Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity

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ABSTRACT

Assessments of anthropogenic impacts on marine wildlife often concentrate on large-scale displacement. However, changes in the activity patterns of animals that do not flee could also affect their energy balance. Increasing boat traffic raises concerns for exposed marine mammals. Understanding risk perception is critical for effective mitigation and management, but it is hard to disentangle the effect of noise, physical presence of boats, and context. We used passive acoustic techniques to quantify how boat disturbance affected bottlenose dolphin foraging activity, and characterized the conditions influencing responses. To account for potential masking effects of boat noise on foraging vocalizations (buzzes), we developed a novel procedure to estimate the relationship between buzz detection probability and noise levels in particular 1/3 octave bands. Bayesian hierarchical modeling was then used to assess the effect of boat presence on buzz occurrence, as well as potential interactions with noise level, location, year, day, hour, dolphin group size, and boat type and number. Our results indicate that boat presence was associated with a short-term 49% reduction in foraging activity, but there was no relationship with noise level. Differences between sites and between years suggested a variable susceptibility depending on foraging conditions. This effect increased for increasing number of boats and depended on boat type. This is the first study conclusively showing that boat physical presence, and not just noise, plays a large role in disturbance.

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1. Introduction

Human disturbance can affect the behavior of exposed wildlife (Frid and Dill, 2002; Beale and Monaghan, 2004a), but responses vary depending on the animals' overall ecological landscape (Gill et al., 2001; Beale and Monaghan, 2004b). The quality of a foraging patch, social context, condition of an individual and its previous encounters with specific stressors can all influence the onset and intensity of any response (e.g. Blumstein, 2006). As a result of such trade-offs, individuals might decide to tolerate disturbance rather than flee from exposed areas (Bejder et al., 2009). This chronic exposure can elicit less overt responses, such as a change in activity budgets (Gill et al., 2001; Bejder et al., 2009). If foraging time is reduced, this could affect energy intake, with potential implications for an individual's energy balance or their condition and vital rates (Kerley et al., 2002; McClung et al., 2004; New et al., 2013). Understanding the mechanisms that mediate risk perception and how these interact with the overall context of potential disturbances is critical for the development of effective mitigation and management strategies (Beale and Monaghan, 2004a).

Commercial shipping is increasing worldwide, substantially contributing to overall ocean noise (Hildebrand, 2009). In coastal habitats, boat numbers are also predicted to rise (McCarthy, 2004) as human activities in the marine environment develop and diversify (Halpern et al., 2008). Alongside industrial development, recreational boating and wildlife tourism have also been expanding (McCarthy, 2004; O'Connor et al., 2009). This has resulted in concerns over the effects of anthropogenic noise on marine mammals, especially for species that use sound to navigate and find prey (Nowacek et al., 2007). Boat noise can mask important acoustic cues (Clark et al., 2009), affect the behavior of the animals (Pirotta et al., 2012) or their prey (Popper et al., 2003)

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and cause stress (Wright et al., 2007). In addition to noise, the physical presence of boats may disrupt activity patterns, particularly when boats seek direct interactions (e.g. whale watching). In these cases, theoretical studies suggest that individuals often perceive boats as a risk (Frid and Dill, 2002), and therefore respond through avoidance and other anti-predatory tactics (e.g. Nowacek et al., 2001; Lusseau, 2003a; Constantine et al., 2004; Williams et al., 2006; Dans et al., 2012; Christiansen et al., 2013). However, it is hard to disentangle the combined effects of noise and boat physical presence (Pirotta et al., 2013). Because of its physical interference with echolocation processes, boat noise alone could act as the disturbing factor, so that animals respond to elevated noise levels regardless of the nature of the source (Nowacek et al., 2007). Alternatively, the presence of a boat and its movement pattern could affect the animals, irrespective of the noise that it produces, as suggested by kayaks having significant impacts on cetacean activity (Lusseau, 2006; Williams et al., 2011). Most likely, source type and behavior, noise characteristics and context all interact in a complex way to determine a gradient of risk perceived, and combined measures of these factors may be required to appropriately describe and predict animal responses (Ellison et al., 2012). It is also possible that other mechanisms lead to changes in behavior, such as indirect effects through responses by their prey (e.g. Popper et al., 2003) or predator inspection behavior (e.g. FitzGibbon, 1994).

