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# Impact of air gun noise on the behaviour of marine fish and squid

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#### ABSTRACT

In this study various species of captive marine fish and one species of squid were exposed to the noise from a single air gun. Six trials were conducted off the coast of Western Australia with each trial using a different noise exposure regime. Noise levels received by the animals ranged between 120 and 184 dB re 1  $\mu$ Pa<sup>2</sup>.s (SEL).

Behavioural observations of the fish and squid were made before, during and after air gun noise exposure. Results indicate that as air gun noise levels increase, fish respond by moving to the bottom of the water column and swimming faster in more tightly cohesive groups. Significant increases in alarm responses were observed in fish and squid to air gun noise exceeding 147–151 dB re 1 µPa SEL. An increase in the occurrence of alarm responses was also observed as noise level increased.

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## 1. Introduction

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Noise

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Underwater noise generated by anthropogenic activities has come under scrutiny as there is concern for the impacts it may be having on surrounding marine life. Much of the research on the ecological impacts from underwater noise has focused on the impacts on marine mammals. However, underwater anthropogenic noise has been shown to impact on the behaviour of fish and, in some cases, has been used to control their behaviour (Hawkins, 1986; Popper, 2002; Slabbekoorn et al., 2010; Yan et al., 2010).

A major source of underwater anthropogenic noise is the seismic surveys that are used in offshore exploration for fossil fuel reserves. They involve the use of a noise source, usually an array of air guns, being towed behind a ship and fired at regular intervals producing a high intensity, low frequency (20–500 Hz) noise. The sound generated by the air gun arrays is within the detectable frequency range for fish of known hearing capabilities (Popper and Fay, 1993; Slabbekoorn et al., 2010) and, although the acoustic energy is directed towards the seabed, considerable energy is propagated horizontally, travelling for many kilometres from the source (McCauley, 1994).

Most previous research indicates that underwater noise from seismic surveys using air guns does affect the behaviour of fish (Dalen and Knutsen, 1987; Engas and Lokkeborg, 2002; Greene, 1985; Ketchington, 2000; Lokkeborg and Soldal, 1993; Pearson et al., 1992; Slotte et al., 2004; Wardle et al., 2001). However, reported behavioural alterations are variable and are often difficult

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to extrapolate and to relate to real impacts due to factors such as differences in noise sources and reporting of noise levels, sampling techniques and other limitations in methodology which are common to research in the marine environment.

There is relatively little information on the effect of underwater noise on the behaviour of marine invertebrates. Recent studies have indicated that offshore seismic survey activity has no effect on catch rates of crustaceans in the surrounding area (Andriguetto-Filho et al., 2005; Parry and Gason, 2006). Wardle et al. (2001) observed little effect on invertebrate (crustaceans, echinoderms and molluscs) populations inhabiting a reef that was exposed to air gun noise. However, low frequency noise has reportedly been used to successfully deter barnacle larvae from settling on ship hulls (Branscomb and Rittschof, 1984) and there is anecdotal evidence of squid being attracted to intermittent, low frequency noise (Maniwa, 1976). Strandings of giant squid have also been reported in the vicinity of seismic survey activity (Guerra et al., 2004). It has also been shown that at least some species of cephalopods and crustaceans are capable of 'hearing' within the frequency range of seismic survey noise (Hanlon and Budelmann, 1987; Hu et al., 2009; Lovell et al., 2005; Packard et al., 1990). Therefore, the noise generated by air guns has the potential to impact on the behaviour of surrounding invertebrate populations.

However, although fish and marine invertebrates may be able to hear air gun signals, previous studies on fish have indicated that the sound may have to be well above the detection threshold to elicit a significant change in behaviour (Blaxter et al., 1981; Knudsen et al., 1992). Therefore, behavioural reactions and the noise levels required to induce them need to be characterised so that, if required, effective mitigation techniques can be designed and





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applied. The aims of the present study are to: (i) determine if exposure to air gun noise can elicit a change of behaviour in fish and squid and (ii) to characterise any behavioural responses in terms of their nature and the noise level required to induce them.

## 2. Materials and methods

Six trials involving two species of schooling demersal/pelagic fish and one species of squid were conducted in Jervoise Bay, Western Australia. Information on the experimental animals used in the trials is shown in Table 1.

During the trials experimental animals were housed in a 10 m (length)  $\times$  6 m (width)  $\times$  3 m (depth) steel framed, mesh lined sea cage deployed in a water depth of 9 m. Animals were acclimated to the cage for a minimum of 7 days prior to any experimentation and were fed daily with bait fish while being held in the cage. The animals were exposed to varying levels of noise from an airgun, with each trial having a different exposure regime (Fig. 1).

