# Longfin squid reproductive behaviours and spawning withstand wind farm pile driving noise

**Ian T. Jones** ⓘ[1,2,*,‡]**, Madison Schumm**[1,§]**, Jenni A. Stanley**[1,¶]**, Roger T. Hanlon**[3]**, and T. Aran Mooney**[1]

[1]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[2]Massachusetts Institute of Technology-Woods Hole Oceanographic Institution Joint Program in Oceanography/Applied Ocean Science and Engineering, Cambridge and Woods Hole, MA 02139, USA
[3]Marine Biological Laboratory, Woods Hole, MA 02543, USA

*Corresponding author: tel: +1 603 862 0092;* e-mail: ian.t.jones@unh.edu.
‡ Present address: Center for Acoustics Research and Education, University of New Hampshire, Durham, NH 03824, USA.
§ Present address: University of Texas at Austin, Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, USA.
¶ Present address: University of Waikato, Tauranga 3110, New Zealand.

Pile driving noise is an intense, repetitive, far-reaching sound that is increasing in many coastal habitats as the offshore wind energy industry expands globally. There is concern for its impacts on keystone species and vital fisheries taxa such as squids. In controlled laboratory conditions, we investigated whether exposure to pile driving noise from offshore wind farm construction altered reproductive behaviours in the short-lived semelparous species *Doryteuthis pealeii*. Pile driving noise had no significant effects on the occurrence rates of agonistic behaviours, mate guarding, mating, and egg laying, compared with silent control trials. The results contrast starkly with behavioural response rates of the same squid species during feeding and shoaling. The data suggest that squid reproductive behaviours may be resilient to this increasingly pervasive environmental stressor, and that behavioural context guides responses to windfarm noise for this invertebrate taxon. While some non-reproductive behaviours can clearly be disturbed, the results show that species with limited opportunity to reproduce can tolerate intense stressors to secure reproductive success.

**Keywords:** aggression, anthropogenic noise, cephalopod, marine invertebrate, mating, offshore wind.

## Introduction

Humans are increasingly utilizing and developing coastal environments, with many activities having the potential to impact marine taxa. The offshore wind energy industry is expanding globally, inducing concern over how anthropogenic noise pollution associated with construction, operation, and maintenance of wind farms will adversely impact aquatic wildlife (Mooney *et al.*, 2020). Support vessels, sonars used for seismic surveys, construction equipment, and operational turbines emit anthropogenic noise during offshore wind farm development (Mooney *et al.*, 2020). Impact pile driving during construction is considered the most intense and pervasive noise (Amaral *et al.*, 2020). Pile driving involves repeated hammering of cylindrical piles into the seabed to support foundations for wind turbines, generally for those in water shallower than 60 m (Musial *et al.*, 2019). It is a widespread noise source as pile driving is used not only for installation of windfarm turbine pilings, but also within harbours and coastal areas for a myriad of construction activities, in sum making it a sound of primary concern. To minimize negative impacts to marine life, studies investigating effects of pile driving noise on animal behaviours are crucial, especially behaviours that have direct implications for survival and reproduction.

Many studies have demonstrated effects of pile driving and other noise sources on the behaviour of marine mammals and fish (Bruintjes *et al.*, 2016; Nedelec *et al.*, 2017; Graham *et al.*, 2019), but far fewer have studied effects on marine invertebrates (Wale *et al.*, 2021). Among fish, impulsive (i.e. short and pulsed) noise alters group cohesion and swimming dynamics of European seabass shoals (*Dicentrarchus labrax*; Neo *et al.*, 2015, 2016; Herbert-Read *et al.*, 2017). Fish exposed to pile driving noise also suffer temporary injuries to hearing structures and organs in close proximity to swim bladders (Casper *et al.*, 2013a, 2013b). For invertebrates (a diverse group of taxa), substrate vibrations (as opposed to water-borne noise) from pile driving cause filter-feeding scallops (*Placopecten magellanicus*) to reduce valve gape, (Jézéquel *et al.*, 2022), elicit startle behaviours in hermit crabs (*Pagurus bernhardus*; Roberts *et al.*, 2016) and impair hermit crabs' (*Pagurus acadianus*) abilities to find key resources, i.e. empty shells (Roberts and Laidre, 2019).

There are fewer comparable data regarding impacts of far-reaching water-borne pile driving sound on invertebrates. The limited knowledge regarding impacts on numerous ecologically vital invertebrate taxa is both a concern and a risk as offshore windfarm construction progresses (Gedamke *et al.*, 2016; Mooney *et al.*, 2020). Furthermore, while ecological and behavioural contexts have been argued as critical to the management of anthropogenic noise pollution faced by marine mammals (Ellison *et al.*, 2012; Harris *et al.*, 2018), such context-based approaches have not been addressed for most other marine taxa, including invertebrates.

Given this paucity of data, it is particularly important to examine anthropogenic noise impacts on cephalopods (in-

cluding squid, cuttlefish, and octopuses) in part because of their high ecological and commercial relevance. They made up 4.5% of global capture production (tonnes) and 6.2% of global fishery export values (USD) from 2012 to 2018 (FAO, 2021), and are key central trophic links in food webs (Boyle and Rodhouse, 2005a, 2005b). Squid can constitute >50% of regional seabird diets and up to 95% of odontocete diets (Boyle and Rodhouse, 2005a). Longfin squid (*Doryteuthis pealeii*) on the east coast of USA are of particular concern with respect to potential impacts of wind farm construction. Commercially, this species has average annual landings of ∼11000 mt and annual values of $30 million since 2010 (NMFS, 2021). Lease areas for offshore windfarms in the northeast United States overlap or are adjacent to inshore spawning and fishing areas for *D. pealeii* (MARCO, 2021), and construction is currently underway or is planned to begin within many of these areas by 2025 (Musial *et al.*, 2020; BOEM, 2021). These squid detect and behaviourally respond to sounds at frequencies <1000 Hz (Mooney *et al.*, 2010, 2016), suggesting sound-sensitivity that overlaps with the typical peak frequencies of pile driving noise. Ecological functions of cephalopods' sound detection are unknown; however, they are thought to utilize sound and vibration for predator avoidance (Hanlon and Messenger, 2018) and possibly for developing an "auditory scene" to orient to and navigate in their environment, as has been discussed for fish (Fay, 2009; York and Bartol, 2014).

Moreover, key studies of their behaviour, reproduction, and sound-sensitivity provide a vital foundation enabling this taxon to act as a model to address invertebrate noise impacts. Several studies have reported disruptive behavioural and physical effects of anthropogenic noise on cephalopods. Squid display alarm responses normally utilized for predator evasion, such as inking and jetting, during air gun (*Sepioteuthis australis*) and pile driving noise (*D. pealeii*; Fewtrell and McCauley, 2012; Jones *et al.*, 2020; Cones *et al.*, 2022). These alarm responses are dramatic, brief, and typically limited to the first few impulses during a pile driving period, and disruptive to the animals' gate during that time (Cones *et al.*, 2022). Pile driving noise also causes *D. pealeii* to cease their pursuit of prey (Jones *et al.*, 2021). Additionally, noise may cause physical damage to cephalopods' sound detection structures (statocysts; André *et al.*, 2011; Solé *et al.*, 2013, 2017). To the authors' knowledge, to date no studies have addressed impacts of anthropogenic noise on reproductive behaviours of cephalopods, nor any marine invertebrate.