Assessing marine mammal responses to disturbance is challenging, and impact assessments have generally focused on whether animals are displaced from exposed areas (Nowacek et al., 2007; Thompson et al., 2013). Some studies have highlighted the importance of changes in activity budgets of individuals that do not flee (Lusseau, 2003a; Pirotta et al., 2014a), but visual identification of different activities is difficult when feeding events take place at depth (Mann, 1999). Because odontocetes rely on echolocation to navigate and find their prey, passive acoustic techniques can provide a more robust method for monitoring underwater activity (Van Parijs et al., 2009; Marques et al., 2013). Different rates of click repetition identify different functional echolocation processes (Madsen and Surlykke, 2013). In particular, trains of discrimination clicks with short inter-click interval, or foraging buzzes, have been associated with attempted prey captures and used as a measure of foraging activity (Miller et al., 2004; Madsen et al., 2005; Pirotta et al., 2014b). The problem with using such techniques to assess responses to human activities is that human-generated noise may itself interfere with the detection of animal vocalizations (Marques et al., 2013). Ignoring potential detection masking effects can lead to falsely classifying samples where vocalizations are missed because of noise and overestimating the intensity of any response. Effective use of passive acoustic techniques in behavioral response studies therefore requires solutions for estimating whether signals of interest are masked by anthropogenic noise.

This study aimed to characterize the effect of boat disturbance on the activity of Atlantic bottlenose dolphins (*Tursiops truncatus*). We used passive acoustic techniques to quantify dolphin foraging activity from the presence of foraging buzzes. A novel analytical framework was then developed to account for the masking effect of noise on the detection of the buzzes. Acoustic data were combined with visual observations to investigate whether dolphin responses varied under different disturbance, context and social conditions.

2. Materials and methods

2.1. Study area

Our study focused on an isolated coastal population of bottlenose dolphins that ranges along the east coast of Scotland (Cheney et al., 2013). We selected study sites in two deep narrow channels within the Moray Firth: the Sutors (57°41.15′N, 3°59.88′W) and Chanonry (57°35.12′N, 4°05.41′W) (Fig. 1). These sites were known to be used regularly by foraging dolphins (Hastie et al., 2004; Bailey and Thompson, 2010; Pirotta et al., 2014b) and both were exposed to commercial and leisure boat traffic (Merchant et al., 2014). Existing evidence from this area suggests that boat interactions can alter bottlenose dolphins' behavior (Janik and Thompson, 1996; Hastie et al., 2003).

2.2. Acoustic data

Single passive acoustic monitoring (PAM) devices (Wildlife Acoustics SM2M Ultrasonic; http://www.wildlifeacoustics.com) were repeatedly deployed at the two sites during summer 2012 and 2013 (Appendix, Table A1). Gaps in the acoustic time series resulted from equipment failure and logistic constraints. Units were moored in the water column ∼1.5 m above the seafloor, and recorded continuously at a sampling rate of ⩾192 kHz and 16 bits (see Merchant et al. (2014) for calibration details).

2.3. Visual data

Alongside acoustic data collection, land-based observations were conducted from an elevated vantage point overlooking the Sutors in 2013 (Fig. 1). Two trained observers each collected data for one three-hour period per day. Observations were limited to good weather conditions (good visibility and Beaufort < 4). Visual scan samples every 15 min recorded dolphin presence (Altman, 1974) and the number and type of boats. Boats were grouped into four classes: (1) non-interacting motor boats, which included all motor boats that transited through the channel without directly seeking interaction with dolphins; (2) interacting boats, which included tour, research and private boats that directly targeted the dolphins; (3) sailing boats (with sails on); (4) stationary boats. Observation effort covered a radius of ∼1.5 km around the observation point. If dolphins were sighted, additional five-minute scans were performed to record the number of dolphins and the number and type of boats.

2.4. Acoustic analysis

We used the 'Click detector' module in PAMGuard software (Gillespie et al., 2009) to detect clicks from downloaded PAM recordings. From these recordings, we selected a series of training files with varying number and intensity of dolphin clicks and varying levels of noise to develop a custom click classifier. Based upon these data, clicks were classified as being produced by a dolphin when they were shorter than 0.2 ms (with a threshold of 20 dB below the maximum of the smoothed click analytic waveform), the energy in the frequency band 15–50 kHz was 18 dB greater than the energy in the control band 0–5 kHz, the mean frequency for the integration range 0–96 kHz was between 10 and 96 kHz, and the click showed a maximum of 10 zero crossings. Whilst conservative, these settings gave us confidence that false positives were excluded, and only louder and closer clicks were retained. Since we were not interested in assessing the overall number of clicks, this was not expected to affect our conclusions.

