

# Sound sensitivity of the giant scallop (*Placopecten magelanicus*) is life stage, intensity, and frequency dependent

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# Sound sensitivity of the giant scallop (*Placopecten magellanicus*) is life stage, intensity, and frequency dependent

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## ABSTRACT:

There is increasing concern that anthropogenic sounds have a significant impact on marine animals, but there remains insufficient data on sound sensitivities for most invertebrates, despite their ecological and economic importance. We quantified auditory thresholds (in particle acceleration levels) and bandwidth of the giant scallop (*Placopecten magellanicus*) and subsequently sought to discern sensitivity among two different life stages: juveniles (1 yr olds) and subadults (3 yr olds). We also leveraged a novel valvometry technique to quantify the amplitude of scallop valve gape reductions when exposed to different sound amplitudes and frequencies. Behavioral responses were obtained for lower frequencies below 500 Hz, with best sensitivity at 100 Hz. There were significant differences between the auditory thresholds of juveniles and subadults, with juveniles being more sensitive, suggesting ontogenetic differences in hearing sensitivity. Scallops showed intensity and frequency dependent responses to sounds, with higher valve closures to lower frequencies and higher sound levels. To our knowledge, these are the first data highlighting life stage, intensity, and frequency responses to sound in a marine benthic invertebrate. These results demonstrate clear sound sensitivity and underscore that the potential impacts of anthropogenic sound in valuable ecological resources, such as scallops, may be dependent on sound characteristics. © 2023 Acoustical Society of America.

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## I. INTRODUCTION

Anthropogenic sound is now recognized as a major source of underwater pollution (Duarte *et al.*, 2021). Several studies have described the various impacts of sound on marine taxa, such as mammals and fishes, ranging from temporary changes in behavior to mortality (Williams *et al.*, 2015). Comparatively, there are substantially few data available on marine invertebrate sound sensitivity, creating a paucity of empirical knowledge on subsequent potential sound impacts (Wale *et al.*, 2021). This is surprising given that marine invertebrates are widespread and ecologically vital within an ocean that is awash with sound cues and potential sound stressors (Duarte *et al.*, 2021). Addressing marine invertebrate sound sensitivity is crucial to better understand their sensory biology, how it may enact key behaviors, and how sound pollution may be disrupting important ecological processes.

The sensory systems of marine invertebrates are sensitive to particle acceleration rather than sound pressure (Popper and Hawkins, 2018). For example, bivalves can detect both water- and substrate-borne vibrations through their abdominal sense organs and statocysts (Roberts and Elliott, 2017). Responses to stimuli include siphonal retraction, valve closures, and swimming behaviors (Mosher, 1972; Ellers, 1995; Kastelein, 2008), although in many cases, the

precise particle acceleration levels were unspecified. Studies showed blue mussels and oysters respond to low frequency particle acceleration below 1000 Hz, with higher sensitivity (i.e., lower thresholds) below 100 Hz (Roberts *et al.*, 2015; Charifi *et al.*, 2017). A recent field study also highlighted that the giant scallop (*Placopecten magellanicus*) reacted to pile driving particle acceleration with juveniles being more sensitive than adults (Jézéquel *et al.*, 2022). This result suggests there may be ontogenetic variations in response to particle acceleration, although frequency responses were not addressed. In addition, these scallops reacted to close (i.e., <10 m), but not far (i.e., 50 m), sources highlighting potential intensity-dependent responses (Jézéquel *et al.*, 2022). There are no audiograms available for scallops thus sound sensitivities must be extrapolated from distant species with divergent morphologies, leaving such estimations tenuous at best. Defining how response types and rates may vary based upon sound level and frequency would broaden an understanding of the sensory ecology of this important bivalve, and for invertebrates, in general. Such information would also empirically support extrapolations regarding how different anthropogenic sound sources may affect this ecologically and economically vital taxon (Newell, 2004; Wijsman *et al.*, 2019). In addition, mollusks present a complex pelago-benthic cycle with higher sensitivity of earlier life stages (i.e., larvae and juveniles) to environmental stressors, such as acidification (Kroeker *et al.*, 2013). Assessing contrasting sound sensitivities across different life stages would be particularly important to better understand sound impacts on scallops (Hawkins *et al.*, 2015).

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Sound detection in marine invertebrates, largely crustaceans and cephalopods, has often been measured using auditory evoked potentials, a means to estimate hearing abilities by measuring neurophysiological responses, often from a selected auditory structure (Mooney *et al.*, 2010; Jézéquel *et al.*, 2021). Behavioral methods are an alternate means to examine hearing; these methods, while diverse, can produce lower thresholds and reflects the perception of sound, an important metric which addresses sound sensitivity (Ladich and Fay, 2013; Popper *et al.*, 2014). Yet marine invertebrates are diverse and it is not often clear how behavioral methods can be applied to these taxa (but see Goodall *et al.*, 1990). Bivalves can make good candidates for invertebrate behavioral sound sensitivity measures considering their low mobility and several acoustically mediated responses (e.g., valve closures) which can be precisely measured (e.g., Roberts *et al.*, 2015). Valvometry is an emerging method that uses inertial measurement units to quantify bivalve valve angles at relatively high resolution (Charifi *et al.*, 2017; Comeau *et al.*, 2018; Hubert *et al.*, 2022). While it has never been used to construct an audiogram in scallops, valvometry has the potential to assess intensity-dependent responses to sound at a fine behavioral scale. Such data are key to better evaluate anthropogenic sound impacts in marine invertebrates (Hawkins *et al.*, 2015).

The aim of this study was to integrate the valvometry method with traditional (video-based) behavioral observations to provide novel insight into scallop sensory ecology and specifically address three key questions: (1) What are the sound detection thresholds (in particle acceleration levels) of the giant scallop (*P. magellanicus*), (2) Do these thresholds vary across different life stages, and (3) How responses vary based on sound level and frequency?