The air gun used in the trials was a 0.33 L Bolt PAR 600B that was deployed at a depth of 5 m and operated at 1500 psi. At this operating pressure the air gun had a source level at 1 m of 192 dB re 1  $\mu$ Pa<sup>2</sup>.s. A signal rate of 1 signal per 10 s was used in all trials. The air gun was suspended from a pontoon which was towed with a small dinghy (18 Hp) at slow speed towards and then away from the cage to emulate a survey vessel approaching and then departing an area. The distance between the air gun and the cage ranged from 5 m to 800 m. The noise level received at the cage was measured by two hydrophones (GEC Marconi SH101X) situated along the long axis of the cage at a depth of 2-3 m. The hydrophones were cabled to shore where signals were sent through a preamplifier with attenuation applied and then stored on a Sony DAT D3 or D8 tape deck. Systems were calibrated using white noise at a known level. All signals were analysed on a Data Physics 430 signal analyser. The difference in sound level of the air gun signal at the surface (0.5 m) and bottom (3 m) of the cage was measured in trial 2 and 3. The mean difference was approximately 12 dB. An example of the power spectra of the air gun signal is shown in Fig. 2.

## 2.1. Collection and analysis of behavioural data

Animal behaviour during the experimental period was recorded using two cameras (Panasonic 1/3" CCD, WV-BP312 with a 4.5 mm

### Table 1

Details of the experimental animals used in the six trials conducted in Jervoise Bay, Western Australia. The standard lengths of the fish in trial 1 were not recorded due to fish escaping prior to retrieval after trials. Squid were stocked into the cage over a number of days as they were caught.

Trial	Species	Number of animals	Standard length (mm)	Acclimation period (days)	Source
1	Trevally (Pseudocaranx dentex)	15	-	14	Wild caught (endemic)
2	Pink snapper (Pagrus auratus)	50	230 ± 24	24	Aquaculture (endemic)
3	Pink snapper (P. auratus)	32	250 ± 8	70	Trial 2
4	Squid (Sepioteuthis australis)	12	166 ± 23	7–18	Wild caught (endemic)
5	Squid (S. australis)	19	185 ± 14	7–10	Wild caught (endemic)
6	Squid (S. australis)	19	185 ± 14	11-14	Trial 5

focal length lens and a Sony 1/3" CCD DC10P with a 4 mm focal length lens) positioned at diagonally opposite corners of the cage. Cameras had horizontal and vertical fields of view of 114° and 87°, and 132° and 101° for the Panasonic and Sony cameras respectively. Both cameras were cabled to shore where data was logged and an operator could observe animal behaviour in real time. behaviour of experimental animals before, during and subsequent to noise exposure was observed and collated from playback of the recordings.

Behavioural observations of groups of animals were the main focus, rather than the behaviour of individuals. Types of behavioural responses were coded along with a time stamp using a simple programme on a PC while watching the experimental footage. Codes fell into the general groups of: position in water column, swimming patterns, swimming speed, schooling patterns, animal colouration, alarm responses and interactions between animals. The definitions of the behaviours discussed in this paper are shown in Table 2. The data collected was used to show differences in the animal's responses between periods before, during and after air gun noise and changes in behavioural responses that occurred as the level of air gun noise increased.

Behaviours were divided into two groups, that is, behaviours that could be analysed as number of occurrences per period (e.g. alarm responses) and behaviours that involved calculating the time spent actually performing that behaviour (e.g. swimming speed and vertical position in water column).

To analyse differences in frequency of occurrence of a particular behaviour between periods (i.e. air gun off and air gun on) the behaviour index (I) for each period was calculated as the ratio of the number of times that particular behaviour was observed (s) to the total number of behavioural counts (S) (Eq. (1)).

$$I = \frac{s}{5} \tag{1}$$

To analyse the relationship between noise level and behavioural response, noise level thresholds were designated. The noise level thresholds (*T*) chosen were;  $100 < T_1 < 147$ ,  $146 < T_2 < 151$ ,  $150 < T_3 < 157$ ,  $156 < T_4 < 162$  and  $T_5 > 161$  dB re 1 µPa<sup>2</sup>.s with 100 dB re 1 µPa<sup>2</sup>.s corresponding to zero air gun noise as air gun signals were always above this level. A behaviour index was then calculated for each noise level threshold.