From the time series of detected clicks, we calculated the time elapsed between each consecutive click (inter-click interval; ICI). A Gaussian mixture-model was fitted to the log-transformed ICIs to identify different echolocating processes (Pirotta et al., 2014b). Each ICI was classified as either a regular ICI (regular clicking for navigation and prey searching), a buzz ICI (buzzes associated with attempted prey captures), or an inter-train ICI (pauses between click trains) (Madsen and Surlykke, 2013). The occurrence of buzz
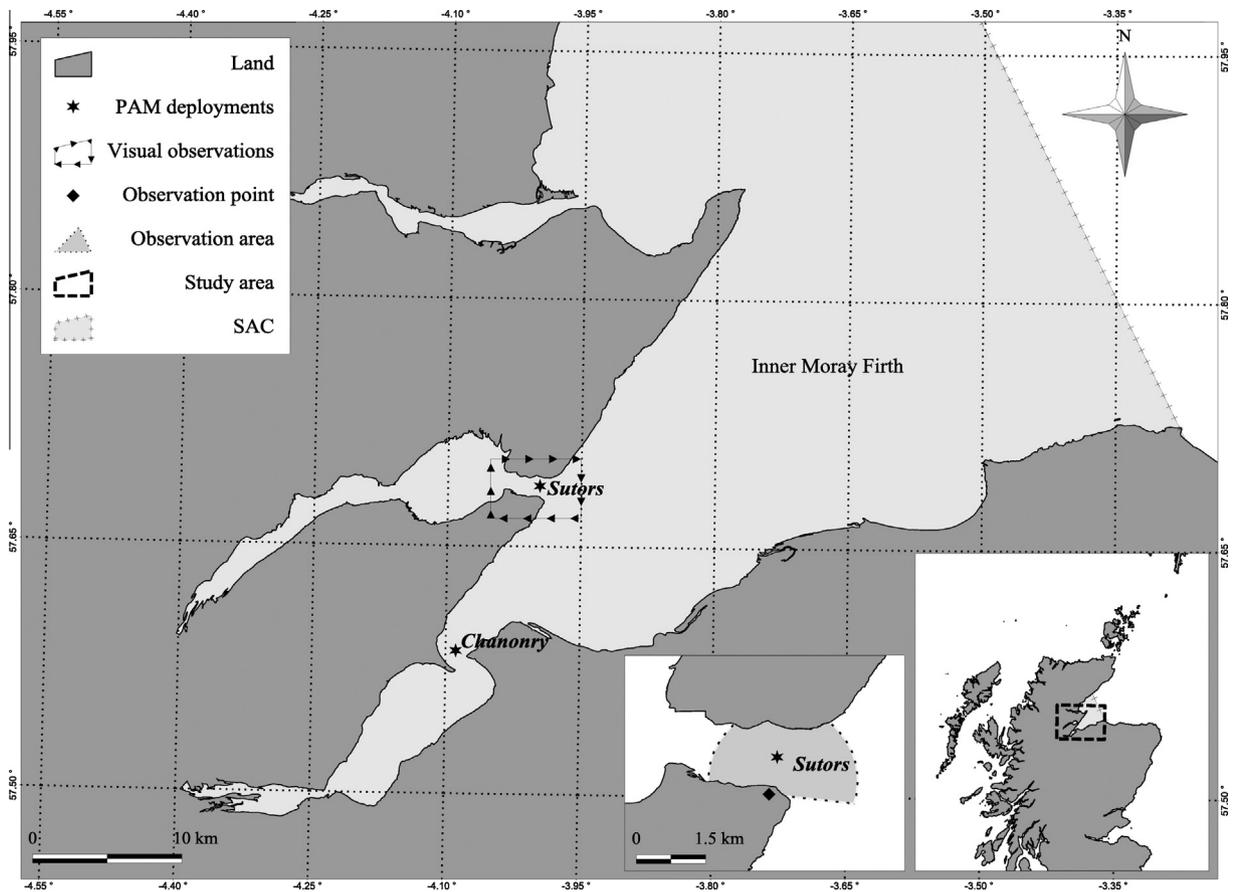
Fig. 1. Map of the study area, with deployment locations and the observation area in the Sutors.

ICIs was evaluated in each minute where at least one ICI was detected.

Acoustic recordings were also analyzed to quantify natural and anthropogenic noise, following the procedure described in Merchant et al. (2014). The boat-detection algorithm described in Merchant et al. (2012) was used to identify boat passages at 1-min resolution, using a 12 dB threshold and a 60-min window.

2.5. Noise masking

We considered the occurrence of buzz ICIs in those samples where at least one ICI was detected. However, masking by boat noise could bias these results because buzz clicks have lower source levels (Madsen and Surlykke, 2013) and are more likely to be masked than regular clicks. To avoid confusing any reduction in buzzing rates with the selective masking, we needed to account for differential masking in our modeling. This was achieved through a novel procedure whereby we determined the relationship between: (i) the ratio of foraging buzzes to regular clicks detected; and (ii) boat noise level. We constructed a training dataset with buzz and regular clicks overlaid on sample recordings with varying levels of boat noise. We then determined the frequency band of boat noise that best indicated buzz detection probability as outlined below.