## II. MATERIALS AND METHODS

Experiments were conducted in May and June 2022 at the research facilities of the Environmental Systems Laboratory (ESL), Woods Hole Oceanographic Institution (WHOI) (Woods Hole, MA, USA). Experiments with scallops are not subject to restriction for animal scientific research according to the United States legislation. Animals were handled with care during the experiments and their health statuses were checked daily by the authors.

### A. Animal collection, characteristics, and care

This study was performed using two scallop sizes reflecting contrasting life stages. We purchased 16 subadults ( $7.5 \pm 0.5$  cm) and 19 juveniles ( $3.3 \pm 0.4$  cm) from the Pine Point Oyster Company (Cape Elizabeth, USA) on September 2, 2021. We defined these life stages according to their age, with juveniles being 1 yr old and subadults being 3 yrs old. After collection, all animals were transferred to ESL facilities where they were acclimatized in tanks. Holding tanks were continuously supplied with nonfiltered flow-through seawater (temperature =  $10^\circ\text{C}$ ), and were exposed to a natural light cycle. Scallops were not fed throughout the holding period.

However, the seawater supply to the tanks was unfiltered; therefore it is likely that some algae were present in the water, allowing some feeding for the animals. Scallops were held in these lab conditions for 8 months before they were used for the experiments.

### B. Experimental setup

Sound detection experiments were performed in a dedicated rectangular opaque fiberglass-sided tank ( $0.6 \times 0.4 \times 0.5$  m;  $0.12 \text{ m}^3$ ) placed in a quiet room within the ESL. One side of the tank was made of transparent glass to visually assess scallop behaviors during sound exposures. The experimental tank rested on rubber gaskets and a dense wooden table, both of which further isolated the tank from surrounding vibrations. Prior to each experiment, the tank was filled with the same fresh, aerated, chilled seawater as for the holding tanks. A UW-30 underwater speaker (Electro-Voice, Fairport, NY, USA) was suspended, facing horizontally towards the scallops, 15 cm from the surface, and 10 cm from the closest tank wall.

Prior to an experiment, one scallop was taken from its holding tank and glued on a flat rock platform, ventral side down, to prevent the animal from moving. The individual was placed in the middle of the tank, raised 10 cm above the bottom and faced the underwater speaker at a distance of 15 cm. Then, a GoPro (San Mateo, CA) HERO6 black camera was introduced in the tank and laid 30 cm in front of the tested scallop. Prior to sound exposure, the scallop was acclimatized for at least 15 min in the tank to recover from handling. Each individual was used only once during the study.

### C. Acoustic stimuli

We focused our study on scallop responses to water-borne sounds generated by an underwater speaker. Here, we did not consider the potential role of substrate-borne vibrations arising from sound exposure that could have also stimulated the animals. Sound exposures were performed using amplitude-modulated tone pips (0.5 s duration) of 100, 150, 200, 300, 500, and 1000 Hz with the same setup as in Jézéquel *et al.* (2021). The presentation order of the frequencies was random. Acoustic stimuli were played from a laptop connected to an amplifier (PLA2378, Brooklyn, NY, USA) which was connected to the underwater speaker. Measurements started at maximum particle acceleration levels (PALs), the values of which were frequency dependent because of the characteristics of the underwater speaker: 96–110 dB re  $1 \mu\text{m s}^{-2}$ . The PALs were then gradually decreased by 3 or 6 dB depending on the amplitude of the behavioral response using audio files in Audacity<sup>®</sup> (Version 3.1.3., Audacity Team 2021, Carnegie Mellon University, USA), until there was no longer detectable response (see Sec. II E). The ambient sound levels in the experimental tank were below that of the acoustic stimuli used during sound exposures (63 dB re  $1 \mu\text{m/s}^{-2}$ ).

The theoretical minimum resonant frequency of our experimental tank was 2.7 kHz (Akamatsu *et al.*, 2002). This was far above the highest frequency of the acoustic



stimuli used during sound exposures (1 kHz), indicating that the acoustic stimuli were not distorted (see Jézéquel *et al.*, 2021 for spectral shapes). However, these low frequencies rapidly attenuated because their wavelengths were larger than the tank size (Rogers *et al.*, 2016). Hence, after the acoustic calibration, we carefully positioned each scallop at the same distance (15 cm) from the speaker to enable comparisons between individuals.

#### D. Acoustic calibration

We quantified sound thresholds, defined as the minimum sound level at which a response was detected, in root-mean square PAL (PAL<sub>rms</sub>, in dB re  $1 \mu\text{m/s}^{-2}$ ) as this is the primary stimulus for sound detection in marine invertebrates (Popper and Hawkins, 2018); scallops and other marine invertebrates are not known to detect sound pressure. PAL<sub>rms</sub> values were measured using a tri-axial accelerometer with a custom-built waterproof housing (model W356B11, PCB Piezotronics, Depew, NY) (sensitivity:  $x = 10.31 \text{ mV m/s}^{-2}$ ;  $y = 10.38 \text{ mV m s}^{-2}$ ;  $z = 10.58 \text{ mV m/s}^{-2}$ ). The device was suspended in the experimental tank in the absence of animal at 15 cm from the speaker, i.e., the same location as the hearing tests. It was wired through a signal conditioner (model 480B21, PCB Piezotronics), which multiplied the recorded voltage by a factor of 100. The accelerometer signal was input to two analog filters (model 3382, Krohn-Hite Corporation, Brockton, MA), which each applied a lowpass filter at 2 kHz and a 20 dB gain. Outputs of the filters were input to a data acquisition board (USB 6251, National Instruments, Brockton, MA), which was in turn connected to a laptop that ran a custom MATLAB (MathWorks, Natick, MA, USA) script to record the audio files. Voltage values in root-mean square for each axis ( $x$ ,  $y$  and  $z$ ) were calibrated to the sensitivity of the accelerometer and used to calculate the magnitude of particle acceleration over the length of each acoustic stimulus (i.e., 0.5 s). Calculations were performed with custom-written MATLAB scripts (v9.1; MathWorks).