Like many cephalopods, *D. pealeii* is short-lived, and has an average lifespan of less than a year (Brodziak and Macy, 1996; Macy and Brodziak, 2001), mating for a short time period from May to October. Although they can mate and lay eggs multiple times over several weeks (Maxwell *et al.*, 1998; Hanlon *et al.*, 2013), they are considered semelparous because they only breed for one season then senesce, making mating events highly important to individual fitness (Shashar and Hanlon, 2013). Complex behavioural dynamics are associated with inshore mating and spawning of *D. pealeii* around communal egg beds and spawning dynamics are well described (Shashar and Hanlon, 2013; Hanlon and Messenger, 2018). Briefly, females lay many gelatinous capsules containing eggs into the substrate; these form large bundles called "egg mops". Males are visually attracted to and approach egg mops. The capsules contain a contact pheromone that elicits heightened aggression in males, leading to subsequent agonistic behaviours

as they fight to compete for female mates (Buresch *et al.*, 2003, 2004; Cummins *et al.*, 2011). Males take on flexible mating roles according to their size relative to nearby males, and their success or failure in agonistic bouts (Hanlon *et al.*, 1997; Shashar and Hanlon, 2013). "Consort males" (usually larger males) will pair with and swim parallel to a female, and "guard" her from other males. Consort males perform the majority of successful mating. "Sneaker males" are usually smaller and keep their distance from larger males, but quickly jet towards a female and occasionally achieve a successful mating. The complexity of this dynamic mating system rivals that of most vertebrates.

The present study investigated anthropogenic noise impacts on reproductive behaviours of small mixed-sex groups of longfin squid *Doryteuthis pealeii*, via controlled laboratory experiments using underwater playbacks of pile driving sound recorded during wind farm construction. To determine whether this noise impacted reproduction, we measured a suite of reproductive behaviours including: mate guarding (when consort males actively position themselves between a female and other males and defend that female resource), as well as male–male agonistic behaviours, mating, and egg laying. To evaluate behavioural context-dependent effects, we compared the response rates during reproductive activities to those of parallel studies with similar methods addressing noise-induced disturbances during feeding and resting (Jones *et al.*, 2020, 2021).

## Methods

### Animal husbandry

Squid were collected by trawl in Vineyard Sound, MA, USA, from May to July 2019 by the Marine Biological Laboratory (Woods Hole, MA, USA). Squid were transported to the nearby Environmental Systems Lab (ESL) at Woods Hole Oceanographic Institution and housed in flowing-seawater tanks prior to testing. Males and females were kept in separate tanks and male squid were further separated by relative size ("large" and "small"). Water temperature in holding tanks was maintained at 18–20°C and squid were exposed to a natural light cycle. Squid were fed killifish (*Fundulus* spp.) *ad libitum* daily and kept in holding tanks for 1–5 days before experimentation. Only visibly healthy squid with minimal skin damage were tested. All procedures regarding use of animals in research followed local guidelines and were approved by the Woods Hole Oceanographic Institution's Institutional Animal Care and Use Committee (approval to TAM).

### Experimental setup

Experiments occurred in a cylindrical, 1.8-m-diameter tank (Figure 1) in the ESL between sunrise and sunset, when *D. pealeii* are reproductively active (Shashar and Hanlon, 2013). Water was maintained at a depth of 0.82 m and temperature of 18.0 ± 1.2°C (mean ± *SD*). A slow water inflow maintained tank temperature and high dissolved oxygen levels. The bottom of the tank had a 3-cm layer of sand. An Aqua-30 speaker (DNH, Netherlands; frequency response: 0.08–20 kHz) and hydrophone (High Tech Inc., USA; sensitivity: −165 dB re 1 V/μPa; frequency response: 0.002–30 kHz) were inserted into the tank to project and monitor sound, respectively, during experiments. The speaker was positioned hor-
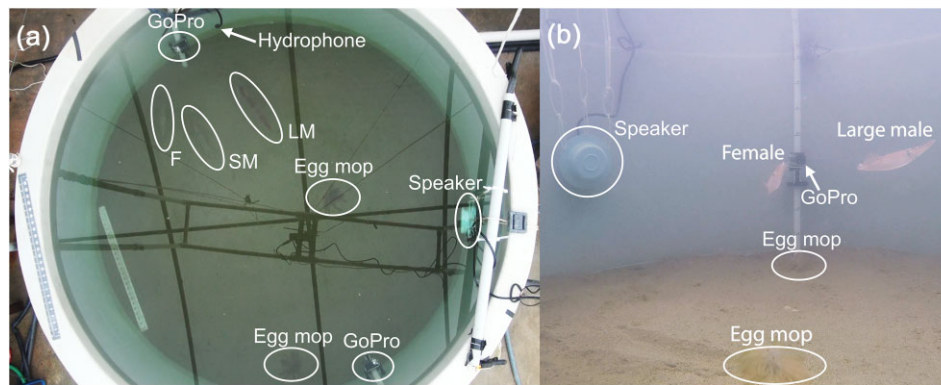
**Figure 1.** Top–down (a) and underwater (b) views of the experiment tank, showing locations of the underwater cameras (GoPro), hydrophone, speaker, egg mops, and squid (F = female, SM = small male, LM = large male). The reflection of scaffolding holding the overhead camera is visible on the water surface in (a). The top–down view was used for real-time monitoring during experiments, whereas the underwater footage was used for quantitative behaviour analyses.

izontally at mid-depth (0.41 m), 12 cm forward of the tank wall behind it, and its main axis of projection faced the centre of the tank. The hydrophone was placed at mid-depth, 5 cm from the tank wall, and 150 cm away from the speaker. The hydrophone was connected to a SoundTrap ST4300 acoustic recorder (Ocean Instruments, NZ; 4 dB gain) located outside the tank. Trials were recorded with an overhead camera (Sony Handycam HDR-XR550), and two underwater cameras (Go-Pro Hero 4) facing each other from opposing sides of the tank at mid-depth, so that video of the entire inside of the tank was captured.