The calculated behaviour indices assume that the behavioural responses of fish were induced solely by the air gun noise. However, observations showed that the same behavioural responses could occur in the absence of the stimuli during the air gun off periods. To take this into account a behavioural response index (BRI) was calculated as the difference between the indices  $I_p$  and  $I_n$  for air gun on and off periods (Eq. (2)).  $I_n$  includes data from all air gun off periods.

$$BRI = I_p - I_n \tag{2}$$

where BRI = behavioural response index;  $I_p = s_p/S_p$ ;  $I_n = s_n/S_n$ ;  $s_p$  = specific behaviour (e.g. alarm responses) counts per period above threshold;  $S_p$  = total behavioural counts per period above air gun threshold;  $s_n$  = specific behaviour counts per period with no air gun noise;  $S_n$  = total behavioural counts per period with no air gun noise

Therefore, a positive BRI indicated that the particular behavioural response was observed more often during air gun noise exposure at or above the specified air gun threshold than when the air gun was off.

Changes in swimming behaviour and vertical position were calculated by the same methods, except that the time spent exhibiting the behaviour to be analysed was calculated (BRI<sub>t</sub>) rather



Fig. 1. Signal intensity received for each trial. The absence of data points represents the period that behaviour was monitored while the air gun was inactive. Noise levels are presented as sound exposure level (SEL). (a) Trial 1; (b) Trial 2; (c) Trial 3; (d) Trial 4; (e) Trial 5; (f) Trial 6.

than the frequency of observations. The BRI for these responses was calculated as shown in Eq. (3).

$$BRI_t = I_p - I_n \tag{3}$$

where BRI<sub>t</sub> = behavioural response index of behaviours measured in time;  $I_p = t_p/T_p$ ;  $I_n = t_n/T_n$ ;  $t_p$  = time spent displaying particular behaviour for period above specified air gun noise threshold;  $T_p$  = time species in view for period above specified air gun noise

threshold;  $t_n$  = time spent displaying specific behaviour for period with no air gun noise;  $T_n$  = time species in view for period with no air gun noise

The relationship between the BRI and the specified air gun noise threshold was plotted and then analysed using regression models. Statistically significant differences in behaviours between air gun on and off periods within each trial could not be calculated due to lack of suitable replication. However, pooled data from trials 4, 5 and 6 (i.e. squid trials) was subjected to an analysis of variance



**Fig. 2.** Power spectra of the signal produced by the airgun used in the six trials as received at the experimental sea cage. Signal spectra shown are from an air gun distance of 50 m (top curve) and 100 m (bottom curve) from the cage.

 Table 2

 Behaviours that were used to describe the response of captive fish and squid to air gun noise.

Category	Behaviour	Description
School cohesion	Loose group	Animals in a cohesive group; <sup>a</sup> polarised or unpolarised; individuals >2 body lengths apart
	Tight group	Animals in tightly cohesive group; polarised or unpolarised; individuals <2 body lengths apart
Alarm responses	Flash expansion	Cohesive groups quickly separating and then reforming a tightly cohesive group (usually polarised)
	Parting	Cohesive group quickly expanding
	Burst swim	Short period of sudden, rapid
		acceleration in a polarised conesive
Swimming speed	Stationary	Animals displaying no detectable
		horizontal or vertical movement
	Slow swimming	Animals swimming non-
		purposefully; usually nonpolarised
	Fast swimming	Animals swimming at faster than
Vortical position	Uppor	Animals observed in upper 1/2 of
vertical position	Орреі	cage
	Mid	Animals observed in middle of cage
	Lower	Animals observed in lower 1/3 of cage
Vertical	Mid to upper	Vertical swimming direction of
movements	Mid to lower	animals
Squid specific	Ink ejected	Squid observed ejecting ink
(alarm	Jetting	Squid observed moving quickly
responses)		backwards in jerking motion

<sup>a</sup> Individuals in 'polarised' groups are of similar size, uniformly spaced and swim in the same direction at approximately the same speed (Shaw, 1978).

(ANOVA) with each trial treated as a replicate. Prior to analysis ratio data was transformed (arcsine square root) and determined to be homogeneous (Levene's test). Significant differences (p < 0.05) between air gun off and on periods were found using Tukey's test.

## 3. Results

## 3.1. Fish

In trial 1 (trevally) alarm responses (i.e. burst swimming) were observed only during air gun operation. During the first exposure more observations of this behaviour were recorded at times of higher noise levels (approximately 163–169 dB re 1  $\mu$ Pa<sup>2</sup>.s). The first exposure to air gun noise resulted in a higher frequency of alarm responses than in the second exposure (21 as opposed to

9). Alarm responses in the second exposure coincided with the commencement of shooting and then again at the higher intensities of noise of the first pass of the air gun. The number of alarm responses increased exponentially as noise level increased, with a coefficient of determination of 0.996 (Fig. 3a).