Firstly, we selected three 1-min recordings with many regular and buzz clicks and no boat (dolphin samples). Then, we identified two 1-min samples corresponding to boat passages where no dolphin was detected (boat samples). These vessels were chosen as representative examples of loud vessel types observed during the study. The first sample corresponded to the passage of a tanker (Betty Knutsen, Shuttle tanker), generating noise predominantly at the low fre-

quencies (Appendix, Fig. A1). The second sample contained the passage of a smaller boat (Fugro Saltire, Offshore industry support vessel), characterized by higher frequency noise (Appendix, Fig. A1). While other vessel types could be identified, these were not loud enough or with a sufficiently different frequency spectrum to justify inclusion. The two boats chosen were considered the extremes of a spectrum of loud vessels emitting noise at variable frequencies. Boat broadband (0.1–10 kHz) noise level was incrementally reduced until its contribution was similar to ambient, i.e. from 158 to 110 dB re 1 μPa^2 (for the large boat sample) and from 145 to 112 (for the smaller boat sample) in steps of 3 dB using a custom-written script in MATLAB, generating a series of 1-min files with decreasing noise level for each boat sample (noise files).

We then overlaid each noise file with each dolphin sample, and processed the resulting files (87 in total) following the procedure described in Section 2.4. For each file, we calculated the total number of clicks and the number of buzz clicks detected using PAM-Guard. We initially plotted the proportion of buzz clicks over the total number of clicks as a function of the broadband level of noise and found that, because of the different frequency composition in the two boat samples (Appendix, Fig. A1), the two types of boat noise had a different masking effect on the buzzes (Fig. 2a). Since broadband noise level did not offer a representative measure of signal masking, we instead identified the 1/3 octave frequency band that minimized the difference in estimated detection probability between the two boat samples. In other words, we tested how buzz detection probability declined with noise level in different 1/3 octave bands, and selected the band where this relationship was consistent for the two boat types, i.e. regardless of how the energy was distributed across the other frequency bands. To do so, we calculated the noise level in each 1/3 octave band for each
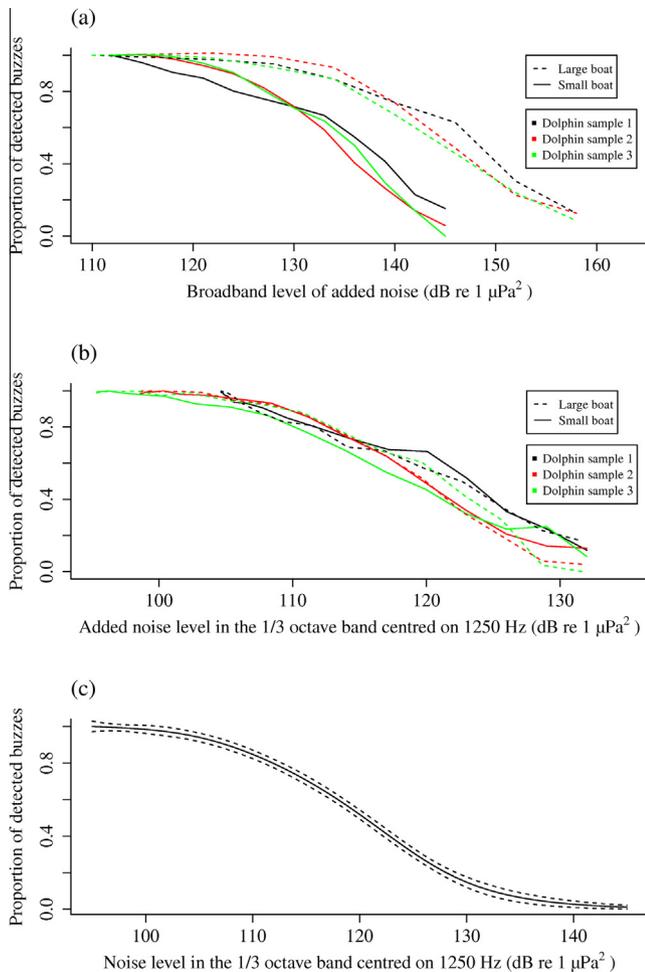
Fig. 2. Results of the estimation of buzz detection probability. (a) Relationship between broadband noise level (0.1–10 kHz) and buzz detection probability for the two boat samples; (b) relationship between noise level in the 1/3 octave band centered on 1250 Hz and buzz detection probability for the two boat samples; (c) estimated buzz detection probability as a function of noise level in the 1/3 octave band centered on 1250 Hz.

file, and fitted a binomial Generalized Additive Model (GAM) (Hastie and Tibshirani, 1990) to the proportion of buzzes in each file using package mgcv in R (R Development Core Team, 2013). Dolphin sample number was also included in the model as a factor to account for the different original proportion of buzz clicks in each dolphin sample. For every model, the percentage deviance explained and R^2 value were calculated as a measure of goodness-of-fit to the data. The model with the highest percentage deviance explained and highest R^2 corresponded to the optimal 1/3 octave band to describe buzz detection probability, i.e. the one yielding a consistent relationship between detection probability and noise level irrespective of boat type.