## Mate guarding experiment

During experiments, squid were exposed to either 5-min long pile driving playbacks or 5-min long silent control playbacks (hereafter referred to as "pile" and "control" trials, respectively). Originally, pile driving impulses recorded in the field had inter-pulse intervals of about ∼1.8 s, peak-to-peak amplitudes of 194 dB re 1 $\mu$Pa, and were recorded from a hydrophone array 500 m away from a pile driven for the Block Island Wind Farm, 1 m above the seabed, in water 26 m deep (Amaral *et al.*, 2018, 2020). These field data, along with particle acceleration calculated from hydrophones in the field, were provided to the authors (see "Acknowledgements"). Three separate playback files were prepared using Adobe Audition (version 3.0): First, an ∼1-min long sequence of 30 pile impulses was sampled from the original field audio data. These 30 impulses had equal peak–peak amplitude to each other. This file was then edited to have a consistent inter-pulse interval of 2 s, resulting in a length of 1 min. To avoid pseudoreplication of playback stimuli, three new 1-min long files were created by rearranging the 30 pile impulses in different random orders. Finally, each of the three 1-min files was copied and pasted five times, resulting in a 5 min duration for each playback file. See the supplementary information (Supplementary Figure S1) for a diagrammatic description of this playback file preparation.

Squid were tested in groups of three, consisting of a large male, a small male, and a female, with respective mean ± *SD* mantle lengths of 22.5 ± 3.3 cm, 15.6 ± 2.2 cm, and 14.3 ± 1.5 cm. Mantle lengths of each large male and small male pair differed by at least 3.5 cm (mean ± *SD*: 6.9 ± 2.1). Field and lab studies show that large males act

as consorts, and small males act as sneakers when large males are present (Hanlon *et al.*, 1997; Shashar and Hanlon, 2013). All cameras were in place and recording before squid were added to the experiment tank. Squid were added sequentially to the tank at intervals of 2 min in a consistent order of large male, small male, then female. Immediately following the addition of the female to the tank, the SoundTrap was turned on to start monitoring sound levels in the tank. Two minutes after the female was added, an egg mop was added to the centre of the tank, and a second egg mop was added near the tank wall (approximately a quarter of the tank's circumference away from the speaker). The addition of the egg mops marked the start time of each trial. Egg mops induced male aggression and mate guarding (Buresch *et al.*, 2003; Cummins *et al.*, 2011).

Fifty-five trials were conducted. Of these, 30 trials had males that mate guarded (15 pile trials, 15 control trials) and were used for analyses; squid that did not mate guard were not played noise or control files and were excluded from analysis to avoid biasing results with individuals not motivated to reproduce. For all trials, squid were given at least 10 min to habituate to the experiment tank before starting playback. An experimenter was stationed out of view of the squid and watched the trial on a screen to monitor the occurrence of mate guarding. Criteria for mate guarding were that the male remained within two body lengths of the female and actively positioned itself between the female and other male (Shashar and Hanlon, 2013). Playback was started when mate guarding was observed occurring for 15 s continuously (after the 10-min habituation period had passed). Although this meant the duration between the start of the trial and start of the first playback varied (median [IQR]: 14.3 [11.1–21.3] min), this playback start criterion was chosen because the experimental design was focused primarily on testing whether noise disrupted mate guarding. Fast habituation (reduced response over time to the repeated noise) within 1 min of noise exposure was anticipated based on observations of individual squids' startle responses to pile driving in an earlier study (Jones *et al.*, 2020). To test for potential habituation, playbacks were repeated up to three times if squid resumed mate guarding after the first and second exposure, with a minimum of 10 min of quiet (i.e. no playback) in between. Only one control trial and one pile trial had a single playback period; the remaining 28 trials had three playback periods. Agonistic behaviours, in-

cluding the number of chases (forward acceleration in pursuit of another squid) and lunges (forward acceleration followed by attempt to grab another squid) by males were also quantified, as defined previously (Cummins *et al.*, 2011).

Two trained observers (50% overlap of analysed trials) watched videos and recorded time spent mate guarding, number of chases, and number of lunges during 5-min-long "playback" periods, and 5-min-long periods just preceding the second and third playback periods ("quiet1" and "quiet2", respectively). Inter-observer reliability was high for both mate guarding and agonistic behaviours ($r > 0.96$, Pearson correlation). Mating and egg-laying events were also scored by an observer who watched the entire (1–2 h) duration of each trial.

### Acoustic calibration of the experimental tank

Mapping of the sound field in the experimental tank involved similar methods and instrumentation used in prior studies (Jones *et al.*, 2020, 2021). Briefly, 1 min of a pile driving file (same as used in experiments) was played through the speaker and recorded in 20 cm increments in all three dimensions (240 recording positions total). Cephalopods detect acoustic particle acceleration rather than pressure (Budelmann, 1992; Budelmann and Tu, 1997; Mooney *et al.*, 2010), therefore, particle acceleration was recorded, as well as sound pressure for comparison with other studies. Recording instruments were affixed at the end of a PVC probe in the following configuration: a PCB triaxial accelerometer (model W356B11, frequency response: 0.5 Hz–5 kHz, sensitivity of each axis: 1.04 mV/m s$^{-2}$) was centred at the recording position, and a Reson hydrophone (model TC4013, frequency response: 1 Hz–170 kHz, sensitivity: −211 dB re 1 V/$\mu$Pa) was spaced 1.5 cm to the left of the accelerometer (facing the speaker).

Acoustic data analyses were performed following previous methods (Jones *et al.*, 2020), and are briefly summarized here. Zero-to-peak levels of individual pile pulses, in decibels (dB), were calculated for particle acceleration ($SAL_{z-pk}$) and sound pressure ($SPL_{z-pk}$) as follows:

$$SAL_{z-pk} \text{ or } SPL_{z-pk} = 20*\text{Log}_{10}\left(X_{pk}\right),$$

where $X_{pk}$ is the maximum absolute acceleration ($\mu$m s$^{-2}$) or pressure ($\mu$Pa). For simplicity, the 3D vector (Euclidean) norm of particle acceleration was calculated, and its magnitude is reported. Power spectral density (PSD) was calculated to visualize these magnitudes across frequencies. All acoustic metrics were limited to 20–1000 Hz, encompassing the hearing range of *D. pealeii*. Acoustic analysis results can be found in the electronic Supplementary Material, which show the underwater speaker in the experiment tank projected lower pressure but similar particle acceleration levels to those recorded in the field.

### Statistical methods

Statistics were performed in R version 4.0.4 using the lme4 (Bates *et al.*, 2015), car (Fox and Weisberg, 2019), and glmmTMB (Brooks *et al.*, 2017) packages. The significance threshold for all tests was $\alpha = 0.05$. Generalized linear mixed effects models (GLMMs) were used to fit mate guarding and agonistic data with repeated measures. Proportion of time spent mate guarding was fit with a beta distribution, and counts of chases and lunges were fit with a negative binomial

distribution. Treatment (pile vs. control) and period ("playback" periods 1, 2, and 3, and "quiet" periods 1 and 2) were included as main effects and squid individual was a random effect. Interactions between treatment and period were kept in final models if they were significant. Model best fit was selected according to Akaike information criteria (AIC). Post-hoc Wald type II $\chi^2$ tests were used to test significance of fixed factors.

## Results

### Sound field of experiment tank

The sound field of pile driving playback in the experiment tank was spatially variable, with highest zero-to-peak levels (up to 145 dB re 1 $\mu$m s$^{-2}$) nearest the speaker, and a 20–40 dB drop-off horizontally towards the centre of the tank). See the supplementary information (Supplementary Figure S2a) for detailed results of acoustics in the experiment tank.