The fish in trial 1 were also observed to swim faster, in tighter groups and towards the bottom of the cage during air gun exposure. The increase in these three behaviours as noise levels increased above 147 dB re 1  $\mu$ Pa<sup>2</sup>.s can be described with a linear relationship with coefficients of determination of 0.9999, 0.9999 and 0.9257, respectively (Fig. 3b). The fish returned to their prenoise exposure position in the water column within 31 min after the final air gun signal of the trial.

The analysis of results for the pink snapper (trial 2 and 3) was effected by:

- (i) The fish being out of view of the cameras for the majority of air gun operations in trial 2, and
- (ii) Lack of response of the fish to air gun noise in trial 3.

However, there were some observations of note (Fig. 4). In trial 2, the main observations were that on the onset of air gun exposure (131 dB re 1  $\mu$ Pa<sup>2</sup>.s) the fish in view 'fast swam' from the top to the bottom of the cage. The fish then remained out of view of camera 1 for the remainder of the first air gun exposure. However, during the first air gun exposure the fish were occasionally in view of camera 2. Every time the fish were in view of camera 2 they were observed at the bottom of the cage. During the time between the two air gun exposures, the cameras were lowered by approximately 0.5 m. With the cameras lowered, the fish were in view for most of the second exposure and were observed spending the majority of the time swimming in a loosely cohesive group at the bottom of the cage. Fish were observed 'fast swimming' almost exclusively during air gun operation. During the second air gun exposure alarm responses coincided with the air gun firing.

In trial 3 the same fish were used as in trial 2, therefore the fish in trial 3 had been previously exposed to air gun noise 58 days prior. Alarm responses (i.e. flash expansion) were observed during the second half of the trial just prior, during and after air gun noise exposure. There was no difference observed in the time spent between the different vertical positions of the cage prior, during or after air gun exposure.

There were no correlations of the difference ratios of any observed behaviour which could be linked to air gun noise levels in trial 3. The behavioural results of this trial need to be considered in conjunction with the damage to the ear (i.e. saccular macula) observed in experimental fish that were sampled from the cage and examined at the conclusion of trial 2 and 3 (described in McCauley et al. (2003)).

## 3.2. Squid

In trial 4 the squid in view of the camera ejected ink at the first air gun signal (162 dB re 1  $\mu$ Pa<sup>2</sup>.s) (Fig. 5). They were then observed moving backwards, away from the air gun, in the upper section of the cage. The backward movement consisted of a series of 'jetting' motions, each movement corresponding to an air gun signal (Fig. 5). The animals then disappeared from view of the cameras. Observations from the surface revealed that the squid were aggregated at the end of the cage furthest away from the air gun in the upper section of the water column for the majority of the first period of air gun exposure. The squid remained out of view of the cameras until the second exposure where they were observed in the top portion of the cage. Alarm responses were observed only when the air gun was in operation.

During trial 5 the squid displayed what appeared to be aggressive behaviour with much of the interest directed at camera 2 after



Fig. 3. Behavioural response indices (BRI) for trevally (*Pseudocaranx dentex*) in trial 1 at specified noise levels. (a) Number of alarm responses observed (all points included in regression analysis). (b) Time spent fast swimming in tight groups in the lower section of the cage. Points included in the regression are circled.



Fig. 4. Pink snapper (Pagrus auratus) behavioural responses of note during trial 2. Data displayed are the results of summed data from both cameras.

the first period of air gun noise exposure, and then at camera 1 after the second air gun exposure. Colour changes (light to dark colouration) were also observed throughout the trial but particularly during the final hour of observation. Also, a white oval patch was clearly visible on the mantle of many of the squid at various times during the trial. At the conclusion of trial 5, a mass of squid eggs were found attached to the moorings of camera 1.

Except for one event, alarm responses were only observed when the air gun was in operation in trial 5. More alarm responses were observed during the first exposure to air gun noise when compared to the second (see comparison in Fig. 7). An increase in the frequency of alarm responses as noise level increased above 147 dB re 1  $\mu$ Pa<sup>2</sup>.s was observed. Above noise levels of 147 dB re 1  $\mu$ Pa<sup>2</sup>.s the frequency of alarm responses increased exponentially with a coefficient of determination of 0.9737 (Fig. 6a).

