Marine Mammal Science
April 2013, Volume 29, Issue 2, pages E46–E59
http://dx.doi.org/10.1111/j.1748-7692.2012.00587.x

Delphinid whistle production and call matching during playback of simulated military sonar

Stacy L. DeRuiter[1, a, *], Ian L. Boyd[2], Diane E. Claridge[3], Christopher W. Clark[4], Chuck Gagnon[4], Brandon L. Southall[5], Peter L. Tyack[6]

[1] Service Acoustique et Sismique, Ifremer Centre de Brest, BP 70, 29280 Plouzané, France
[2] Scottish Oceans Institute, East Sands, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom
[3] Bahamas Marine Mammal Research Organisation, PO Box AB-20714, Marsh Harbour, Abaco, Bahamas
[4] Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850, U.S.A.
[5] SEA, Inc., 911 Center Street, Suite B, Santa Cruz, California 95060, U.S.A.
[6] Scottish Oceans Institute, East Sands, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom.

[a] Present address: Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews, Fife KY16 9LZ, United Kingdom.

*: Corresponding author : Stacy L. DeRuiter, email address : stacy_deruiter@yahoo.com

Abstract :

In 2007 and 2008, controlled exposure experiments were performed in the Bahamas to study behavioral responses to simulated mid-frequency active sonar (MFA) by three groups of odontocetes: false killer whales, *Pseudorca crassidens*; short-finned pilot whales, *Globicephala macrorhynchus*; and melon-headed whales, *Peponocephala electra*. An individual in each group was tagged with a Dtag to record acoustic and movement data. During exposures, some individuals produced whistles that seemed similar to the experimental MFA stimulus. Statistical tests were thus applied to investigate whistle-MFA similarity and the relationship between whistle production rate and MFA reception time. For the false killer whale group, overall whistle rate and production rate of the most MFA-like whistles decreased with time since last MFA reception. Despite quite low whistle rates overall by the melon-headed whales, statistical results indicated minor transient silencing after each signal reception. There were no apparent relationships between pilot whale whistle rates and MFA sounds within the exposure period. This variability of responses suggests that changes in whistle production in response to acoustic stimuli depend not only on species and sound source, but also on the social, behavioral, or environmental contexts of exposure.

Keywords : noise ; Sonar ; mid-frequency sonar ; whistle ; behavioral effects ; sound production ; *Pseudorca crassidens* ; *Globicephala macrorhynchus* ; *Peponocephala electra* ; false killer whale ; pilot whale ; melon-headed whale

INTRODUCTION

Anthropogenic sound in the ocean is recognized as a potential threat to marine mammal welfare and population sustainability (National Research Council 2005, Southall *et al.* 2007). As a specific example, a link has been observed between the operation of powerful, military, mid-frequency sonar systems (MFA, operating at about 1 to 10 kHz) and atypical mass strandings and deaths of cetaceans in certain conditions; several species of beaked whales are particularly affected (Frantzis 1998, Simmonds and Lopez-Jurado, 1991, Balcomb and Claridge, 2001, Evans and England, 2001, Fernández *et al.*, 2005, Hildebrand, 2005, Parsons *et al.*, 2008, Filadelfo *et al.*, 2009). Research to date suggests that behavior changes prompted by the sonar are probably one component of the mechanism linking sonar to strandings (Houser *et al.* 2001, Cox *et al.* 2006, Zimmer and Tyack 2007), so several studies have focused on the behavioral responses of cetaceans to military sonars (Tyack *et al.* 2011, Kvadsheim *et al.* 2009). Here, we present data from the Behavioral Response Study 2007-2008 (BRS 07-08) (Tyack *et al.* 2011) in which beaked whales and other toothed whales were intentionally exposed to controlled, simulated MFA sonar signals.