### Mate guarding

Large males mate guarded the female squid in 25 of the 30 trials (12 control, 13 pile), and the small male mate guarded in eight trials (5 control, 3 pile). In three trials (2 control, 1 pile), the small male mate guarded first, then the large male later took over as consort and mate guarded for the rest of the trial. The consort role shift in the pile treatment took place before playback1, and the role shifts in the two control trials took place during playback2 and quiet2 periods. The number of mate-guarding small males was too low to perform GLMMs, including all period and treatment groups, thus statistics were limited to large males.

There was no significant effect of the pile driving sound on time spent mate guarding by large males. Inter-quartile ranges of time spent mate guarding in pile and control treatments largely overlapped, whether comparing these treatments within playback periods, within quiet periods, or comparing playback and quiet periods within a given sound treatment (Figure 2). This reflects the similarity of behaviours in noise vs. quiet conditions, despite the high amplitude pile driving sound (Supplementary Figure S2). Analysing all large males (Figure 2), period was a significant factor ($\chi^2 = 10.01$, df = 4, $p = 0.04$), treatment was not significant ($\chi^2 = 0.88$, df = 1, $p = 0.35$), and the interaction between period and treatment was significant ($\chi^2 = 14.0$, df = 4, $p < 0.01$; Supplementary Table S1). Post-hoc Tukey tests revealed the significant interaction was most likely driven by differences among periods in control trials: playback2 vs. playback1 ($p = 0.017$), quiet2 vs. playback1 ($p = 0.002$), and quiet2 vs. quiet1 ($p = 0.049$). We analysed large males in trials where small males did not mate guard to determine whether the significant period effect may have been due to consort role shifts from the small male to large male. In this subset of trials ($n = 10$ control, $n = 12$ pile), period was not a significant factor ($\chi^2 = 2.69$, df = 4, $p = 0.61$), nor was treatment ($\chi^2 = 0.01$, df = 1, $p = 0.93$; Supplementary Table S2). This suggests that the delay of two control large males in taking on a consort role led to the significant period factor and significant interaction between period and treatment for data in Figure 2. Overall, these results suggested that consort males' time spent mate guarding was not significantly affected by noise, and that the increase over time of mate guard-
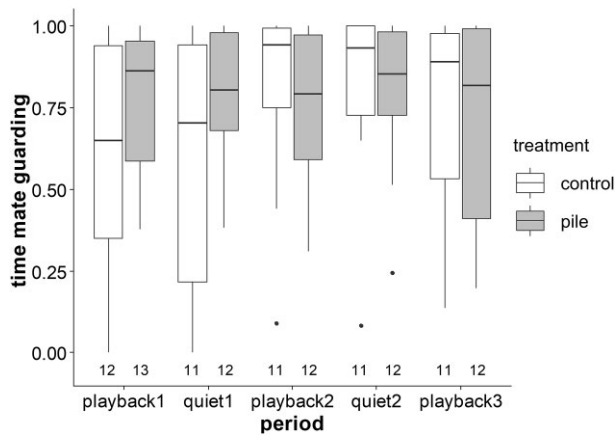
**Figure 2.** Proportion of time spent mate guarding in playback and between-playback (quiet) time periods for large males. Periods each had 5 min duration and are listed in the sequence they were presented to the squid. Numbers under each box are sample sizes. Horizontal lines represent medians, boxes extend from the 25th to 75th percentile, and dots represent outliers, defined as values <1.5 times the inter-quartile range.

ing in control trials was likely influenced by variation of individual male squid behaviour rather than the squids' acoustic environment.

## Agonistic behaviours

Pile driving noise did not have a significant effect on the agonistic behaviours of large males, in terms of number of chases and number of lunges towards competing males (Figure 3). For number of chases, neither period ($\chi^2 = 1.43$, df $= 4$, $p = 0.84$) nor treatment ($\chi^2 = 1.88$, df $= 1$, $p = 0.17$) were significant factors (Supplementary Table S3). Similarly, for number of lunges, period ($\chi^2 = 1.05$, df $= 4$, $p = 0.90$) and treatment ($\chi^2 = 0.19$, df $= 1$, $p = 0.67$) were not significant (Supplementary Table S4). There were no significant interactions between periods and treatment for chase or lunge behaviours. Small males did not chase or lunge at large males. Overall, these results indicated that aggressive behaviours of male squid were unaffected by the noise treatment.

## Mating and egg laying

Mating and egg laying continued to occur during and after noise exposure. Mating occurred in 30% of trials (5 control, 4 pile), and was always between the large male and female. Mating between a given consort pair occurred once in six trials, twice in two trials, and thrice in one trial. There was no significant difference in duration of mating events between pile and control trials (U $= 18$, $p = 0.10$, Mann–Whitney U test). Overall, the median duration of the typical male parallel mating position was 17 s (IQR: 15–18), and durations ranged from 9 to 33 s, within those observed in squid in the wild (Shashar and Hanlon, 2013). In two pile trials, noise playback (playback1 or playback3) started during mating, and mating continued. The durations of these two mating events were 18 and 28 s, within the duration range of mating events that occurred in "quiet" periods and control playbacks. Egg laying (by females) also occurred after mating at statistically similar rates in pile and control trials (mean ± SD: 0.90 ± 0.30, and 0.74 ± 0.14

eggs capsules min$^{-1}$, respectively; U $= 21$, $p = 0.41$, Mann–Whitney U test).

## Discussion

### Resilience of reproductive behaviours during noise

Here, we present the first empirical dataset addressing the potential effects of anthropogenic noise on reproductive behaviours of a marine invertebrate. Overall, there was no indication that the high-intensity, repeated pile driving noise impacted any of the suite of reproductive behaviours measured, including agonistic, mate guarding, mating, or egg-laying behaviours. Typical behavioural dynamics (Shashar and Hanlon, 2013) of sexually active longfin squid continued to occur despite the repeated, high-intensity, impulsive noise treatment. These results are perhaps surprising given the array of impacts seen in other behaviours of cephalopods and in other taxa (Mooney et al., 2020); however, they underscore the exceptionally strong motivation of these squid to reproduce. Squid engaging in these behaviours are nearing the end of their brief lifespan; females may continue to mate with multiple males and spawn over a few weeks, but both sexes will soon senesce (Maxwell and Hanlon, 2000; Hanlon et al., 2013). From an evolutionary standpoint, persistence of reproductive behaviours during environmental stressors is advantageous for species with limited opportunity to reproduce in their lifetime. The present results are consistent with theory that reproductive behaviours of semelparous species should be relatively uninfluenced from potentially inhibitory effects of stress (Wingfield and Sapolsky, 2003; de Jong et al., 2020). Based on these data, one might conclude that mating behaviours of semelparous species are at a lower risk of adverse effects from noise exposure.

