from larger-scale commercial windfarms and *P. magellanicus* distribution data, we estimated that physiological impacts noted in this study may impact over a million scallops per turbine during future construction in productive Mid-Atlantic Bight habitats.

However, there is high scallop density variability across multiple spatial scales that may be exploited by ocean use regulators to selectively avoid productive habitats, mitigating disruptions to ecologically-important and abundant scallops, safeguarding one of the most lucrative fisheries in the U.S. and allow nations to meet renewable energy needs.

CRediT authorship contribution statement

Seth F. Cones: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Youenn Jézéquel:** Writing – review & editing, Supervision, Software, Methodology, Conceptualization. **Sierra Jarriel:** Writing – review & editing, Investigation. **Nadège Aoki:** Writing – review & editing, Data curation. **Hannah Brewer:** Writing – review & editing, Resources, Investigation, Data curation. **John Collins:** Writing – review & editing, Resources, Data curation. **Laurent Chauvaud:** Writing – review & editing, Resources, Methodology. **T. Aran Mooney:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2024.124709.

References

Amaral, J.L., Miller, J.H., Potty, G.R., Vigness-raposa, K.J., Frankel, A.S., 2020. Characterization of impact pile driving signals during installation of offshore wind turbine foundations. J. Acoust. Soc. Am. 147, 2323–2333. https://doi.org/10.1121/10.0001035.

Barbeau, M.A., Scheibling, R.E., 1994. Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)). J. Exp. Mar. Biol. Ecol. 180, 103–136.

Chauvaud, L., Thouzeau, G., Paulet, Y.M., 1998. Effects of environmental factors on the daily growth rate of *Pecten maximus* juveniles in the Bay of Brest (France). J. Exp. Mar. Biol. Ecol. 22, 83–111. https://doi.org/10.1016/S0022-0981(97)00263-3.

Cones, S., Ferguson, S.R., Jezequel, Y., Aoki, N., Mooney, T.A., 2022. Pile driving noise induces transient gait disruptions in the long fin squid (*Doryteuthis pealeii*). Front. Mar. Sci. 9, 2256. https://doi.org/10.3389/fmars.2022.1070290.

Cones, S., Youenn, J., Mooney, T.A., 2023. Marine bivalve sound detection and associated noise impacts. In: The Effects of Noise on Aquatic Life. Springer, pp. 1–11. https://doi.org/10.1007/978-3-031-10417-6_32-11.

Day, R.D., McCauley, R.D., Fitzgibbon, Q.P., Hartmann, K., Semmens, J.M., 2017. Exposure to seismic air gun signals causes physiological harm and alters behavior in the scallop *Pecten fumatus*. Proc. Natl. Acad. Sci. U.S.A. 114 (40), E8537–E8546. https://doi.org/10.1073/pnas.1700564114.

Deruiter, S.L., Southall, B.L., Calambokidis, J., Zimmer, W.M.X., Sadykova, D., Falcone, E.A., Friedlaender, A.S., Joseph, J.E., Moretti, D., Schorr, G.S., Thomas, L., Tyack, P.L., 2013. First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. Biol. Lett. 9 (4), 20130223 https://doi.org/10.1098/rsbl.2013.0223.

Duarte, C.M., Chapuis, L., Collin, S.P., Costa, D.P., Devassy, R.P., Eguiluz, V.M., Erbe, C., Gordon, T.A.C., Halpern, B.S., Harding, H.R., Havlik, M.N., Meekan, M.G., Merchant, N.D., Miksis-Olds, J.L., Parsons, M., Predragovic, M., Radford, A.N., Radford, C.A., Simpson, S.D., et al., 2021. The soundscape of the Anthropocene ocean. Science 371, eaba4658. https://doi.org/10.1126/science.aba4658.

Elner, R.W., Jamieson, G.S., 1979. Predation of Sea Scallops, *Placopecten magellanicus*, by the Rock Crab, *Cancer Irroratus*, and the American Lobster, *Homarus Americanus*, vol. 36. Journal of the Fisheries Research Board of Canada, pp. 537–543. https://doi.org/10.1139/f79-077.

FAO, 2016. The State of the World Fisheries and Aquaculture. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fewtrell, J.L., McCauley, R.D., 2012. Impact of air gun noise on the behaviour of marine fish and squid. Mar. Pollut. Bull. 64 (5), 984–993. https://doi.org/10.1016/j.marpolbul.2012.02.009.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7 (11), 1325–1330. https://doi.org/10.1111/2041-210X.12584.

Garcia-March, J.R., Jiménez, S., Sanchis, M.A., Monleon, S., Lees, J., Surge, D., Tena-Medialdea, J., 2016. In situ biomonitoring shows seasonal patterns and environmentally mediated gaping activity in the bivalve, Pinna nobilis. Mar. Biol. 163, 1–12. https://doi.org/10.1007/s00227-016-2812-3.