#### E. Threshold determination

Sound detection thresholds were initially visually determined by an experienced observer looking through the tank window. Behavioral reactions (full, partial valve closure, or no response) were noted for each acoustic stimulus exposure. The presentation order of the frequencies was random. For a given frequency, scallops were exposed to five consecutive acoustic stimuli of identical amplitude separated by at least 30 s to allow the animal to recover (i.e., re-open its valves). At least three positive responses (out of five) were used to validate sound detection at this particular level. Then, the PAL<sub>rms</sub> was gradually decreased and the corresponding responses were visually monitored. The PAL<sub>rms</sub> were first decreased in 6 dB increments depending on the amplitude of the behavioral response, and in 3 dB increments when close to the thresholds until the stereotypical behavioral response was no longer detectable. Then, one to two additional recordings at 3–6 dB below the visually

determined thresholds were made to ensure that low responses were not missed. Nondetection was determined by at least three negative responses. The minimum sound level at which an animal responded was calculated as its thresholds. After a threshold was determined and before changing to a different acoustic frequency, the tested scallop was exposed again to the highest level of acoustic stimuli. This ensured that scallops responded back by stronger valve closures and habituation or other change in response rate or amplitude did not occur, underscoring that the animals did not become conditioned to the acoustic stimulus.

There was little ambiguity in the response, given the well-defined criteria for open, closed, and partially closed valves. However, all experiments were video recorded and subsequent data were archived on a laptop and viewed to confirm the responses and thresholds previously obtained.

#### F. Quantification of intensity and frequency dependent responses

Valve gap and closure behaviors in response to acoustic stimuli were also measured continuously in subadult scallops via a bio-logger. Each individual was affixed with a small ( $15 \times 10 \times 4 \text{ mm}$ , mass 1.7 g) Axy 5 XS bio-logging tag (Technosmart Europe srl, Rome, Italy), which contained both an accelerometer and a magnetometer.

Tags were attached as in Jézéquel *et al.* (2022). To attach the tags, the outer surface of the valves on each scallops was first dried with a paper towel and lightly sanded at the attachment site. A tag was then glued with 3 min underwater epoxy to the outer surface of the upper curved valve at a maximum possible distance from the hinge. A small neodymium magnet (11 mm diameter, 1.7 mm thickness) was then epoxied to the lower flat valve directly below the sensor. The voltage of the magnetometer (in mV) was recorded at a 2 Hz sampling rate. Total handling time in air for each individual was less than 15 min. Then, tagged individuals were relocated to their holding tanks for an acclimatization period of at least 3 days before sound exposure tests.

After the experiments, tagged individuals were retrieved and data were downloaded using Open Movement GUI software, Newcastle University, UK (v1.0.0.37). We then calibrated each magnetometer sensor to compute the relationship between the recorded voltage and the valve gap opening distance to account for morphometric differences among individuals (Nagai *et al.*, 2006). First, the adductor muscle of each scallop was severed, and the voltage was measured for 20 known inter-valve distance values from 0 (corresponding to a closed shell) to 20 mm in 1 mm increments. These distances were obtained by inserting sequentially a series of 1 mm-thick glass slides between the valves. The recorded data were then used to create an observed calibration curve for each individual using the following equation:

$$d = \left( \frac{x1}{Uh(d) - x3} \right)^{0.5} - x2,$$

where  $d$  is the measured inter-valve distance (in mm),  $Uh(d)$  is the sensor output values (in mV), and  $X = \{x1, x2, x3\}$  is a set of parameters to estimate.

The relationships between voltage and wedge height (i.e., valve opening) were strong ( $r^2 \geq 0.98$ ). Valve opening data were then converted into valve gap angles ( $\vartheta$ , in degrees) using the equation from Wilson *et al.* (2005):

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

where  $W$  is the valve opening (in mm) and  $L$  (in mm) is shell length of the scallop.

This standardization approach accounts for varying shell heights and thus minimizes the influence of scallop size on the behavioral metric.

### G. Statistical analyses

Sound detection threshold data were distributed normally (Kolmogorov–Smirnov test,  $p < 0.001$ ), thus two-way repeated analyses of variances (ANOVAs,  $\alpha = 0.05$ ) were used to determine the effects of life stage (juvenile and subadult) on the sound detection thresholds (PALrms) across frequencies at 100, 150, and 200 Hz (frequencies of greatest sensitivity). When significant effects were detected, pairwise Tukey tests were used to assess whether differences were observed among all groups ( $p = 0.05$ ). Least-squares linear regressions were applied on the different datasets of sound detection thresholds to test for potential relationships with scallop sizes, changes in valve angle with sound levels. Finally, we used logistic regressions to address the relationship between the scallop response rate and sound levels at particular frequencies. The goodness of models' fits and how well the response rate was predicted were assessed using the Hosmer–Lemeshow test ( $p = 0.05$ ). We also used one-way ANOVA to assess whether valve angle in tagged scallops depended on frequency of similar sound level. Because the speaker response was frequency dependent, we choose to compare valve angles at 96 dB re  $1 \mu\text{m/s}^{-2}$ , which was the same sound level where scallops responded at all tested frequencies.