It is not possible to generalize these trends to all semelparous species, all cephalopods, or all noise types, since responses may be specific to species and noise characteristics. For instance, females of one semelparous goby species (Pomatoschistus microps) significantly delayed their inspection of nests, delayed spawning, and laid fewer eggs during noise from air stones (Blom et al., 2019). These differences only occurred when gobies were presented with continuous, rather than impulsive, noise. It is possible that longfin squid behaviours in the present study may have differed if presented a different noise type (e.g. boat noise). Based on studies of fish, continuous noise with irregular amplitude and frequency characteristics is thought to be more likely to cause stress compared to impulsive sounds that have more consistent amplitude and frequency spectra (de Jong et al., 2020). Impulses played in the present study were similar to each other in amplitude and spectra and may be considered "regular", although amplitudes received by squid varied spatially in the tank. Effects of continuous or irregular noise on squid behaviour remain to be tested. Considering species with currently published particle motion audiograms, cephalopods tend to have lower particle acceleration sensitivities (higher thresholds) than many fish species (Horodysky et al., 2008; Wysocki et al., 2009; Mooney et al., 2010, 2016; Wright et al., 2011; Samson et al., 2014). Such differences in hearing sensitivity could also contribute to different responses to noise across taxa, although this should not be assumed a priori (Hawkins and Popper, 2018).

Laboratory-based studies allow detailed observation of behaviour in a well-controlled environment without confound-
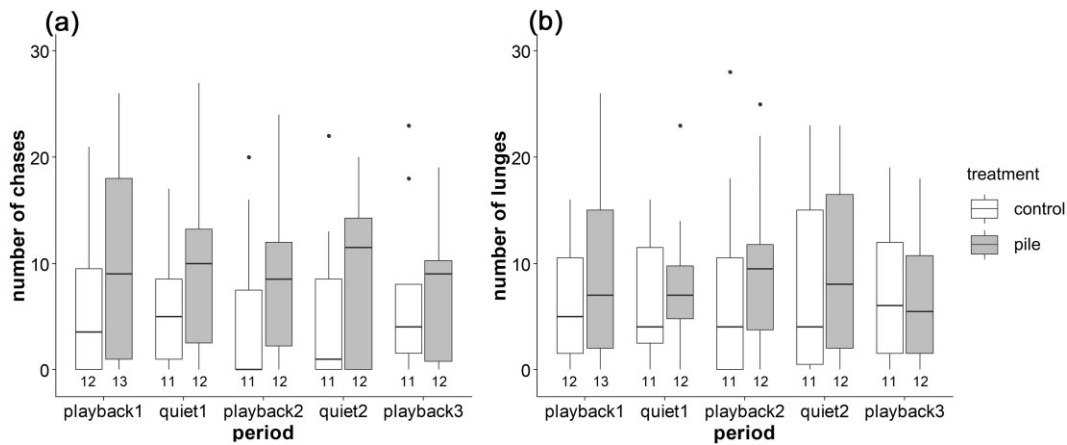
**Figure 3.** (a) Number of chases, and (b) number of lunges towards small males by the same large males shown in Figure 2, in playback and between-playback (quiet) time periods. Periods each had 5 min duration and are listed in the sequence they were presented to the squid. Numbers under each box are sample sizes. Horizontal lines represent medians, boxes extend from the 25th to 75th percentile, and dots represent outliers, defined as values >1.5 times the inter-quartile range.

ing influence of extraneous noise sources and other environmental factors. Peak particle acceleration levels in the experiment tank (see electronic Supplementary Material) were similar to or exceeded those measured at 500 m from Block Island Wind Farm piles (1 m above seabed, 26 m depth), thus representing acceleration levels predicted within a 500-m radius (Amaral et al., 2018). Importantly, sound propagation from piles depends on multiple engineering and environmental factors, including pile dimensions, angle with respect to the seabed, hammer strike energy, bathymetry, sediment properties, and seasonally dependent sound speed profiles; however, propagation of particle acceleration from piles is poorly understood (Lippert and von Estorff, 2014; Tsouvalas and Metrikine, 2016; Lin et al., 2019). In-tank underwater acoustics cannot exactly replicate in-situ acoustic propagation (Parvulescu, 1964; Rogers et al., 2016; Jézéquel et al., 2019; Jones et al., 2019). Yet the experimental acoustic field can be measured precisely in high spatial resolution (perhaps more so than in the field), and careful effort was made to represent similar amplitudes and frequency spectra that squid may experience from in-situ pile driving.

## Behavioural context-dependent noise impacts on squid: cross-study comparisons

Comparisons to response rates of longfin squid in other behavioural conditions underscores that behavioural context of the noise exposure greatly affects responses exhibited (Figure 4). Note that these comparisons are conceptual; these experiments were necessarily performed with unique (although similar) experimental procedures as each study required its own contextual design, and necessarily on squid from different cohorts, which may contribute to variability in responses to stressors (Zakroff et al., 2018). Previous laboratory studies of individual squid either simply swimming, resting, or otherwise not engaged in specific tasks (Jones et al., 2020), or during feeding events, showed substantially higher rates of alarm and flight responses (Jones et al., 2021). Alarm responses included inking, jetting, other locomotor startle behaviours, and body pattern changes, which are all employed

by squid as anti-predator defences (Hanlon and Messenger, 2018). Comparatively, noise effects on feeding behaviours were more nuanced. There were no statistically significant differences between noise and control treatments in the proportion of squid that ultimately captured prey during the trial. Yet noise played during squids' pursuit of prey led to a significant increase in missed or abandoned prey capture attempts.

In the present study, trios of squid exposed to high intensity noise did not demonstrate any significant changes in reproductive behaviours. Although the same playback equipment and audio were retained across these lab studies, tests in the present study with multiple squid required using a larger tank. Maximum zero-to-peak particle acceleration levels in the tank were about 5–10 dB lower in the present study than in the tank used in prior studies, thus the acoustic field may in part account for behavioural differences across studies. However, in the present study, sound levels of the pile driving playback were within those that elicited alarm responses and missed prey capture attempts in prior studies, and alarm responses such as jetting were observed in (although not the focus of) the present study (Jones et al., 2020, 2021; Cones et al., 2022). Therefore, behavioural context (solitary squid, solitary squid with a prey item, or groups of squid engaged in reproduction) likely influenced differences in responses across studies.