The squid in trial 5 were stationary for less time during periods of air gun operation when compared to the time spent stationary when the air gun was not operating. There was no observed difference in swimming speed and vertical position in the water column between periods of air gun exposure and no air gun exposure.



Fig. 5. Squid (Sepioteuthis australis) behavioural responses of note during trial 4. Data displayed are the results of summed data from both cameras.

There was a general trend for the squid in trial 5 to increase their swimming speed above noise levels of 147 dB re 1  $\mu$ Pa<sup>2</sup>.s and then slow their swimming speed or become relatively stationary at the surface during the most intense air gun signals (Fig. 6b).

The same animals were used in trials 5 and 6. Therefore, the squid in trial 6 had been previously exposed to air gun noise five days prior to trial 6. In trial 6 the squid were observed fast swimming more often during air gun operation than they were when the air gun was off. It is also interesting to note that at each of the highest six levels of exposure either the jetting or flash expansion of the group was observed. As noise levels exceeded 147 dB re 1  $\mu$ Pa<sup>2</sup>.s the frequency of alarm responses increased with a linear relationship giving a coefficient of determination of 0.9981 (Fig. 6c).

The trend of the squid increasing swimming speed as the air gun approached and then becoming stationary in the top section of the cage at the highest noise intensities that was observed in trial 5 was also noted in trial 6 (Fig. 6d).

The behaviour index (*I*) for frequency of alarm responses in each of the air gun on/off periods for trials 4, 5 and 6 is shown in Fig. 7. The analysis of pooled data from these trials identified a significantly (p < 0.05) higher frequency of alarm responses in the squid during air gun operation. This analysis also revealed a significantly (p < 0.05) higher number of alarm responses during the first exposure to air gun noise when compared to subsequent exposures.

## 4. Discussion

The behavioural observations in this study indicate that air gun noise does result in alterations in fish and squid behaviour. The types of behaviour observed in response to noise are similar to



**Fig. 6.** Behavioural response indices (BRI) for squid (*Sepioteuthis australis*) in trials 5 and 6 at specified noise levels. (a) Alarm responses of squid in trial 5. Points included in regression analysis are circled. (b) Time spent fast swimming by the squid in trial 5. (c) Alarm responses of squid in trial 6. Points included in regression analysis are circled. (d) Time spent fast swimming by the squid in trial 5. (c) Alarm responses of squid in trial 6. Points included in regression analysis are circled.



**Fig. 7.** Frequency of alarm responses in squid (*Sepioteuthis australis*) for periods of no air gun noise compared with periods of air gun noise. Frequency is calculated as alarm responses per period divided by the total behavioural counts per period (*I*). Off and on refer to the air gun status.

those reported in fish by other researchers including: alarm responses and changes in schooling patterns, position in the water column and swimming speeds. A relationship between behavioural responses and noise level was also demonstrated.

While not discussed in detail here, an important consideration in these types of experiments which has not been addressed by any studies is the size of the experimental cage. In this study, a relatively large cage (approximately 40-50 body lengths long for most experimental species) was used. Initially a cage 18 m in length was used but was found to be difficult to work with and had limited camera coverage using the two systems available. The optimum cage size for experiments of this nature will be dependent on practical factors (e.g. maintenance requirements, animal retrieval, suitable visual coverage) while being large enough such that the animal's behaviour is not completely compromised, so maintaining some semblance of normal swimming patterns and allowing for interactions with co-specifics in a normal fashion. Small cages would be expected to significantly alter fish behaviour from their normal pattern and so to their response to stimuli, thus it is likely that experimental regimes that are identical except for cage size may yield different results.

## 4.1. Fish

In this study changes in schooling behaviour and vertical position in trevally were observed at 147–151 dB re 1  $\mu$ Pa<sup>2</sup>.s. Specifically, at these noise levels the fish began to swim faster and form more tightly cohesive groups towards the bottom of the cage. From the data collected in trial 2, the pink snapper also moved to the lower section of the cage. However, the behaviour of the pink snapper differed from the trevally in trial 1 in that loosely cohesive groups was observed more often during exposure to noise. Also, although alarm responses in the pink snapper were observed more often during noise exposure there was a decrease in their frequency when compared to the trevally.