Silencing and avoidance are among the expected responses of marine mammals to military MFA sonar, especially for species like beaked whales that rely on acoustic and behavioral crypsis to avoid threats (Johnson *et al.* 2004, Zimmer *et al.* 2005, Tyack *et al.* 2006) and are thus particularly wary of acoustic stimuli (Barlow and Cameron 2003, Carretta *et al.* 2008). Indeed, beaked whales respond to anthropogenic noise with premature cessation of echolocation clicks and prolonged ascent during foraging dives (Aguilar Soto *et al.* 2006, Tyack *et al.* 2011). Porpoises and other toothed whales that produce narrow-band, high-frequency echolocation clicks may have similar risk-avoidance strategies (Madsen *et al.* 2005*a*, Morisaka and Connor 2007).

However, many delphinid species are highly social. They live in relatively large groups, make frequent use of sound to communicate in both affiliative and agonistic contexts, and may rely in some contexts on social defenses against predators or conspecific competitors rather than fleeing threats or employing acoustic crypsis (Tyack 2000). It is possible that these species respond to acoustic stimuli by modifying their sound production or social behavior, for example by changing group cohesion or whistle production patterns (Lesage *et al.* 1999).

A change in whistle production patterns could involve whistling in response to the sound stimulus, perhaps even imitating it. In contrast to most mammals, there is abundant evidence that dolphins can produce rare spontaneous or consistent trained imitations of anthropogenic (Caldwell and Caldwell 1972, Taylor and Saayman 1973, Herman 1980, Richards *et al.* 1984, Reiss and McCowan 1993) and conspecific sounds (Tyack 1986, Janik and Slater 1998, Janik 2000, Fripp *et al.* 2005). Initial examination of the BRS 07-08 Dtag sound recordings revealed several instances in which, just after exposure to the MFA signal, false killer whales (*Pseudorca crassidens*) produced whistles that sounded similar to the MFA to human listeners (see Fig. 1 for an example). We therefore conducted a quantitative analysis to test whether delphinids exposed to simulated MFA signals responded vocally to the MFA, specifically considering a response in which animals produce a burst of whistles immediately after hearing an MFA sound, which are more similar to the MFA than whistles produced at other times.

METHODS: DATA COLLECTION & FIELD EXPERIMENTS

The data analyzed here were collected during BRS 07-08 at the U.S. Navy's Atlantic Undersea Test and Evaluation Center (AUTEC) in the Tongue of the Ocean, Bahamas. During these experiments, beaked whales and delphinids were tagged with Dtags (Johnson and Tyack 2003, Johnson *et al.* 2006), which recorded sound (192 kHz sampling rate, overall frequency response flat within 3 dB between 0.5 and 67 kHz) and movement data during exposure to a simulated MFA sonar signal.

The MFA signal was a 1.4 s tonal signal with 3 parts: a 0.5 s upsweep from 3.1 to 3.2 kHz, a 0.5 s tone at 3.3 kHz, a 0.1 s silence, and finally a 0.3 s tone at 3.4 kHz (Fig. 1). During each exposure experiment, the signal was transmitted every 25 s, with a total of 30 to 44 transmissions per exposure. The initial sound source level (SL) was 160 dB re 1 µPa rms at 1 m. SL was increased by 3dB with each successive ping to a maximum level of 211 dB re 1 µPa at 1 m.

A subset of the BRS data are considered here, including three datasets from tags placed on a pilot whale (*Globicephala macrorhynchus*, gm07_229b), a false killer whale (*Pseudorca crassidens*, pc08_272a), and a melon-headed whale (*Peponocephala electra*, pe08_273b). Datasets were also available from another pilot whale (gm08_273a) and false killer whale (pc08_270a), but those will not be considered in detail because the animals remained nearly silent throughout the exposure, producing five and four whistles, respectively. Another pilot whale (gm07_229a) was also tagged and exposed concurrently with gm07_229b, but since the two datasets were not independent samples, 229b was selected arbitrarily for analysis and 229a for exclusion.