## III. RESULTS

### A. Sound detection thresholds

Clear valve closures were observed in all scallops in response to acoustic stimuli. No reactions occurred in the absence of sound. Acoustic response thresholds were obtained from the 35 tested scallops between 100 and 500 Hz. Responses were presented in units of PALrms in Fig. 1. These acoustically mediated responses were not detected at the highest frequency tested (1000 Hz). Frequency and life stage had both significant effects on thresholds (two-way

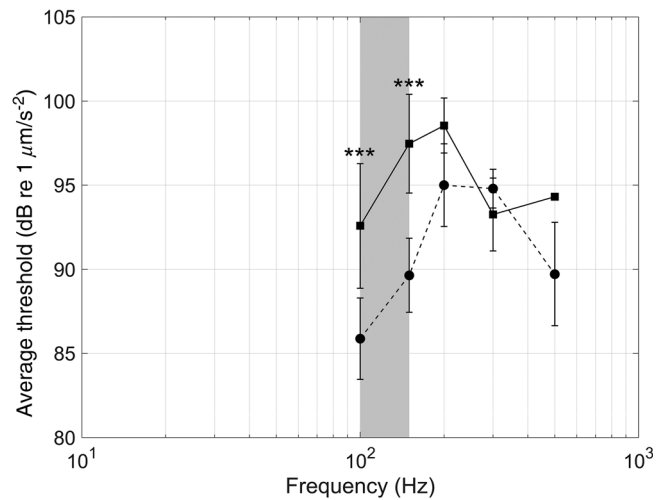


FIG. 1. Behavioral sound detection thresholds (in PALrms) of juvenile (dashed line,  $n = 19$ ) and subadult (continuous line,  $n = 16$ ) scallops. Valve closures were used to assess detection at a given sound frequency and level. Error bars are s.d. and stars highlight significant differences between juveniles and subadults using Tukey tests ( $p < 0.001$ ). The shaded area highlights the frequencies where 100% of scallops responded. No differences were found at 200 Hz. Only 43% and 12% juveniles and subadults, respectively, responded at 300 Hz, while 16% and 6% of juveniles and subadults, respectively, responded at 500 Hz. Background sound level was 63 dB re  $1 \mu\text{m/s}^{-2}$  over the 100–1000 Hz frequency range.

repeated measures ANOVA; frequency:  $F_{2,95} = 30.3$ ,  $p < 0.001$ ; life stage:  $F_{1,95} = 49.8$ ,  $p < 0.001$ ).

Overall, scallops significantly displayed a greater sensitivity (i.e., lower thresholds) at the lowest tested frequency (i.e., 100 Hz; Tukey test,  $p < 0.001$ ). In addition, juveniles showed significantly lower thresholds compared to subadults (Tukey test,  $p < 0.001$ ). This was further confirmed as linear regressions between thresholds and scallop sizes showed significant effects at the three frequencies of greatest response rates (100, 150, and 200 Hz) (see Fig. 2). While all scallops responded to 100 and 150 Hz, the percentage of responses then decreased with increasing frequency (Table I). For example, 75% of subadults reacted at 200 Hz, while only 6% reacted at 500 Hz (Table I). Logistic regressions were performed to estimate models that adequately explained the relationship between valve angle and PALrms at 100, 150, and 200 Hz (Fig. 3). The models were significant at all three tested frequencies (Hosmer–Lemeshow test,  $p < 0.001$ ).

### B. Intensity- and frequency-based responses

Subadults, at a given frequency, showed a positive correlation between the amplitude of the valve angle reduction and sound intensity (Fig. 4). Linear relationships between valve angle and PALrms were significant at 100, 150, and 200 Hz (see Fig. 5 for statistics). Finally, at the same sound level, there was a significant effect of frequency in the valve angle closures (one-way ANOVA;  $F_{3,51} = 11.1$ ,  $p < 0.001$ ), with scallops closing their valves more at 100 Hz compared to higher frequencies (Tukey test,  $p < 0.05$ ).

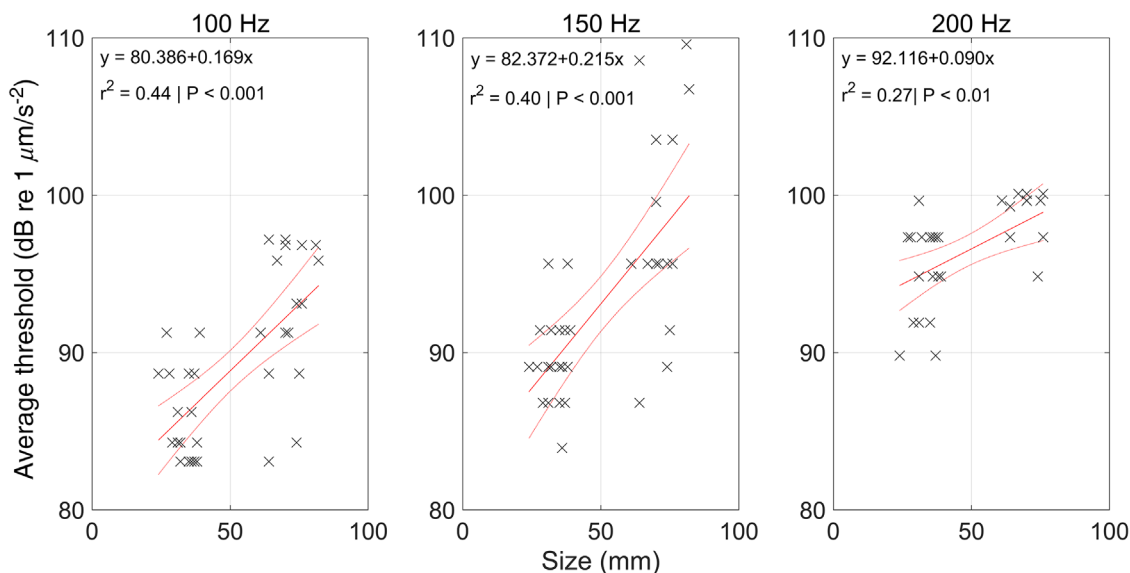


FIG. 2. (Color online) Linear relationships between sound detection thresholds (in PALrms) and scallop sizes ( $n = 35$ ) for different frequencies. Each point represents the value for one individual. Dashed red lines show 95% confidence intervals around the models.

#### IV. DISCUSSION

We constructed behavioral audiograms of two life stages of the giant scallop. We can discern three key results from these data. First, scallops detect underwater sounds with greater sensitivity at lower frequencies ( $< 200$  Hz). Second, juveniles showed lower thresholds (i.e., greater sensitivity) compared to subadults, suggesting ontogenetic differences in scallop sensitivity to sound. Third, scallops showed both sound level and frequency dependent responses, with stronger valve closures to lower frequencies and higher sound levels. To our knowledge, this is the first paper highlighting life stage, intensity, and frequency response to sound in a marine benthic invertebrate.