These differences could be attributed to a number of factors. Firstly, observations of pink snapper behaviour in trial 2 were based on the second exposure to air gun noise in this trial as the fish were out of view of the cameras for the first exposure. Therefore, habituation to the noise from the first exposure could have resulted in differences in behavioural responses. Secondly, species naturally differ in their behavioural responses to noise exposure and in hearing sensitivity (Hawkins, 1981, 1986; Kastelein et al., 2008; Popper et al., 2003). Thirdly, the noise regime used in trial 2 differed from that in trial 1. Lastly, it should be noted that while the trevally were wild caught, the pink snapper were sourced from

aquaculture. Evidence suggests that behavioural responses in fish of the same species will differ, depending on whether the individuals were hatchery reared or wild caught (Knudsen et al., 1992; Woodward and Strange, 1987). Factors such as habituation to high noise levels and familiarity to the captive environment could lead to the behavioural differences observed (Bart et al., 2001; Johnsson et al., 2001; Knudsen et al., 1992; McDonald et al., 1998). However, with the exception of the formation of tightly cohesive groups during noise exposure, the general behavioural responses to air gun noise for the two species were comparable.

Pearson et al. (1992) reported similar behaviours in captive rockfish (Sebastes spp.) at 180 dB re 1 µPa mean peak. Converting the sound exposure levels (SEL) used in this study to mean peak values, using factors derived and outlined in McCauley et al. (2000), places the change in behaviours observed in this study at 168–173 dB re 1 µPa mean peak. This is lower than the noise levels required to induce alarm responses in the rockfish used in Pearson et al. (1992). However, after extrapolation of their results it was suggested that 'subtle' changes in behaviour, such as the vertical position in water column, could occur at 161 dB re 1 µPa mean peak which is comparable to the results of the present study. The differences in results between these, and other studies, could be caused by factors such as differences in behavioural definitions, species, cage size and acclimation procedures (in Pearson et al. (1992) the experimental fish were wild caught and transferred into the cages one day prior to the trials) or because of the approachdepart air gun regime used in the present study as opposed to the stationary air gun used by Pearson et al. (1992).

Similar results have been reported in experiments using wild unrestrained fish being exposed to noise. Fish huddling in groups and swimming towards the lower part of the water column in response to approaching vessel noise (Handegard et al., 2003; Olsen, 1990) and air gun noise (Chapman and Hawkins, 1969; Dalen and Knutsen, 1987; Dalen and Raknes, 1985; Slotte et al., 2004) are reported in the literature. Alarm behaviours in fish are common in response to noise and have been reported by many authors (Blaxter and Hoss, 1981; Boeger et al., 2006; Kastelein et al., 2008; Pearson et al., 1992; Wardle et al., 2001). Sudden fast behavioural alterations such as startle responses and flash expansions of schools (classified as alarm responses in this study) and changes in schooling behaviour such as individuals forming a tight group or huddling are comparable with the behaviour of fish avoiding predators (Godin, 1997; Pitcher and Parish, 1993; Shaw, 1975).

It is interesting to note that, in this study, the fish were observed to aggregate at the bottom of the cage where the airgun noise levels were highest. Bottom dwelling has reportedly been used as a behavioural indicator of general anxiety in fish (Cachat et al., 2010; Maximino et al., 2010). This suggests that the observation of fish bottom dwelling in this study is in fact a generic 'anxiety' response to an unknown stressor approaching from the water's surface, rather than specifically to noise.

The study by Wardle et al. (2001) exposed a small reef system to the noise from three 2.5 L air guns (195–218 dB re 1 µPa peak pressure). Interestingly, although alarm responses were exhibited by fish, no other significant avoidance behaviours were observed. A factor that could have contributed to this result is that the reef system exposed consisted mainly of resident species. The results may have been different for fish not territorial to a specific area or in an area without structural refuge. The air gun being stationary and therefore, providing no approaching danger signals to the animals inhabiting the reef and the relatively long gap between signals (i.e.  $\ge 1$  min) in Wardle et al. (2001) may have also influenced the behavioural reactions of the fish.

Although the same fish were used in trials 2 and 3, each trial resulted in different behavioural responses to air gun noise. In trial 2 the fish swam to the bottom of the cage where they remained for the duration of noise exposure and fast swimming was observed in relation to noise exposure. In trial 3 the fish did not display a preference for any portion of the cage and fast swimming was occasionally observed but was not related to noise exposure. There are several possible explanations for this difference in behaviour. For example, the fish may have become habituated to the noise from trial 2 and did not associate the noise with danger. Also, in trial 3 a different air gun noise regime was used, with air gun noise levels beginning 5 dB lower that in trial 2 which may have resulted in the fish becoming habituated to the noise before higher noise levels were reached. Alternatively, the damage that resulted to the ears of the fish in trial 2 and reported in McCauley et al. (2003) compromised the fishes hearing ability. Finally, it is possible that the longer acclimation time to the cage (i.e. 70 days) by the time trial 3 had begun, had an effect on fish behaviour.