We used the GAM fitted to the most representative 1/3 octave band to predict the expected proportion of detected buzz clicks over the range of noise levels in that band recorded across our entire dataset. These proportions were divided by the maximum predicted proportion to scale them to 1, producing a detection probability function.

2.6. Statistical analysis

2.6.1. Acoustic-only

We used Bayesian hierarchical models fitted in OpenBUGS 3.2.1 (Thomas et al., 2006) to test the effect of several covariates on

dolphin buzzing activity. A hierarchical model is composed of a process model, describing the underlying (and unobservable) biological process, and an observation model that probabilistically formulates the mechanisms generating the observable data (Royle and Dorazio, 2008). Specifically, we developed a binary process model, where the response variable was the presence or absence of buzz ICIs in each minute of recording when dolphins were present (i.e. where at least one ICI was recorded). Because we expected buzzing activity to be temporally autocorrelated (Pirotta et al., 2014b), we constructed an autoregressive correlation structure (defined by the autocorrelation parameter ρ) for model residuals within each day of data collection (see Appendix). We then formulated the observation component of the hierarchical model. Particularly, we wanted to account for noise potentially compromising the detection of the buzzes. The detection probability function we previously estimated (Section 2.5) described the probability of detecting a buzz given the recorded noise level in the selected 1/3 octave band. This was used as the binary observation model, so that a presence data point (i.e. a minute with recorded buzz ICI) could be incorrectly classified as an absence (i.e. no buzz ICI detected) based on the detection probability associated with the concurrent noise level in the band of interest (Appendix). Once the modeling framework was finalized, we tested the effect of the presence of a boat (as determined by the boat-detection algorithm) on the probability of buzz ICI occurrence in each 1-min sample. We also assessed the occurrence of buzz ICIs in the five minutes before and after a boat passage, as opposed to the occurrence of buzz ICIs at any other time (for this analysis we excluded the periods where a boat was present, and the after/before periods, respectively). Moreover, we tested the effect of the broadband level of noise, the noise level in the selected 1/3 octave band, the hour of the day and its interaction with the boat effect. To assess any temporal or spatial trend in the response, and because of the uneven effort coverage between the two sites and across time, we ran the following models on subsets of the data. We used only the data from 2012 to investigate the effect of the interaction between boat presence and the location of the deployment. We tested the effect of the Julian day and its interaction with boat presence only in 2013 in the Sutors, and in 2012 in Chanonry. We also tested whether this relationship was not linear, by including a quadratic and a cubic polynomial term for Julian day. Finally we assessed whether there were any differences between the two years, considering only the data from the Sutors.

We used indicator variables to measure the evidence for the inclusion of each effect in the model, as described by Dellaportas et al. (2002) and Kuo and Mallick (1998). Under this procedure, each regression coefficient β is multiplied by a binary indicator w_β that has a Bernoulli prior with $p = 0.5$. The posterior of w_β is a measure of the probability that the associated effect should be retained in the model. Posterior parameter estimates were model-averaged based on these probabilities (Kéry, 2010).

For each model, Markov Chain Monte Carlo (MCMC) algorithms were iterated until the parameters of interest converged. Convergence and appropriate burn-in were identified by visually inspecting trace plots. Once burn-in iterations were removed, we checked that the absolute value of Geweke's diagnostic was below 1.96 for all parameters (Geweke, 1992). This diagnostic was calculated using the package coda in R. We retained every 10th sample in the chain to reduce sample autocorrelation.

2.6.2. Acoustic and visual

Where acoustic sampling periods were concurrent to visual observations, we associated the total number of boats present, dolphin group size and prevailing boat type (i.e. the type of boats present in the greatest number) with each 1-min recording. We then tested the effect of these variables and other temporal covariates

(Julian day and hour of the day), on the occurrence of buzz ICIs. Interactions between the total number of boats and other covariates were also assessed. The total number of boats and hour of the day were also tested in a non-linear form, using a quadratic and a cubic term. We followed the same modeling procedure described for the analysis of the acoustic-only data, and included indicator variables to investigate covariate effects.

3. Results

Acoustic sampling covered 101 days, of which 65 were in 2012, and 36 in 2013, 43 were in Chanonry, and 58 in the Sutors. Dolphins were detected in 67,055 min. 33% of these 1-min samples contained buzz ICIs, and 5% contained a boat passage. The duration of boat passages varied between 1 and 62 min in the Sutors (median = 3), and between 1 and 49 min in Chanonry (median = 3). Longer boat passages may have resulted from overlapping passages of multiple boats (Merchant et al., 2012). Boat passages mainly occurred during the day in Chanonry, but had a less evident diel pattern in the Sutors (Appendix, Fig. A2). Visual observations from land were carried out on 27 days with concurrent acoustic sampling. Dolphins were detected in 3094 min of the concurrent acoustic samples, and 30% of these samples contained buzz ICIs. The analysis of natural and anthropogenic noise at the two sites based on a subset of these data is described in Merchant et al. (2014).