Collectively, these studies emphasize the importance of behavioural context when predicting anthropogenic noise effects on marine taxa. This theme has been demonstrated across vertebrate and invertebrate taxa (Ellison et al., 2012; Bruintjes and Radford, 2013; Filiciotto et al., 2018). For example, boat noise caused cichlid fish (Neolamprologus pulcher) to change rates of digging and attack behaviours when eggs were not present, but there were no significant changes to these behaviours when eggs were present (Bruintjes and Radford, 2013). In the case of longfin squid, evidence from laboratory experiments indicate noise exposure is potentially more disruptive to anti-predator responses and feeding behaviours than to reproductive activities. Notably, noise effects on feeding behaviour may indirectly influence reproductive behaviours in ways not yet assessed; for instance, a reduced
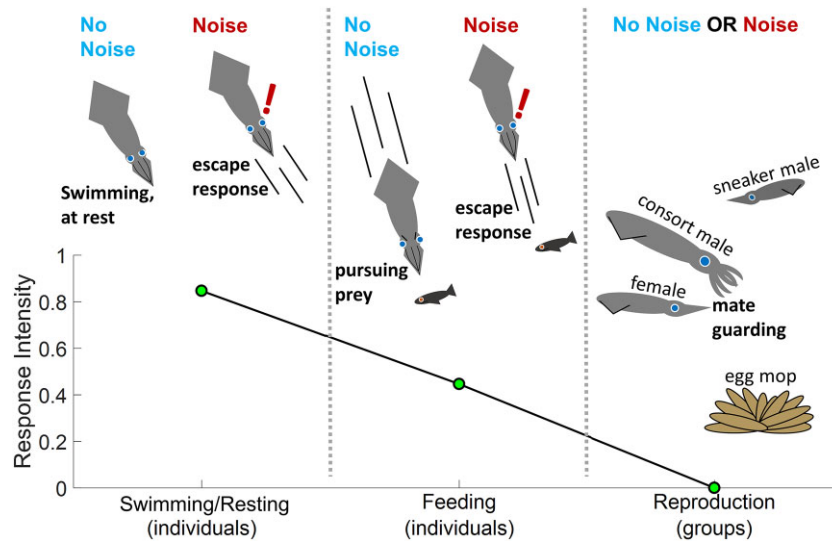
**Figure 4.** Comparison of relative response rates of *D. pealeii* to pile driving noise across studies measuring alarm/defence behaviours (Jones *et al.*, 2020), feeding behaviours (Jones *et al.*, 2021), and reproductive behaviours (present study). Response intensity is the quantified proportion of noise exposure trials with a response subtracted by the proportion of control trials with a response. For the alarm/defence study, a response was defined as at least one occurrence of inking, jetting, startle, or body pattern change. For the feeding study, a response was defined as at least one missed predation attempt. Since there were no significant noise effects on any reproductive behaviours, response intensity for the present study is set at zero. Example videos showing these behaviours during noise are in the electronic Supplementary Material.

caloric intake could lead to reduced energy put towards reproduction.

## Conclusions and future directions

The present study indicates that reproductive behaviours of longfin squid may be less at risk of being disrupted by noise relative to anti-predator defence and feeding behaviours. Together with previous studies on *D. pealeii*, these results reinforce the importance of considering multiple behavioural contexts in which animals' responses to anthropogenic noise may differ. While generally understood for mammals (Ellison *et al.*, 2012), such a perspective is new for invertebrates, which are often considered monotonic in their responses to noise stressors (Hawkins and Popper, 2018). Given the evolutionary pressure of fitness and reproduction, those species that are semelparous or otherwise limited in reproductive opportunities may be particularly resilient to noise-mediated responses during reproduction. How such "tolerance" then impacts an animal physiologically, epigenetically, or otherwise is yet to be determined.

To address wind farm effects in more ecologically and acoustically relevant scenarios, additional complementary field studies on squid behavioural responses to noise and habitat changes due to wind farms are needed. These should (i) be longer term, as animals' responses to chronic exposure may differ (Radford *et al.*, 2016), (ii) investigate potential displacement (i.e. swimming away) from wind farms during construction and operation, (iii) include monitoring of physiological changes in addition to behaviour, and (iv) be conducted on multiple populations. Laboratory studies have provided valuable information on the behavioural contexts in which longfin squid may be adversely affected by anthropogenic noise and can inform research foci for field studies addressing *in-situ* and population-level impacts. These research efforts and the results of the present study are of central impor-

tance to the fishing industry, regulators, and energy industry seeking to assess and address risks that offshore energy expansion poses to ecologically and commercially key marine fauna.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

## Author contributions

ITJ: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing—original draft, Writing—review & editing. MS: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing—review & editing. JAS: Funding acquisition, Conceptualization, Methodology, Writing—review & editing. RTH: Conceptualization, Methodology, Writing—review & editing. TAM: Funding acquisition, Conceptualization, Methodology, Supervision, Writing—review & editing.

## Conflict of interest statement

The authors have no conflicts of interest to declare.

## Data availability

The data underlying this article are available in the article and in its online Supplementary Material.

## References

Amaral, J. L., Beard, R., Barham, R. J., Collett, A. G., Elliot, J., Frankel, A. S., Gallien, D. et al. 2018. Field observations during wind turbine foundation installation at the Block Island Wind Farm, Rhode Island, Appendix D: underwater sound monitoring reports. https://www.boem.gov/environment/field-observations-during-wind-turbine-foundation-installation-block-island-wind-farm (last accessed 18 July 2023).

Amaral, J. L., Miller, J. H., Potty, G. R., Vigness-Raposa, K. J., Frankel, A. S., Lin, Y-T., Newhall, A. E. et al. 2020. Characterization of impact pile driving signals during installation of offshore wind turbine foundations. The Journal of the Acoustical Society of America, 147: 2323–2333.

André, M., Solé, M., Lenoir, M., Durfort, M., Quero, C., Mas, A., Lombarte, A. et al. 2011. Low-frequency sounds induce acoustic trauma in cephalopods. Frontiers in Ecology and the Environment, 9: 489–493.

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67: 1–48.

Blom, E., Kvarnemo, C., Dekhla, I., Schöld, S., Andersson, M. H., Svensson, O., and Amorim, M. C. P. 2019. Continuous but not intermittent noise has a negative impact on mating success in a marine fish with paternal care. Scientific Reports, 9: 1–9.

BOEM. 2021. BOEM renewable energy lease and grant information. https://www.boem.gov/renewable-energy/lease-and-grant-information (last accessed 24 March 2021).

Boyle, P., and Rodhouse, P. 2005a. Cephalopods as prey. In Cephalopods: Ecology and Fisheries, pp. 234–258. Blackwell Science, Oxford, UK.

Boyle, P., and Rodhouse, P. 2005b. Cephalopods as predators. In Cephalopods, Ecology and Fisheries, pp. 222–233. Blackwell Science.

Brodziak, J. K. T., and Macy, W. K. 1996. Growth of long-finned squid, Loligo pealei, in the northwest Atlantic. Fishery Bulletin, 94: 212–236.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J. et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal, 9: 378–400.

Bruintjes, R., Purser, J., Everley, K. A., Mangan, S., Simpson, S. D., and Radford, A. N. 2016. Rapid recovery following short-term acoustic disturbance in two fish species. Royal Society Open Science, 3: 150686.

Bruintjes, R., and Radford, A. N. 2013. Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish. Animal Behaviour, 85: 1343–1349.

Budelmann, B. U. 1992. Hearing in nonarthropod invertebrates. In The Evolutionary Biology of Hearing, 1st edn, pp. 141–155. Ed. by D. B. Webster, R. R. Fay, and A. N. Popper. Springer-Verlag, New York, NY.