Fifty eight days separated trial 2 and 3 and, although studies have suggested that fish are capable of long term memory, it is unlikely that the fish would remember the noise without some sort of association, for example with pain or food reward (Gleitman and Rozin, 1971). If pain was associated with the air gun noise then a more pronounced behavioural response would be expected as would a physiological stress response (Schreck, 1990). The acclimation time for the fish in trial 2 was 24 days. This time period is generally accepted as sufficient for fish to become acclimated to a new environment, especially as the pink snapper had been reared in a captive environment (Pottinger and Pickering, 1992). Therefore, it is most likely that the ear damage observed at the conclusion of trial 2 resulted in altered hearing capabilities and is responsible for the lack of behavioural response to air gun noise in trial 3. The effect, if any, that the observed damage had on hearing capabilities was not investigated. However, some of the alarm responses that were observed in trial 3 appeared to be in response to the noise. Therefore, it can be assumed that, if the damage to the ears did compromise hearing, it did not prevent all fish from sensing the air gun noise at high levels.

## 4.2. Squid

The behaviours observed in the squid in response to air gun noise exposure could be classified into the same categories as the observed fish behaviour. That is, alarm responses and changes in swimming patterns and vertical position. The response of squid to air gun noise has not been previously reported in the literature.

The squid in trial 4 were observed ejecting ink at the first air gun signal. The primary function of this response in squid is thought to be predator evasion (Hanlon and Messenger, 1996a). The dense cloud of ink can either act as a facade or decoy (i.e. pseusdomorphs). Squid ink contains L-DOPA and dopamine which are both molecules that act as olfactory stimuli (Lucero et al., 1994). Therefore, squid ink may also act as an alarm substance. Subsequent to ejecting the ink the animals were observed jetting away from the direction of the air gun. Jetting in squid is a known escape response usually mediated by the 'giant fibres' (Hanlon and Messenger, 1996a; Otis and Gilly, 1990; Wells and O'dor, 1991). It is assumed that, if the squid had not been held captive, they would have fled the area.

The ejection of ink was not observed in trial 5 or 6. The first air gun signal in trial 4 was received at the cage at 162 dB re 1  $\mu$ Pa<sup>2</sup>.s whereas in trial 5 and 6 the air gun was started further away from the cage and therefore the signal received by the squid was lower at the beginning of the trials that is, 136 dB re 1  $\mu$ Pa<sup>2</sup>.s and 144 dB re 1  $\mu$ Pa<sup>2</sup>.s, respectively. However, although the intensity of the air gun signal did exceed 162 dB re 1  $\mu$ Pa<sup>2</sup>.s in both trial 5 and 6, the squid did not display the inking behaviour. This result is only preliminary, but it would appear that the responses displayed by the squid are somewhat dependant on the animals becoming accustomed to the noise at low levels.

This effect has been reported in fish and marine mammals (Blaxter and Hoss, 1981; McCauley, 1994). Blaxter et al. (1981) found that exposing herring (*Clupeaharengus*) to a sound signal that took many cycles to reach maximum amplitude increased the threshold for the sound to induce a startle response. It is interesting to note that in trial 4, although the noise level did exceed 162 dB re 1  $\mu$ Pa<sup>2</sup>.s after the first signal as the air gun approached the cage, the inking response was not observed again. Either the squid had depleted their ink reserves or it was the habituation to the noise that reduced the startle response. General habituation (i.e. response to predators) has been reported in squid (Long et al., 1989) and the pooled results from all squid trials indicate a significant decrease in alarm responses in the second exposure to air gun noise when compared with the first, supporting this line of thought.

An alternative explanation for the decrease in the severity and number of alarm responses to successive air gun signals is that the noise exposure resulted in impaired hearing and therefore affected the subsequent behavioural responses of the squid. Recent research has shown that exposure to low frequency sounds can result in damage to the sensory epithelium of the organ thought to be responsible for hearing in cephalopods, that is the statocyst (Andre et al., 2011). If this was the case, it appears that any alteration in hearing ability resulting from the noise exposure is not permanent, as the same squid were used in trial 5 and 6 with similar number of alarm responses observed in both trials.