The best GAM, including the noise level in the 1/3 octave band centered on 1250 Hz (1122–1413 Hz), explained almost 97.7% of the deviance in the detected proportion of buzz clicks ($R^2 = 0.99$), yielding a consistent relationship between buzz detection probability and noise level irrespective of boat type (Fig. 2b). Therefore, we constructed the buzz detection function based on this relationship (Fig. 2c).

Bayesian hierarchical analysis on the acoustic data (Appendix, Table A2) showed that the presence of boats negatively affected the occurrence of buzzes, with an average reduction in buzzing probability of 49% (Fig. 3a). The corresponding indicator variable suggested that this effect should be retained in the model. Conversely, the occurrence of buzz ICIs did not appear to vary substantially in the five minutes before or after the passage of a boat. The broadband level of noise and noise in the 1250 Hz band were not associated with the occurrence of buzz ICIs, nor was the hour of the day, both in the presence and absence of boats. The effect of Julian day on the response was negligible at both sites, and there was no interaction with boat presence. Allowing for a non-linear relationship did not alter this result. However, when considering only data from 2012, there was an interaction between boat presence and deployment location, suggesting that the boat effect on buzzing activity was relatively stronger in Chanonry (average reduction in buzzing probability by 51%) than in the Sutors (average reduction in buzzing probability by 43%) (Fig. 3b). In the Sutors, buzz occurrence also tended to be higher and more variable (Fig. 3b). The interaction between boat effect and year in the Sutors showed that boat presence had a proportionally stronger effect on buzz occurrence in 2013 than in 2012, and that buzz occurrence was higher and more variable in 2012 (Fig. 3c).

The hierarchical analysis for combined acoustic and visual data (Appendix, Table A2) showed that the total number of boats present had a negative effect on the probability of buzz ICI occurrence, going from 0.22 when no boat was present to <0.11 for five or more boats (Fig. 4a). This effect was retained with a probability of 92%. The quadratic and cubic term for the total number of boats were not estimated to be different from 0, suggesting that the relationship was linear on the link scale (although sigmoid on the response scale). There was no interaction between boat effect and group
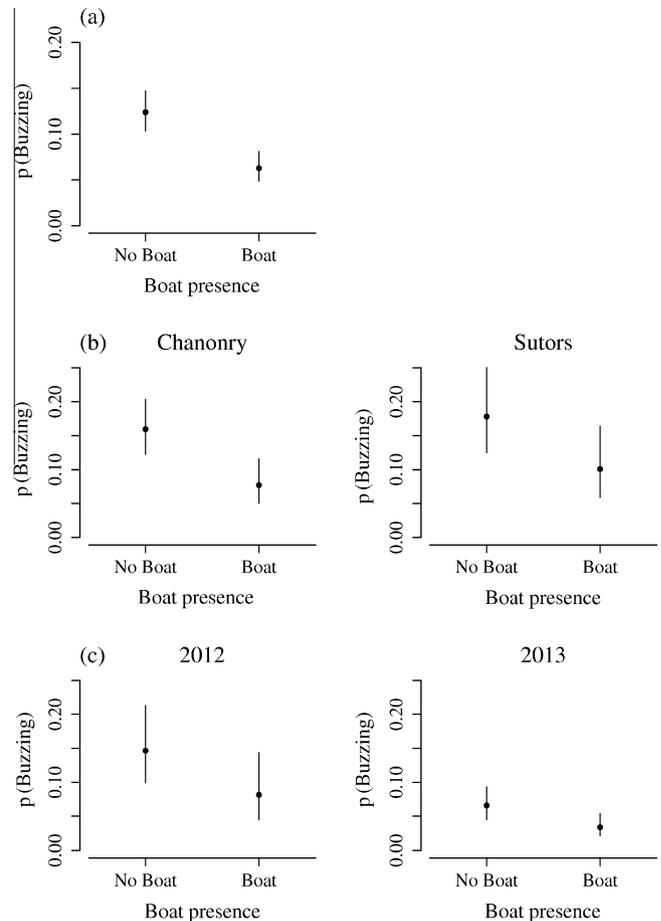

Fig. 3. Results of the Bayesian hierarchical analysis of acoustic-only data. (a) Estimated effect of boat presence on the probability of buzz occurrence. (b) Estimated interaction between the effect of boat presence and location (in 2012). (c) Estimated interaction between the effect of boat presence and year (in the Sutors).

size, although larger groups were associated with a higher probability of detecting a buzz ICI. This probability almost doubled (from 0.22 to 0.39 in the absence of boats) for group size going from 1 to 18. Interacting boats had a relatively stronger effect than non-interacting motor boats, while both sailing and stationary boats had an almost negligible effect (Fig. 4b). Neither Julian day nor hour of the day were associated with buzz occurrence, and their interaction with total number of boats was negligible. Including hour as a non-linear effect did not alter this result.