Budelmann, B. U., and Tu, Y. 1997. The statocyst-oculomotor reflex of cephalopods and the vestibulo-oculomotor reflex of vertebrates: a tabular comparison. Vie et Milieu, 47: 95–99.

Buresch, K. C., Boal, J. G., Knowles, J., Debose, J., Nichols, A., Erwin, A., Painter, S. D. et al. 2003. Contact chemosensory cues in egg bundles elicit male–male agonistic conflicts in the squid Loligo pealeii. Journal of Chemical Ecology, 29: 547–560.

Buresch, K. C., Boal, J. G., Nagle, G. T., Knowles, J., Nobuhara, R., Sweeney, K., and Hanlon, R. T. 2004. Experimental evidence that ovary and oviducal gland extracts influence male agonistic behavior in squids. The Biological Bulletin, 206: 1–3.

Casper, B. M., Smith, M. E., Halvorsen, M. B., Sun, H., Carlson, T. J., and Popper, A. N. 2013a. Effects of exposure to pile driving sounds on fish inner ear tissues. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 166: 352–360.

Casper, B. M., Halvorsen, M. B., Matthews, F., Carlson, T. J., and Popper, A. N. 2013b. Recovery of barotrauma injuries resulting from exposure to pile driving sound in two sizes of hybrid striped bass. PLoS One, 8: e73844.

Cones, S. F., Jézéquel, Y., Ferguson, S., Aoki, N., and Mooney, T. A. 2022. Pile driving noise induces transient gait disruptions in the longfin squid (Doryteuthis pealeii). Frontiers in Marine Science, 9: 1–13.

Cummins, S. F., Boal, J. G., Buresch, K. C., Kaunpradit, C., Sobhorn, P., Holm, J. B., Degnan, B. M. et al. 2011. Extreme aggression in male squid induced by a beta-MSP-like pheromone. Current Biology, 21: 322–327.

de Jong, K., Forland, T. N., Amorim, M. C. P., Rieucau, G., Slabbekoorn, H., and Sivle, L. D. 2020. Predicting the effects of anthropogenic noise on fish reproduction. Reviews in Fish Biology and Fisheries, 30: 245–268.

Ellison, W. T., Southall, B. L., Clark, C. W., and Frankel, A. S. 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conservation Biology, 26: 21–28.

FAO. 2021. FAO fisheries and aquaculture statistics. http://www.fao.org/fishery/statistics/en (last accessed 6 October 2021).

Fay, R. 2009. Soundscapes and the sense of hearing of fishes. Integrative Zoology, 4: 26–32.

Fewtrell, J. L., and McCauley, R. D. 2012. Impact of air gun noise on the behaviour of marine fish and squid. Marine Pollution Bulletin, 64: 984–993.

Filiciotto, F., Paz, M., Moyano, S., Vincenzi, G. De, Hidalgo, F., Sciacca, V., Cielo, M. et al. 2018. Are semi-terrestrial crabs threatened by human noise? Assessment of behavioural and biochemical responses of Neohelice granulata (Brachyura, Varunidae) in tank. Marine Pollution Bulletin, 137: 24–34.

Fox, J., and Weisberg, S. 2019. An {R} Companion to Applied Regression. Sage, Thousand Oaks, CA.

Gedamke, J., Harrison, J., Hatch, L., Angliss, R., Barlow, J., Berchok, C., Caldow, C. et al. 2016. Ocean noise strategy roadmap. https://cetsound.noaa.gov/road-map (last accessed 18 July 2023).

Graham, I. M., Merchant, N. D., Farcas, A., Barton, T. R., Cheney, B., Bono, S., and Thompson, P. M. 2019. Harbour porpoise responses to pile-driving diminish over time. Royal Society Open Science, 6: 190335.

Hanlon, R. T., Buresch, K. C., Moustahfid, H., and Staudinger, M. D. 2013. Doryteuthis pealeii, longfin inshore squid. *In* Advances in Squid Biology, Ecology and Fisheries, Part I, pp. 205–240. Ed. by R. Rosa, R. O'Dor, and G. J. Pierce. Nova Science Publishers, Inc., New York, NY.

Hanlon, R. T., Maxwell, M. R., and Shashar, N. 1997. Behavioral dynamics that would lead to multiple paternity within egg capsules of the squid *Loligo pealei*. The Biological Bulletin, 193: 212–214.

Hanlon, R. T., and Messenger, J. B. 2018. Cephalopod Behaviour. 2nd Edition. Cambridge University Press, New York, NY.

Harris, C. M., Thomas, L., Falcone, E. A., Hildebrand, J., Houser, D., Kvadsheim, P. H., Lam, F. P. A. *et al.* 2018. Marine mammals and sonar: dose-response studies, the risk-disturbance hypothesis and the role of exposure context. Journal of Applied Ecology, 55: 396–404.

Hawkins, A. D., and Popper, A. N. 2017. A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. ICES Journal of Marine Science, 74: 635–651.

Herbert-Read, J. E., Kremer, L., Bruintjes, R., Radford, A. N., and Ioannou, C. C. 2017. Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals. Proceedings of the Royal Society B: Biological Sciences, 284: 1–9

Horodysky, A. Z., Brill, R. W., Fine, M. L., Musick, J. A., and Latour, R. J. 2008. Acoustic pressure and particle motion thresholds in six sciaenid fishes. Journal of Experimental Biology, 211: 1504–1511.

Jézéquel, Y., Bonnel, J., Coston-Guarini, J., and Chauvaud, L. 2019. Revisiting the bioacoustics of European spiny lobsters *Palinurus elephas*: comparison of antennal rasps in tanks and *in situ*. Marine Ecology Progress Series, 615: 143–157.

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*). Scientific Reports, 12: 1–11.

Jones, I. T., Peyla, J. F., Clark, H., Song, Z., Stanley, J. A., and Mooney, T. A. 2021. Changes in feeding behavior of longfin squid (*Doryteuthis pealeii*) during laboratory exposure to pile driving noise. Marine Environmental Research, 165: 1–13.

Jones, I. T., Stanley, J. A., Bonnel, J., and Mooney, T. A. 2019. Complexities of tank acoustics warrant direct, careful measurement of particle motion and pressure for bioacoustic studies. Proceedings of Meetings on Acoustics, 37: 1–11.

Jones, I. T., Stanley, J. A., and Mooney, T. A. 2020. Impulsive pile driving noise elicits alarm responses in squid (*Doryteuthis pealeii*). Marine Pollution Bulletin, 150: 110792.

Lin, Y.-T., Newhall, A. E., Miller, J. H., Potty, G. R., and Vigness-Raposa, K. J. 2019. A three-dimensional underwater sound propagation model for offshore wind farm noise prediction. The Journal of the Acoustical Society of America, 145: EL335–EL340.

Lippert, T., and von Estorff, O. 2014. The significance of parameter uncertainties for the prediction of offshore pile driving noise. The Journal of the Acoustical Society of America, 136: 2463–2471.