Harding, H.R., Gordon, T.A.C., Eastcott, E., Simpson, S.D., Radford, A.N., 2019. Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. Behav. Ecol. 30 (6), 1501–1511. https://doi.org/10.1093/beheco/arz114.

Hawkins, A.D., Roberts, L., Cheesman, S., 2014. Responses of free-living coastal pelagic fish to impulsive sounds. J. Acoust. Soc. Am. 135 (5), 3101–3116. https://doi.org/10.1121/1.4870697.

Heilmayer, O., Brey, T., Pörtner, H.O., 2004. Growth efficiency and temperature in scallops: A comparative analysis of species adapted to different temperatures. Func. Ecol. 18 (5), 641–647. https://doi.org/10.1111/j.0269-8463.2004.00905.x.

Hemery, L.G., Garavelli, L., Copping, A.E., Farr, H., Jones, K., Baker-Horne, N., Kregting, L., McGarry, L.P., Sparling, C., Verling, E., 2024. Animal displacement from marine energy development: mechanisms and consequences. Sci. Total Environ. 917, 170390 https://doi.org/10.1016/j.scitotenv.2024.170390.

Hubert, J., Booms, E., Witbaard, R., Slabbekoorn, H., 2022. Responsiveness and habituation to repeated sound exposures and pulse trains in blue mussels. J. Exp. Mar. Biol. Ecol. 547, 151668 https://doi.org/10.1016/j.jembe.2021.151668.

Jézéquel, Y., Cones, S., Jensen, F.H., Brewer, H., Collins, J., Mooney, T.A., 2022. Pile driving repeatedly impacts the giant scallop (*Placopecten magellanicus*). Sci. Rep. 12, 15380 https://doi.org/10.1038/s41598-022-19838-6.

Jézéquel, Y., Cones, S., Mooney, T.A., 2023a. Sound sensitivity of the giant scallop (*Placopecten magelanicus*) is life stage, intensity, and frequency dependent. J. Acoust. Soc. Am. 153 (2), 1130–1137. https://doi.org/10.1121/10.0017171.

Jézéquel, Y., Cones, S., Ferguson, S.R., Aoki, N., Girdhar, Y., Mooney, T.A., 2023b. Short-term habituation of the longfin squid (*Doryteuthis pealeii*) to pile driving sound. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. https://doi.org/10.1093/icesjms/fsad157 fsad157.

Jones, I.T., Peyla, J.F., Clark, H., Song, Z., Stanley, J.A., Mooney, T.A., 2021. Changes in feeding behavior of longfin squid (*Doryteuthis pealeii*) during laboratory exposure to pile driving noise. Mar. Environ. Res. 165 (November 2020), 105250 https://doi.org/10.1016/j.marenvres.2020.105250.

Livingstone, D.R., de Zwaan, A., Thompson, R.J., 1981. Aerobic metabolism, octopine production and phosphoarginine as sources of energy in the phasic and catch adductor muscles of the giant scallop *Placopecten magellanicus* during swimming and the subsequent recovery period. Comp. Biochem. Physiol. Part B: Biochemistry And 70 (1), 35–44. https://doi.org/10.1016/0305-0491(81)90120-6.

MacDonald, B.A., Thompson, R.J., 1986. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. Mar. Biol. 93 (1), 37–48. https://doi.org/10.1007/BF00428653.

Methratta, E.T., 2020. Monitoring fisheries resources at offshore wind farms: BACI vs. BAG designs. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 77 (3), 890–900. https://doi.org/10.1093/icesjms/fsaa026.

Miller, P.J.O., Isojunno, S., Siegal, E., Lam, F.P.A., Kvadsheim, P.H., Cure, C., 2022. Behavioral responses to predatory sounds predict sensitivity of cetaceans to anthropogenic noise within a soundscape of fear. Proc. Natl. Acad. Sci. U.S.A. 119 (13), 1–8. https://doi.org/10.1073/pnas.2114932119.

Mooney, T.A., Andersson, M.H., Stanley, J.A., 2020. Acoustic impacts of offshore wind energy on fishery resources. Oceanography 33 (4), 82–95. https://doi.org/10.5670/oceanog.2020.408.

Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J. Shel. Res. 23, 51–62.

Parsons, M.J.G., Barneche, D.R., Speed, C.W., McCauley, R.D., Day, R.D., Dang, C., Fisher, R., Gholipour-Kanani, H., Newman, S.J., Semmens, J.M., Meekan, M.G., 2023. A large-scale experiment finds no consistent evidence of change in mortality or

commercial productivity in silverlip pearl oysters (*Pinctada maxima*) exposed to a seismic source survey. Mar. Pollut. Bull. 199, 115480 https://doi.org/10.1016/j.marpolbul.2023.115480.