In all models, the estimated autocorrelation parameter ρ (with a mean estimate ranging between 0.96 and 0.99) suggested that there was strong temporal autocorrelation between consecutive residuals within each day of sampling. The MCMCs for the parameters of interest converged after a variable number of iterations depending on the model, ranging from 5000 to 25,000.

4. Discussion

Our results show that the presence of moving motorized boats affected bottlenose dolphin buzzing activity. Boat passages corresponded to a reduction by almost half in the probability of recording a buzz, but this probability did not vary with broadband noise level or with noise in the 1250 Hz 1/3 octave band. The boat effect did not anticipate the arrival of a boat and did not persist following a boat passage, suggesting that it was limited to the time where a boat was physically present in the sampled area. The short median passage duration relative to the size of the study sites indicates
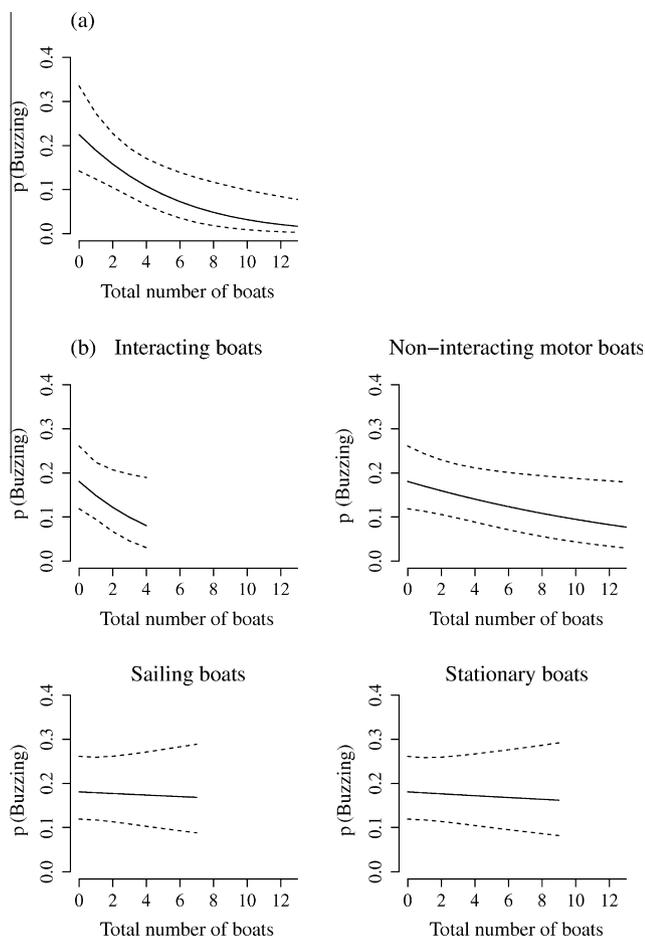
Fig. 4. Results of the Bayesian hierarchical analysis of acoustic and visual data combined. (a) Estimated effect of the total number of boats on the probability of buzz occurrence. (b) Estimated interaction between the effect of the total number of boats and prevailing boat type.

that the acoustically-detected passages corresponded to the time when a boat was close to the hydrophones. Reinforcing the role of boat physical presence, the visual data showed that the effect increased for increasing numbers of boats in the area (Williams and Ashe, 2007; Pirotta et al., 2013). Dolphins appeared to temporarily interrupt their activity when disturbed, staying in the area and quickly resuming foraging as the boat moved away. Environmental impact assessments tend to focus on large-scale behavioral responses and are therefore likely to miss such subtle changes in the activity budget. However, repeated disruptions of foraging activity have the potential to translate into reduced energy intake (New et al., 2013).

This study supports the idea that boats are perceived as a risk and thus elicit evasive tactics (Frid and Dill, 2002; Beale and Monaghan, 2004a). Dolphins might stop foraging to raise vigilance (Li et al., 2011) or to increase their distance from the source of disturbance (Lusseau, 2003a). With the available data, we cannot establish whether the short latency before restarting buzzing resulted from the stressor being known to the animals and thus causing a weaker response, or from the animals being constrained in the amount of time they had to spend foraging. The possibility to compensate for missed feeding opportunities after disturbance might influence the intensity of their response and the drive to resume their previous activity (Stockwell et al., 1991; Stillman and Goss-Custard, 2002). Indirect effects such as responses by dolphins' prey (e.g. Popper et al., 2003) or predator inspection

behavior (e.g. FitzGibbon, 1994) might also have contributed to the observed reduction in foraging activity.