Macy, W. K., and Brodziak, J. K. T. 2001. Seasonal maturity and size at age of *Loligo pealeii* in waters of southern New England. ICES Journal of Marine Science, 58: 852–864.

MARCO. 2021. Mid-Atlantic ocean data portal. https://portal.midatlanticocean.org/ (last accessed 31 March 2021).

Maxwell, M. R., and Hanlon, R. T. 2000. Female reproductive output in the squid *Loligo pealeii*: multiple egg clutches and implications for a spawning strategy. Marine Ecology Progress Series, 199: 159–170.

Maxwell, M. R., Macy, W. K., Odate, S., and Hanlon, R. T. 1998. Evidence for multiple spawning by squids (*Loligo pealei*) in captivity. The Biological Bulletin, 195: 225–226.

Mooney, T. A., Andersson, M. H., and Stanley, J. 2020. Acoustic impacts of offshore wind energy on fishery resources. Oceanography, 33: 82–95.

Mooney, T. A., Hanlon, R. T., Christensen-Dalsgaard, J., Madsen, P. T., Ketten, D. R., and Nachtigall, P. E. 2010. Sound detection by the longfin squid (*Loligo pealeii*) studied with auditory evoked potentials: sensitivity to low-frequency particle motion and not pressure. Journal of Experimental Biology, 213: 3748–3759.

Mooney, T. A., Samson, J. E., Schlunk, A. D., and Zacarias, S. 2016. Loudness-dependent behavioral responses and habituation to sound by the longfin squid (*Doryteuthis pealeii*). Journal of Comparative Physiology A, 202: 489–501.

Musial, W., Beiter, P., Spitsen, P., Nunemaker, J., and Gevorgian, V. 2019. 2018 offshore wind technologies market report.https://nrel.primo.exlibrisgroup.com/permalink/01NREL_INST/1e90bo2/alma991001018188903216 (last accessed 18 July 2023).

Musial, W., Beiter, P., Spitsen, P., Nunemaker, J., Gevorgian, V., Cooperman, A., Hammond, R. *et al.* 2020. 2019 offshore wind technology data update. https://nrel.primo.exlibrisgroup.com/permalink/01NREL_INST/1e90bo2/alma991001009861503216 (last accessed 18 July 2023).

Nedelec, S. L., Radford, A. N., Pearl, L., Nedelec, B., Mccormick, M. I., Meekan, M. G., and Simpson, S. D. 2017. Motorboat noise impacts parental behaviour and offspring survival in a reef fish. Proceedings of the Royal Society B: Biological Sciences, 284: 1–7.

Neo, Y. Y., Hubert, J., Bolle, L., Winter, H. V, Ten Cate, C., and Slabbekoorn, H. 2016. Sound exposure changes European seabass behaviour in a large outdoor floating pen: effects of temporal structure and a ramp-up. Environmental Pollution, 214: 26–34.

Neo, Y. Y., Ufkes, E., Kastelein, R. A., Winter, H. V., Ten Cate, C., and Slabbekoorn, H. 2015. Impulsive sounds change European seabass swimming patterns: influence of pulse repetition interval. Marine Pollution Bulletin, 97: 111–117.

NMFS. 2021. Annual commercial landing statistics. https://www.fisheries.noaa.gov/foss (last accessed 26 March 2021).

Parvulescu, A. 1964. Problems of propagation and processing. *In* Marine Bio-acoustics, pp. 87–100. Ed. by W. N. Tavolga. Pergamon Press, Bimini, Baham.

Radford, A. N., Lébre, L., Lecaillon, G., Nedelec, S. L., and Simpson, S. D. 2016. Repeated exposure reduces the response to impulsive noise in European seabass. Global Change Biology, 22: 3349–3360.

Roberts, L., Cheesman, S., Elliott, M., and Breithaupt, T. 2016. Sensitivity of *Pagurus bernhardus* (L.) to substrate-borne vibration and anthropogenic noise. Journal of Experimental Marine Biology and Ecology, 474: 185–194.

Roberts, L., and Laidre, M. E. 2019. Finding a home in the noise: cross-modal impact of anthropogenic vibration on animal search behaviour. Biology Open, 8: 1–7.

Rogers, P. H., Hawkins, A. D., Popper, A. N., Fay, R. R., and Gray, M. D. 2016. Parvulescu revisited: small tank acoustics for bioacousticians. *In* The Effects of Noise on Aquatic Life II, pp. 933–941. Ed. by A. N. Popper, and A. D. Hawkins Springer Science+Business Media, New York, NY.

Samson, J. E., Mooney, T. A., Gussekloo, S. W. S., and Hanlon, R. T. 2014. Graded behavioral responses and habituation to sound in the common cuttlefish *Sepia officinalis*. The Journal of experimental biology, 217: 4347–4355.

Shashar, N., and Hanlon, R. T. 2013. Spawning behavior dynamics at communal egg beds in the squid *Doryteuthis (Loligo) pealeii*. Journal of Experimental Marine Biology and Ecology, 447: 65–74.

Solé, M., Lenoir, M., Durfort, M., López-Bejar, M., Lombarte, A., and André, M. 2013. Ultrastructural damage of *Loligo vulgaris* and *Illex coindetii* statocysts after low frequency sound exposure. PLoS One, 8: 1–12.

Solé, M., Sigray, P., Lenoir, M., van der Schaar, M., Lalander, E., and André, M. 2017. Offshore exposure experiments on cuttlefish indicate received sound pressure and particle motion levels associated with acoustic trauma. Scientific Reports, 7. http://dx.doi.org/10.1038/srep45899.

Tsouvalas, A., and Metrikine, A. V. 2016. Structure-borne wave radiation by impact and vibratory piling in offshore installations: from

sound prediction to auditory damage. Journal of Marine Science and Engineering, 4: 1–26.

Wale, M. A., Briers, R. A., and Diele, K. 2021. Marine invertebrate anthropogenic noise research—Trends in methods and future directions. Marine Pollution Bulletin, 173: 112958.

Wingfield, J. C., and Sapolsky, R. M. 2003. Reproduction and resistance to stress: when and how. Journal of Neuroendocrinology, 15: 711–724.

Wright, K. J., Higgs, D. M., and Leis, J. M. 2011. Ontogenetic and interspecific variation in hearing ability in marine fish larvae. Marine Ecology Progress Series, 424: 1–13.

Wysocki, L. E., Codarin, A., Ladich, F., and Picciulin, M. 2009. Sound pressure and particle acceleration audiograms in three marine fish species from the Adriatic Sea. The Journal of the Acoustical Society of America, 126: 2100.

York, C. A., and Bartol, I. K. 2014. Lateral line analogue aids vision in successful predator evasion for the brief squid, *Lolliguncula brevis*. The Journal of Experimental Biology, 217: 2437–2439.

Zakroff, C., Mooney, T. A., and Wirth, C. 2018. Ocean acidification responses in paralarval squid swimming behavior using a novel 3D tracking system. Hydrobiologia, 808: 83–106.

*Handling Editor: Francis Juanes*