In trial 5 the squid were observed displaying what was assumed to be aggressive behaviour towards each other and towards camera 1. At the conclusion of the trial a mass of squid eggs were observed on camera 1. The behaviour that was witnessed is classic squid spawning behaviour (Hanlon and Messenger, 1996b; Jantzen and Havenhand, 2003). Sepioteuthis australis are known to spawn in sea grass meadows, attaching their eggs to blades of seagrass (Moltschaniwskyj and Pecl, 2003). Therefore, it is possible that it was the presence of suitable egg deposition structure that is, the camera, in the cage that stimulated them to spawn rather than being a response induced by the air gun noise. However, in some animals, particularly invertebrates, exposure to a stressor stimulates reproductive behaviour (Battaglene et al., 2002; Braley, 1989; Pattipeiluhu and Melatunan, 1998). Although the reproductive behaviour of S. australis found off the coast of Western Australia is not well documented, it is known from populations on the south coast of Australia that spawning during the day is not unusual and does not seem to be restricted by season (Jantzen and Havenhand, 2003; Moltschaniwskyj and Pecl, 2007; Pecl, 2004).

It should also be noted that the reproductive behaviour observed in trial 5 certainly would have affected the scoring of some behaviours. In particular, vertical position and swimming patterns would have been influenced. Also, there was some concern that, as squid are traditionally thought to be semelparous, the experimental animals would become moribund after spawning which could affect the behaviour of the squid in trial 6. However, evidence suggests that *S. australis* is capable of multiple spawning during its short life time of approximately 12 months (Pecl, 2001, 2004) and the animals showed no signs of approaching death in the 5 days after trial 5 or during trial 6.

In general, the only significant behavioural alteration that the squid displayed in response to air gun noise was the frequency of alarm responses, particularly at higher noise levels. However, there was a trend for the squid to increase swimming speed as the air gun approached and then remain relatively stationary towards the water surface as the air gun signal became most intense. A possible explanation for this result is that the animals detected the approximate 12 dB decrease in noise levels at the water's surface compared to the levels at depth and therefore remained at the surface while the air gun signals were most intense (i.e. avoidance behaviour). In support of this theory, becoming motionless is a common component of crypsis, a behaviour that squid are renowned for when threatened (Hanlon and Messenger, 1996a; Smith, 1997).

Although some interesting behaviours were observed in the squid in response to air gun noise in this study, the results are preliminary. From the results it would appear that noise levels greater than 147 dB re 1  $\mu$ Pa<sup>2</sup>.s are required to induce avoidance behaviour in this species. The results also suggest that a ramped (i.e. gradual increase in signal intensity) air gun signal and prior exposure to air gun noise decreases the severity of the alarm responses in this species.

## 5. Conclusions

The behavioural responses observed in this study do not provide conclusive evidence for the responses that air gun noise may have on the behaviour of wild, unrestrained fish and squid. However, the consistency between the types of behaviours induced by air gun noise in this study and in other reports suggests that to some level we can predict the behavioural response of fish to air gun noise and hence, seismic surveys.

There are many factors that must be considered when deciding on the potential effects of seismic survey noise in a specific area including survey duration, array characteristics, ecology of the surrounding area and indirect, as well as, direct effects. The direct effects of air gun noise on the behaviour of exposed captive species have been reported in this study. However, the changes in behaviour observed could have impacts on other aspects of the exposed species. For example, energy expenditure associated with repetitive alarm responses could be an issue (Godin, 1997). Also, the behavioural alterations that occurred to these species would undoubtedly have an effect on other species within the ecosystem. Lokkeborg and Soldal (1993) reported that, while long line and trawl catches of cod (Gadusmorhua) decreased after exposure to noise from an actual seismic survey, the catch of prawns, the natural prey of the cod, increased. Likewise, Engas et al. (1996) observed a greater reduction in the number of large fish than that of small fish in an area exposed to a 5 days seismic survey. A number of explanations for this change in distribution have been put forward, for example, different swimming speeds, differing hearing ability and habituation rates. Whatever the reason, the altered distribution could have significant effects on the entire ecosystem.

Research indicates precise responses to air gun and seismic survey noise are species specific and dependent on the actual noise exposure regime. Therefore, as there is no such thing as a typical seismic survey, mitigation techniques should be developed and appropriate risk assessment needs to be undertaken prior to commencing a survey. Risk assessments should include characteristics of the specific survey to be used, modelling of probable noise propagation in the area to be surveyed and knowledge of the species present and awareness of their biology. Further research into the effects of seismic surveys on marine fish and invertebrates is important so that results can be used to design effective mitigation techniques that benefit the surrounding aquatic life and commercial fisheries, without compromising the economic value of offshore seismic exploration.

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