We did not detect any daily trend in buzz occurrence or in the boat effect, and changes over an intermediate time scale (several days) were also negligible. The effect of Julian day was evaluated over short sampling periods, and longer periods of sampling might be expected to reveal stronger seasonal effects (Pirotta et al., 2014b). Given the temporal distribution of the available data, it is therefore not possible to determine whether the year differences found in the Sutors (sampled in September 2012 and June 2013) correspond to genuine inter-annual variation or a seasonal change in buzz occurrence. Using a separate PAM dataset, Pirotta et al. (2014a) also detected more intense buzzing activity in this area during September. The proportionally smaller reduction in buzz occurrence in September 2012 could suggest a lower propensity of the dolphins to stop their activity when disturbed (Stillman and Goss-Custard, 2002; Blumstein et al., 2005). This propensity could depend on patch quality, which could also explain the higher response variability (Beale and Monaghan, 2004b). Context-dependency could explain the proportionally higher and less variable boat effect in Chanonry, as the overall buzzing activity was also lower. However, this variation could also reflect different habitat or prey characteristics affecting dolphins' response (Frid and Dill, 2002).

Differences in basal buzzing probability between seasons or locations could also depend on temporal and spatial variability in group size, since the combination of acoustic and visual data showed that buzzing activity increased with larger groups. This could also mean observed reductions in buzzing activity could have resulted from some individuals leaving a group when exposed to boat disturbance. However, contrary to expectations (Frid and Dill, 2002), the boat effect did not vary depending on the size of the dolphin group. Moreover, the effect on the animals varied depending on the relative abundance of different boat types. Boats that directly interacted with animals were associated with the greatest reduction in buzz occurrence, followed by non-interacting motor boats. The behavior of the disturbance source is expected to influence the perceived risk, and a boat actively following the animals will be more disruptive than one moving along a predictable route (Williams et al., 2002; Lusseau, 2003b). This likely explains why the effect of sailing and stationary boats on buzzing activity was negligible. These boats are also virtually silent. Therefore, while noise level alone was not found to be affecting buzzing activity, the mere presence of boats is similarly insufficient to elicit an activity change. Noise appears to be the medium through which the animals perceive an approaching risk, and may contribute to the threatening effect of the approaching boat (Frid and Dill, 2002). We can conclude that it is the complex interaction between the physical presence of a boat, its noise and its behavior around the animals that affects the perception of risk and determines the onset of a response (Ellison et al., 2012).

From a methodological perspective, we confirm that anthropogenic and natural noise affects the detection of echolocation signals. Although passive acoustic techniques offer a powerful means for investigating marine mammal responses to human disturbances, the consequences of noise on the detection and classification of the signals of interest cannot be ignored (Marques et al., 2013). In the absence of an observation model, we would have overestimated the intensity and duration of the effect of boats on dolphins, and thus misinformed management solutions. We developed a novel approach to deal with noise masking that uses *post hoc* noise trials. Recorded anthropogenic noise was manipulated and superimposed over dolphin recordings, allowing us to estimate detection biases and account for them in a Bayesian hierarchical model. In the present study, we use this approach to adjust for the relatively stronger masking of buzz clicks, but the procedure

can be easily adapted to estimate absolute masking of other marine mammal vocalizations.

Our study quantifies the reduction in buzzing activity that results from boat interactions, providing an indication of the potential foraging disruption and shedding light on the mechanisms that mediate risk perception. For the first time, we conclusively show that the physical presence of boats, and not just the noise they emit, plays a large role in disturbance. Moreover, we characterize the conditions that can intensify or reduce such an effect, and pinpoint the features of the source that are likely to elicit a response. Given the short duration of the observed response, individual dolphins exposed to boat traffic may be able to compensate for missed foraging opportunities after the boats have moved away (Stockwell et al., 1991). However, their ability to compensate, as well as the availability of suitable ecological conditions to do so, is currently unknown, and an increase in the number of interactions might compromise their foraging efficiency and energy balance. With boat traffic increasing worldwide (Hildebrand, 2009), our study has wider implications for managing the exposure of marine mammals to this disturbance and mitigating their responses. If the perception of boats as a risk and the corresponding perceptual mechanisms are validated in different contexts, our results may be used to parameterize individual-based models that evaluate the relevance of the observed responses and predict long-term population consequences (New et al., 2013), allowing for more robust and focused environmental impact assessments.

Data accessibility

The dataset used in this paper is available in the PANGAEA data repository: http://doi.pangaea.de/10.1594/PANGAEA.837769.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.11.003.

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