Popper, A.N., Hawkins, A.D., Fay, R.R., Mann, D.A., Bartol, S., Carlson, T.J., Coombs, S., Ellison, W.T., Gentry, R.L., Halvorsen, M.B., Løkkeborg, S., Rogers, P.H., Southall, B.L., Zeddies, D.G., Tavolga, W.N., 2014. Sound Exposure Guidelines for Fishes and Sea Turtles: A Technical Report Prepared by ANSI-Accredited Standards Committee S3/SC1 and Registered with ANSI. Springer. https://doi.org/10.1007/978-3-319-06659-2 (Issue July 2015).

Popper, A.N., Hice-Dunton, L., Jenkins, E., Higgs, D.M., Krebs, J., Mooney, T.A., Rice, A., Roberts, L., Thomsen, F., Vigness-Raposa, K., Zeddies, D., Williams, K.A., 2022. Offshore wind energy development: research priorities for sound and vibration effects on fishes and aquatic invertebrates. J. Acoust. Soc. Am. 151 (1), 205–215. https://doi.org/10.1121/10.0009237.

Robson, A.A., Chauvaud, L., Wilson, R.P., Halsey, L.G., 2012. Small actions, big costs: the behavioural energetics of a commercially important invertebrate. J. R. Soc. Interface 9 (72), 1486–1498. https://doi.org/10.1098/rsif.2011.0713.

Robson, A.A., Garcia De Leaniz, C., Wilson, R.P., Halsey, L.G., 2010. Behavioural adaptations of mussels to varying levels of food availability and predation risk. J. Molluscan Stud. 76 (4), 348–353. https://doi.org/10.1093/mollus/eyq025.

Sigray, P., Linné, M., Andersson, M.H., Nöjd, A., Persson, L.K.G., Gill, A.B., Thomsen, F., 2022. Particle motion observed during offshore wind turbine piling operation. Mar. Pollut. Bull. 180, 113734 https://doi.org/10.1016/j.marpolbul.2022.113734.

Simpson, S.D., Purser, J., Radford, A.N., 2015. Anthropogenic noise compromises antipredator behaviour in European eels. Global Change Biol. 21 (2), 586–593. https://doi.org/10.1111/gcb.12685.

Sloan, N.A., Campbell, A.C., 1982. Perception of food. In: Jangoux, M., Lawrence, J.M., Balkema, A.A. (Eds.), Echinoderm Nutrition, pp. 3–23.

Sole, M., Radford, A.N., Nedelec, S.L., Vazzana, M., Wale, M.A., Semmens, J.M., Mccauley, R.D., Andre, M., 2023. Marine invertebrates and noise. March, 1–35. https://doi.org/10.3389/fmars.2023.1129057.

Stokesbury, K.D.E., Bethoney, N.D., 2020. How many sea scallops are there and why does it matter? Front. Ecol. Environ. 18 (9), 513–519. https://doi.org/10.1002/fee.2244.

Stokesbury, K.D.E., Harris, B.P., Marino II, M.C., Nogueira, J.I., 2004. Estimation of sea scallop abundance using a video survey in off-shore US waters. J. Shellfish Res. 23 (1), 33–40.

Thompson, R.J., Livingstone, D.R., de Zwaan, A., 1980. Physiological and biochemical aspects of the valve snap and valve closure responses in the giant scallop *Placopecten magellanicus* - I. Physiology. J. Comp. Physiol. B 137 (2), 97–104. https://doi.org/10.1007/BF00689207.

Trueman, E.R., 1983. Locomotion in molluscs. In: The Mollusca. Elsevier, pp. 155–198.

Tyack, P.L., Zimmer, W.M.X., Moretti, D., Southall, B.L., Claridge, D.E., Durban, J.W., Clark, C.W., D'Amico, A., DiMarzio, N., Jarvis, S., McCarthy, E., Morrissey, R., Ward, J., Boyd, I.L., 2011. Beaked whales respond to simulated and actual navy sonar. PLoS One 6 (3), e17009. https://doi.org/10.1371/journal.pone.0017009.

van der Knaap, I., Slabbekoorn, H., Moens, T., Van den Eynde, D., Reubens, J., 2022. Effects of pile driving sound on local movement of free-ranging Atlantic cod in the Belgian North Sea Auteurs. Environ. Pollut. 300 (October 2021), 118913 https://doi.org/10.1016/j.envpol.2022.118913.

van der Schatte Olivier, A., Jones, L., Vay, L., Christie, M., Wilson, J., Malham, S.K., 2020. A global review of the ecosystem services provided by bivalve aquaculture. Rev. Aqua. 12, 3–25. https://doi.org/10.1111/raq.12301.

Williams, T.M., Blackwell, S.B., Tervo, O., Garde, E., Sinding, M.H.S., Richter, B., Heide-Jørgensen, M.P., 2022. Physiological responses of narwhals to anthropogenic noise: a case study with seismic airguns and vessel traffic in the Arctic. Funct. Ecol. 36 (9), 2251–2266. https://doi.org/10.1111/1365-2435.14119.