Few studies have investigated sound sensitivity in bivalves, and only a handful of them provided detailed measurements of exposure stimuli in particle acceleration levels (See supplementary material for Fig. S1 and the comparisons of auditory thresholds in bivalves.)<sup>1</sup> We found scallops detect sounds up to 500 Hz with the greatest sensitivity (i.e., lowest thresholds) at 100 Hz (Fig. 1), the lowest frequency we tested. This is consistent with oysters (*Magallana gigas*) that detect underwater sounds below 1000 Hz, with better sensitivity between 10 and 200 Hz (Charifi et al., 2017). Previous studies also reported behavioral responses to low frequency sounds in clams (*Donax variabilis*) ( $< 200$  Hz) (Ellers, 1995) and *Macoma baltica* ( $< 50$  Hz) (Mosher,

1972). One study also quantified the responses of blue mussels (*Mytilus edulis*) to substrate-borne vibrations in the same low frequency range ( $< 410$  Hz) (Roberts et al., 2015). Overall, these different studies highlighted low frequency detection of both water- and substrate-borne vibrations in bivalves.

Average auditory thresholds measured for scallops increased with frequency, ranging from 86–99 dB re  $1 \mu\text{m/s}^{-2}$  at 100 and 200 Hz, respectively (Fig. 1). These values are similar to thresholds of water-borne sound for oysters (Charifi et al., 2017). While we did not take into account the potential role of associated substrate-borne vibrations arising from our speaker that could have also stimulated the scallops in the tank, our threshold values are also consistent with substrate-borne vibration levels detected by mussels (Roberts et al., 2015). Further studies should now assess what acoustic component plays a role in bivalve sensory ecology (Roberts and Elliott, 2017).

The decrease in sound sensitivity with increasing frequency found in our study is common in marine invertebrates (Mooney et al., 2010; Charifi et al., 2017; Jézéquel et al., 2021). The scallop dose response curves shown in Fig. 3 are consistent with previous results on oyster sound detection (Charifi et al., 2017). Although our underwater speaker did not allow us to expose scallops to frequencies below 100 Hz, it is likely that they would detect sound, possibly with improving sensitivity, below this frequency (Roberts et al., 2015; Charifi et al., 2017). There is evidence to support this very low frequency sound sensitivity as scallops were also shown to respond to pile driving particle accelerations with peak energies below 100 Hz (Jézéquel et al., 2022).

The two scallop life stages studied showed different sound sensitivities. Sound detection thresholds were significantly lower for juveniles (i.e., 1 yr olds) at 100 and 150 Hz compared to subadults (i.e., 3 yr olds) indicating that

TABLE I. Percentage (%) of scallops responding to each frequency (Hz) across the two tested life stages.

Life stage	Tested frequencies					
	100 Hz	150 Hz	200 Hz	300 Hz	500 Hz	1000 Hz
Juveniles	100	100	100	43	16	0
Subadults	100	100	75	12	6	0

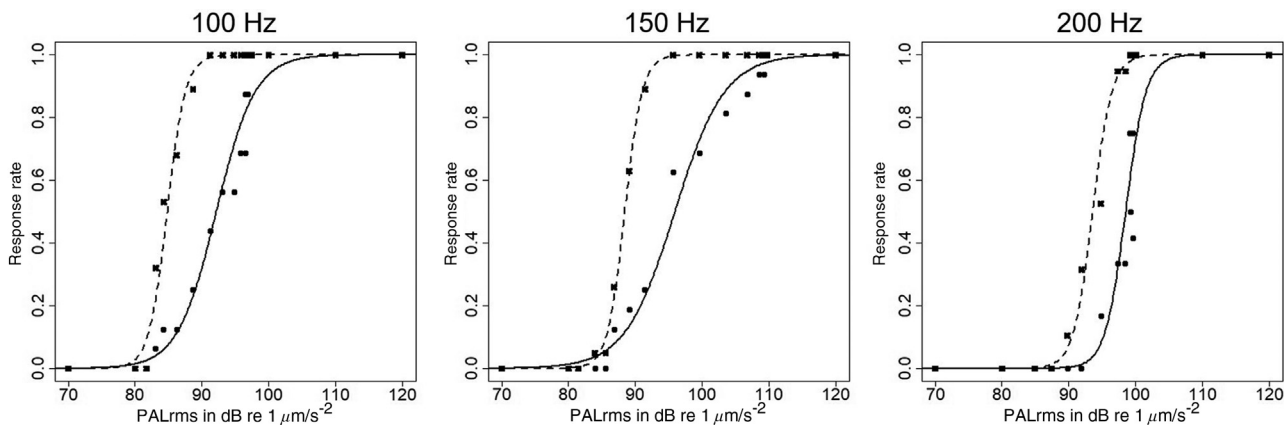


FIG. 3. Dose response curves presented as logistic regressions describing the relationships between the percentage of responding scallops and sound detection thresholds at different frequencies. Juveniles ( $n = 19$ ) are shown by dashed lines and subadults ( $n = 16$ ) are shown by continuous lines. Each point represents the value for one individual.

juveniles are more sensitive to sounds in this lower frequency range. Ontogenetic variation in auditory sensitivity was also found in blue mussels in response to substrate-borne vibrations, although the range of sizes used in this study was narrower (Roberts *et al.*, 2015). These results were expected as both larvae and juveniles are particularly sensitive stages of the complex bivalves pelago-benthic life cycle (Hunt and Scheibling, 1997). This pattern is also consistent with a recent field-based study which showed *P. magellanicus* juveniles were more sensitive to pile driving sound compared to subadults, and it demonstrates that caution should be used when extrapolating species hearing thresholds across ontogeny (Jézéquel *et al.*, 2022).