Details of the tag deployments and controlled exposures of delphinids are presented in Table 1, while more complete descriptions of the experimental protocol (Boyd *et al.* 2008) and the tagging process (Madsen *et al.* 2005*b*) are available elsewhere.

METHODS: ACOUSTIC DATA PROCESSING

We analyzed the time period from the beginning of the MFA exposure period until 25 s after the end of the final transmission. Start times of each whistle and each received MFA signal were determined by inspection of spectrograms produced in Matlab (Mathworks, Natick, MA; nfft = 2048, Hamming window, 50% overlap). All whistles that were visible on the spectrogram were included in the analysis, whether they were produced by the tagged whale or by others in its group. Whistle contours were traced using a semi-automated custom Matlab algorithm. Briefly, the operator clicked on a spectrogram to select the start, end, and several points along the whistle contour. The software traced a smooth curve through the selected points (using the Matlab function "pchip"), displaying results for operator approval. The lowest frequency contour present in the whistle was traced, except in multi-voiced calls where the lowest component only lasted for part of the whistle duration (in such cases, the next-highest-frequency contour that lasted the full call duration was traced). Determination of which calls were overlapping or multi-voiced was made based on relative amplitude and comparison to other calls (most multi-voiced calls occurred many times in the dataset, while pairs of overlapping calls would be chance events). Accuracy of all traced contours was verified by visual inspection of a plot in which the traced contour was overlaid on the whistle spectrogram.

We calculated a similarity index (SI) between each whistle contour and the MFA signal as a function of four measures: duration (absolute value of MFA duration – whistle duration), mean frequency (absolute value of mean MFA frequency – mean whistle frequency), whistle flatness ((Miksis *et al.* 2002), with flatter whistles considered more similar to the MFA), and whistle frequency range (total frequency range covered by whistle divided by median frequency, with smaller values considered more similar to MFA). These four metrics were computed, scaled to range from 0 to 1 by dividing each whistle's score by the maximum observed value for that tag dataset. In cases where lower scores indicated higher similarity to the MFA sound, the scaled values were subtracted from 1 so that higher scores indicated greater similarity to the MFA. Finally, these scores were summed to obtain a SI value for each individual whistle.

METHODS: STATISTICAL ANALYSIS

All statistical tests were applied to each group of whales (that is, each Dtag recording) separately. We used an overall significance threshold of $P = 0.02$ ($P = 0.05$ with a Bonferroni correction factor to account for the three groups tested). We tested for autocorrelation of inter-whistle intervals and calculated Greenwood's test statistic (Greenwood 1946) to verify that whistles occurred in clusters. To test for a correlation between whistle-MFA similarity and the time since the last MFA reception, we fitted a straight line to a scatter plot of SI as a function of time since the last MFA reception, then applied a rotation test (DeRuiter and Solow 2008), using the line's slope as the test statistic. We compared the observed slope of the SI data with those obtained in 100,000 random "rotations" of each dataset. Each rotated dataset was constructed by randomly re-assigning the nominal start time of the exposure period, while maintaining the whistle time-series, the spacing between MFA sounds, and the exposure duration. We chose this test rather than a standard linear regression to account for autocorrelation and clustering in the time series of SI scores caused by variations in call rates with behavior or by call-type matching (Janik 2000, Miller *et al.* 2004).

We carried out a second analysis using a point-process time series model (Truccolo *et al.* 2005) to quantify temporal variation of whistle production rate. This model related whistle rate to time since the most recent MFA reception, time since the first MFA reception, and number of whistles occurring in the preceding time interval. For each group of whales, a whistle time series (with value 1 at whistle start times and 0 at all other times) was constructed using 0.01 s time steps, equal to the time resolution of our spectrograms. These time series were then modeled according to the equation

$$\lambda(t_k|H_k) = \exp\{\mu + \beta_1 T_k + \beta_2 S_k + \beta_3 (N_k - N_{(k-w/\Delta)})\} , \quad (1)$$