The tagged scallops permitted us to assess precise changes in valve angle during sound exposures. The results

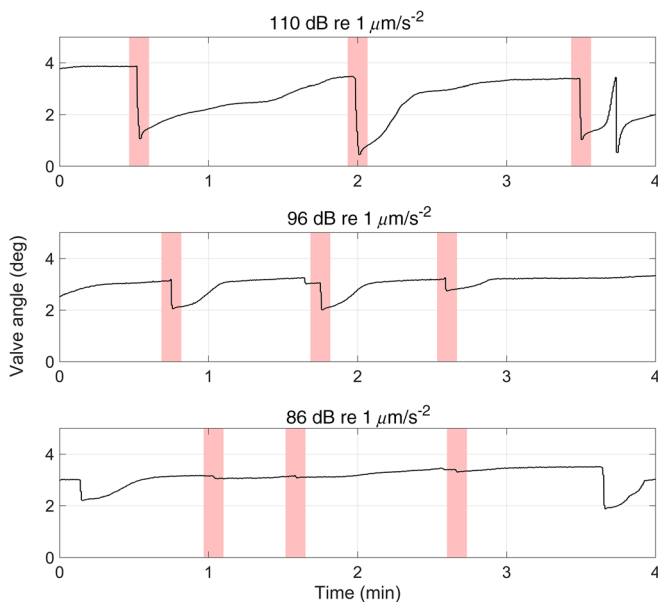


FIG. 4. (Color online) Typical example of valve angle responses from one tagged subadult scallop in response to 150 Hz stimuli played at three different sound levels. Note that the amplitudes of the valve closures decreased with sound level.

highlighted clear differences in behavioral response amplitudes depending on sound levels and frequencies. Indeed, scallops reacted significantly more (i.e., greater valve closures) to elevated sound levels (Figs. 4 and 5). In addition, at the same sound level (i.e., 96 dB re  $1 \mu\text{m/s}^{-2}$ ), scallops exhibited significantly greater valve closures in response to lower (i.e., 100 Hz) frequencies. Previous studies showed that short-duration valve closures are behavioral stresses inducing large energetic costs in scallops (Robson *et al.*, 2012). Hence, our data indicate higher stress is associated with higher acoustic particle acceleration levels and lower frequencies in scallops.

Sound sensitivity may be advantageous for bivalves, especially for detection of water- and substrate-borne vibrations from natural ambient sounds. For example, clams react to low frequency sound generated by waves, which permit them to migrate shoreward during rising tides and seaward during falling tides (Ellers, 1995). Another hypothesis could be the detection of nearby fish predator calls. However, a recent study of reef soundscape levels measured as particle acceleration levels below 80 dB re  $1 \mu\text{m/s}^{-2}$  in the 100–1000 Hz frequency band imply scallops cannot detect ambient soundfield, which was mostly composed of fish sounds (Jones *et al.*, 2022). Hence, this suggests scallops would not be able to detect nearby fish predator calls except perhaps at very close range (<1 m). More studies are needed to address the particle acceleration values and detection ranges of relevant sound cues for bivalves.

Understanding sound detection in a particular species is also informative when addressing the potential impacts of anthropogenic sound. The low frequency sound detection abilities (<500 Hz) of scallops falls within the same frequency range of most anthropogenic activities, such as shipping, pile driving, and seismic surveys (Duarte *et al.*, 2021). Despite the scarce availability of *in situ* particle acceleration measurements of anthropogenic sound sources, we can still compare scallop sound sensitivity with some recent studies. Shipping is the most pervasive underwater sound pollutant, yet data from recreational boats show PALrms would be too



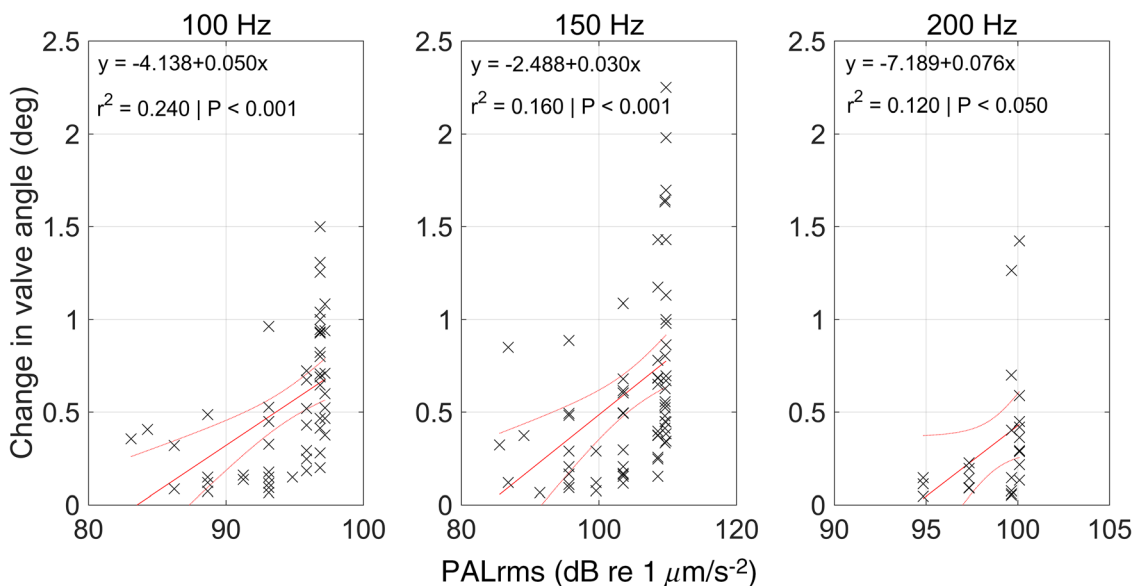


FIG. 5. (Color online) Linear relationships between subadult scallop ( $n = 16$ ) response amplitudes and sound detection thresholds (in particle acceleration levels) for different frequencies. Dashed red lines show 95% confidence intervals around the models.