where $\lambda(t_k|H_k)$ is the conditional intensity function giving the probability of a whistle starting at time interval *k* (t_k), given the history up to that time point (H_k); T_k is the time since the first MFA reception; S_k is the time since the most recent MFA reception; (N_k-$N_{(k-w/\Delta)}$) is the number of whistles that started in a *w*-second interval before time-step *k* (Δ being the time-step size, here 0.01 s); and μ (the background whistle rate), β_1, β_2, and β_3 are parameters to be estimated by the model. The "preceding time interval" term accounts for clustering and is analogous to the ensemble rates modeled by Truccolo *et al.* (2005). Intervals of 1, 5, 10, 20, 30, 40, 50, and 60 s were tested for each dataset. Akaike's information criterion (AIC) was used to select the optimal preceding-interval duration and determine which terms to include in the model for each dataset, including additional terms only if they decreased AIC by at least 2, but selecting the single "preceding time interval" with minimal AIC in all cases. Models were fitted using generalized linear modeling (GLM) methods in R (http://www.R-project.org).

We repeated the point-process analysis considering only MFA-like whistles - a subset of whistles most similar to the MFA. Whistles scoring above the 80th percentile for SI were considered to be MFA-like; this choice of the 80th percentile is relatively arbitrary, but statistical inference regarding the relationship between MFA-like whistle rate and time since the last MFA reception was the same for 7 other thresholds ranging from the 50th to the 95th percentiles (data not shown).

RESULTS

Figure 2 shows all traced whistle contours. The number of whistles detected during the MFA exposure and contour-traced for further analysis was 466 for the false killer whales, 173 for the pilot whales, and 53 for the melon-headed whales (Table 2). Of these, 95, 114, and 11 respectively were classified as MFA-like. Figure 3 shows examples of the SI classification, illustrating that lower-frequency, less-frequency modulated whistles were classed as MFA-like while highly modulated, higher-frequency whistles had the lowest SI scores. The melon-headed whales had fewer whistle contour types (~3) than the other groups, so absolute frequency and duration of the whistles played a larger role in determining SI of that dataset.

For all three groups, whistle times were both clustered and auto-correlated (Table 2), indicating the use of methods such as the rotation test and the point-process model which take such clustering into account.

For the false killer whales, the correlation/rotation test indicated a slight negative relationship between SI and time since last MFA reception, so whistles were most similar to the MFA sound immediately after each MFA reception, then similarity declined until after the next reception ($P = 0.0041$, Fig. 4, Table 2). Figure 2 also shows evidence of this trend, since there are more unmodulated, lower-frequency whistles at short time delays after the MFA sound. Other groups showed no significant trends ($P > 0.02$, Fig. 4, Table 2).

Point process analysis results for the false killer whale (pc08_272a) group confirmed the rotation test findings, as both overall and “MFA-like” whistle rates were inversely proportional to time elapsed since the last MFA reception (Fig. 4, Table 2). In other words, after each MFA reception, the group increased whistle production rate and made more-MFA-like whistles. There was also a slight reduction in the rate of MFA-like whistles, but not the overall whistle rate, as overall time since start of exposure (and thus MFA received levels) increased (Fig. 4, Table 2).

In contrast to the false killer whale pattern, there was an increase in overall whistle rate by the melon-headed whales as a function of time since last MFA reception (that is, a transient reduction in whistle rate immediately following each MFA reception); the pilot whales showed no such trends (Table 2, Fig. 2). In all cases with adequate sample size (n>11), the point process models indicated a dependence of whistle rate at any given moment upon whistle rate in the preceding 10-50 s; they thus indicate the time scale over which individuals are modulating their whistle rates in response to group whistling activity.