low to be detectable by scallops (i.e.,  $< 80$  dB re  $1 \mu\text{m/s}^{-2}$ ) (Jones *et al.*, 2022). In addition, pile driving is associated with the construction of docks, platforms, and offshore wind farms and is of major concern primarily due to the repeated, high-intensity impulsive sound generated underwater (Dahl *et al.*, 2015). In a recent field study, scallops reacted to pile driving particle acceleration levels at a near site with higher sound levels (86 dB re  $1 \mu\text{m/s}^{-2}$ ) but not at a far site where PALrms decreased to 63 dB re  $1 \mu\text{m/s}^{-2}$  (Jézéquel *et al.*, 2022). Interestingly, the PALrms at the farther site was 20 dB lower than the sound detection thresholds found in our study, which is consistent with the non-reaction of the scallops to pile driving particle acceleration levels at this distance. However, particle acceleration levels recorded from offshore windfarm constructions are much higher amplitudes and these results suggest that scallops may be impacted over hundreds of meters from the source (Bruns *et al.*, 2014; Sigra *et al.*, 2022).

Other threats for scallops include seismic surveys that are typically used for underwater gas exploration. Sounds produce by airguns have been found to impact behavior and physiology of *Pecten fumatus* (Day *et al.*, 2017). Underwater recordings highlighted that substrate-borne vibration levels were above 100 dB re  $1 \mu\text{m/s}^{-2}$  at 3 km away from the source, with main energy below 100 Hz (McCauley *et al.*, 2021). These results suggest scallops from our study would show behavioral responses to airgun sound at kilometer scale. Taken together, our results imply different behavioral responses of scallops depending on anthropogenic sound sources and levels. Finally, the ontogenetic variation in sound sensitivity imply scallop juveniles would be more affected to anthropogenic sound compared to subadults and adults. One interesting hypothesis is the lack of acclimation of early life stages to sound compared to older life stages, where juveniles are considered “naive” to this

pollution. Hence, more studies are now needed to assess anthropogenic sound impacts on early scallop life stages (Hawkins *et al.*, 2015).

## V. CONCLUSION

Overall, this study demonstrated low frequency sound detection by scallops, with the greatest sensitivity at 100 Hz. This frequency range highlights that scallops should be able to detect an array of anthropogenic sounds, and provides evidence that sound may be a concern for this taxon (NRC, 2003). In addition, scallop sound sensitivity was life stage, intensity, and frequency dependent, which implies contrasting behavioral responses to different anthropogenic sources, and response rates may be dependent on the characteristics of the acoustic cues. A large body of literature has already shown various impacts in marine mammals, fish, and cephalopods, from temporary changes in animal behaviors to lethal impacts (Madsen *et al.*, 2006; Hawkins *et al.*, 2015; Jones *et al.*, 2020). In marked contrast, the potential impacts on bivalves and other benthically associated invertebrates are still poorly understood (Roberts and Elliott, 2017). These results on sound detection by scallops are an important step in understanding scallop sensory ecology. Further studies are now needed to assess the potential impacts of anthropogenic sound on their behaviors.

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- Akamatsu, T., Okumura, T., Novarini, N., and Yan, H. Y. (2002). "Empirical refinements applicable to the recording of fish sounds in small tanks," *J. Acoust. Soc. Am.* **112**, 3073–3082.
- Bruns, B., Stein, P., Kuhn, C., Sychla, H., and Gattermann, J. (2014). "Hydro sound measurements during the installation of large diameter offshore piles using combinations of independent noise mitigation systems," in *Proceedings of the Inter-Noise Conference*, Melbourne, Australia, pp. 1–10.
- Charifi, M., Sow, M., Ciret, P., Benomar, S., and Massabuau, J. C. (2017). "The sense of hearing in the Pacific oyster, *Magallana gigas*," *PLoS One* **12**, e0185353.
- Comeau, L. A., Babarro, J. M., Longa, A., and Padin, X. A. (2018). "Valve-gaping behavior of raft-cultivated mussels in the Ría de Arousa, Spain," *Aquac. Rep.* **9**, 68–73.
- Dahl, P. H., de Jong, C. A., and Popper, A. N. (2015). "The underwater sound field from impact pile driving and its potential effects on marine life," *Acoust. Today* **11**, 18–25.
- Day, R. D., McCauley, R. D., Fitzgibbon, Q. P., Hartmann, K., and 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**, E8537–E8546.
- Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., Erbe, C., Gordon, T. A., Halpern, B. S., Harding, H. R., Havlik, M. N., Meekan, M., Merchant, N. D., Miksis-Olds, J. L., Parsons, M., Predragovic, M., Radford, A. N., Radford, C. A., Simpson, S. D., Slabbekoorn, H., Staaterman, E., Van Opzeeland, I. C., Winderen, J., Zhang, X., and Juanes, F. (2021). "The soundscape of the Anthropocene Ocean," *Science* **371**, eaba4658.
- Ellers, O. (1995). "Discrimination among wave-generated sounds by a swash-riding clam," *Biol. Bull.* **189**, 128–137.
- Goodall, C., Chapman, C., and Neil, D. (1990). "The acoustic response threshold of the Norway lobster, *Nephrops norvegicus* (L.) in a free sound field," in *Frontiers in Crustacean Neurobiology*, edited by K. Wiese, W.-D. Krenz, J. Tautz, H. Reichert, and B. Mulloney (Birkhauser, Basel), pp. 106–113.
- Hawkins, A. D., Pembroke, A. E., and Popper, A. N. (2015). "Information gaps in understanding the effects of noise on fishes and invertebrates," *Rev. Fish Biol. Fish.* **25**, 39–64.
- Hubert, J., Booms, E., Witbaard, R., and Slabbekoorn, H. (2022). "Responsiveness and habituation to repeated sound exposures and pulse trains in blue mussels," *J. Exp. Mar. Biol. Ecol.* **547**, 51668.
- Hunt, H. L., and Scheibling, R. E. (1997). "Role of early post-settlement mortality in recruitment of benthic marine invertebrates," *Mar. Ecol. Prog. Ser.* **155**, 269–301.
- Jézéquel, Y., Jones, I. T., Bonnel, J., Chauvaud, L., Atema, J., and Mooney, T. A. (2021). "Sound detection by the American lobster (*Homarus americanus*)," *J. Exp. Biol.* **224**, jeb240747.
- Jézéquel, Y., Cones, S., Jensen, F. H., Brewer, H., Collins, J., and Mooney, T. A. (2022). "Pile driving repeatedly impacts the giant scallop (*Placopecten magellanicus*)," *Sci. Rep.* **12**(1), 11.
- Jones, I. T., Gray, M. D., and Mooney, T. A. (2022). "Soundscapes as heard by invertebrates and fishes: Particle acceleration measurements on coral reefs," *J. Acoust. Soc. Am.* **152**, 399–415.
- Jones, I. T., Stanley, J. A., and Mooney, T. A. (2020). "Impulsive pile driving noise elicits alarm responses in squid (*Doryteuthis pealeii*)," *Mar. Pollut. Bull.* **150**, 110792.
- Kastelein, R. A. (2008). "Effects of vibrations on the behaviour of cockles (bivalve molluscs)," *Bioacoustics* **17**, 74–75.
- Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., and Gattuso, J. P. (2013). "Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming," *Global Change Biol.* **19**(6), 1884–1896.
- Ladich, F., and Fay, R. R. (2013). "Auditory evoked potential audiometry in fish," *Rev. Fish Biol. Fish.* **23**, 317–364.
- Madsen, P. T., Wahlberg, M., Tougaard, J., Lucke, K., and Tyack, A. P. (2006). "Wind turbine underwater noise and marine mammals: Implications of current knowledge and data needs," *Mar. Ecol. Prog. Ser.* **309**, 279–295.
- McCauley, R. D., Meekan, M. G., and Parsons, M. J. (2021). "Acoustic pressure, particle acceleration, and induced ground acceleration signals from a commercial seismic survey array and potential implications for environmental monitoring," *J. Mar. Sci. Eng.* **9**, 571–592.
- Mooney, T. A., Hanlon, R. T., Christensen-Dalsgaard, J., Madsen, P. T., Ketten, D. R., and Nachtigall, P. E. (2010). "Sound detection by the long-fin squid (*Loligo pealeii*) studied with auditory evoked potentials: Sensitivity to low-frequency particle acceleration and not pressure," *J. Exp. Biol.* **213**, 3748–3759.
- Mosher, J. I. (1972). "The responses of *Macoma balthica* (Bivalvia) to vibrations," *J. Molluscan Stud.* **40**, 125–131.
- Nagai, K., Honjo, T., Go, J., Yamashita, H., and Oh, S. J. (2006). "Detecting the shellfish killer *Heterocapsa circularisquama* (Dinophyceae) by measuring bivalve valve activity with a Hall element sensor," *Aquaculture* **255**, 395–401.
- Newell, R. I. (2004). "Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review," *J. Shellfish Res.* **23**, 51–62.
- NRC (2003). *Ocean Noise and Marine Mammals* (The National Academies Press, Washington, DC).
- Popper, A. N., and Hawkins, A. D. (2018). "The importance of particle motion to fishes and invertebrates," *J. Acoust. Soc. Am.* **143**, 470–488.
- 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., and Halvorsen, M. B. (2014). "Sound exposure guidelines for fishes and sea turtles: A technical report prepared by ANSI-accredited standards committee S3/SC1 and registered with ANSI," *Spinger Briefs Oceanography* **2**, 23–32.
- Roberts, L., Cheesman, S., Breithaupt, T., and Elliott, M. (2015). "Sensitivity of the mussel *Mytilus edulis* to substrate-borne vibration in relation to anthropogenically generated noise," *Mar. Ecol. Prog. Ser.* **538**, 185–195.
- Roberts, L., and Elliott, M. (2017). "Good or bad vibrations? Impacts of anthropogenic vibration on the marine epibenthos," *Sci. Total Environ.* **595**, 255–268.
- Robson, A. A., Chauvaud, L., Wilson, R. P., and Halsey, L. G. (2012). "Small actions, big costs: The behavioural energetics of a commercially important invertebrate," *J. R. Soc. Interface* **9**, 1486–1498.
- Rogers, P. H., Hawkins, A. D., Popper, A. N., Fay, R. D., and Gray, M. D. (2016). "Parvulescu revisited: Small tank acoustics for bioacousticians," in *The Effects of Noise on Aquatic Life II*, edited by A. N. Popper and A. D. Hawkins (Springer, New York), pp. 933–941.
- Sigray, P., Linné, M., Andersson, M. H., Nöjd, A., Persson, L. K. G., Gill, A. B., and Thomsen, F. (2022). "Particle motion observed during offshore wind turbine piling operation," *Mar. Pollut. Bull.* **180**, 113734.
- Wale, M. A., Briers, R. A., and Diele, K. (2021). "Marine invertebrate anthropogenic noise research—Trends in methods and future directions," *Mar. Pollut. Bull.* **173**, 112958.
- Wijsman, J. W. M., Troost, K., Fang, J., and Roncarati, A. (2019). "Global production of marine bivalves. Trends and challenges," in *Goods and Services of Marine Bivalves*, edited by A. D. Small, J. G. Ferrerira, J. Grant, J. K. Petersen, and O. Strand (Springer, Cham, Switzerland), pp. 7–26.
- Williams, R., Wright, A. J., Ashe, E., Blight, L. K., Brintjes, R., Canessa, R., Clark, C. W., Cullis-Suzuki, S., Dakin, D. T., Erbe, C., and Hammond, P. S. (2015). "Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management," *Ocean Coast. Manag.* **115**, 17–24.
- Wilson, R., Reuter, P., and Wahl, M. (2005). "Muscling in on mussels: New insights into bivalve behaviour using vertebrate remote-sensing technology," *Mar. Biol.* **147**, 1165–1172.