DISCUSSION

Results of the two independent statistical approaches applied in this study (Correlation/Rotation Test and Point Process Method) consistently support the idea that a group of false killer whales increased their whistle rate, and produced more MFA-like whistles, just after hearing each of a series of MFA transmissions. Whistle production rate and whistle-MFA similarity were both highest immediately following each individual MFA reception, then declined over the 25 s period preceding the next MFA reception. This result is consistent with previous anecdotal reports that delphinids whistle back at and imitate sonars and other active acoustic devices (*e.g.*, Hager 2008, S. Baumann-Pickering[1], C. Clark, unpublished observations). Our results complement those of Alves and colleagues, obtained during a study in which long-finned pilot whales (*Globicephala melas*) underwent controlled exposure to military sonar sounds.[2] Alves *et al.* found that some (but not all) pilot whale groups changed their call production patterns during the exposure, increasing their production rate of calls with contours

---

[1] S. Baumann-Pickering, Marine Physical Laboratory, Whale Acoustics, Scripps Institution of Oceanography, 9500 Gilman Dr., La Jolla, CA 92093-0205. Personal Communication, 8/2010.

[2] A. Alves (Bute Building, University of St Andrews, St Andrews, Fife KY16 9TS, UK), R. Antunes,F.-P. A. Lam, P. Kvadsheim, and P. J. O. Miller. Manuscript in review entitled "Vocal matching of frequency-modulations of sonar signals by long-finned pilot whales (*Globicephala melas*)." Personal Communication, 5/2011.

similar to those of the sonar stimuli. Our findings are also consistent with Rendell and Gordon (1999), who reported increased whistle rates from a group of long-finned pilot whales immediately following periodic receptions of 4 to 5 kHz military sonar transmissions, although these whales did not increase production rates of the whistle type most similar to the sonar signal. Finally, the changes here observed in false killer whale whistle production patterns are reminiscent of the call-type matching observed in vocal exchanges between socializing bottlenose dolphins (*Tursiops truncatus*) (Janik 2000), killer whales (*Orcinus orca*) (Miller *et al.* 2004), and pilot whales (Sayigh *et al*. in press).

In contrast to the false killer whales, melon-headed whales had lower whistle rates immediately after each individual MFA reception, while pilot whales showed no trends. Previous research has shown that whistle production rates in pilot whales and other delphinids vary greatly with behavioral state (Taruski 1979, Weilgart and Whitehead 1990, Watwood *et al.* 2005, Quick and Janik 2008). Given the available data, it is not possible to determine whether this observed variability of responses is rooted in differences between individuals/groups, species, or behavioral/social contexts. However, in a similar study of long-finned pilot whale whistle production during mid-frequency sonar exposure, only about 25% of observed groups matched sounds as observed here.[2] The whistle repertoire of pilot whales in particular is extremely varied and encompasses the frequency range of the MFA signal, so the differences between their responses and those of the false killer whales are not likely caused by physiological limitations.

The function of the observed responses to the MFA sound is unknown. Delphinid whistles are used for communication, most often in affiliative contexts (Tyack 1998). The false killer whales made more MFA-like whistles just after MFA signal reception, suggesting that they may have been roughly imitating the sonar or incorporating some features of the MFA sound into their whistles. The hypothesized functions of such acoustic matching by animals vary widely, and include the development of varied repertoires and the use of learned calls to indicate identity or group membership (Krebs and Kroodsma 1980, Tyack 2008). Acoustic matching sometimes plays a role in deterring predators, raising an alarm, or attracting prey (Rowe *et al.* 1986, Chu 2001, Goodale and Kotagama 2006, Barber and Conner 2007, Marshall and Hill 2009). In some social interactions, particularly among songbirds, imitation or matching of a conspecific's call type can function as a challenge or threat (*e.g.*, Krebs *et al.* 1981, Arak 1983, Searcy and Beecher 2009). However, for many species, acoustic matching is an affiliative gesture, with convergence of call characteristics among members of a social group helping to build and sustain social bonds (reviewed by Tyack 2008).

The observed behavior of the false killer whales in response to the MFA might thus be an adaptive mechanism to expand the vocal repertoire, an affiliative or agonistic response, or a predator-avoidance response. We must also consider the possibility that the false killer whales were changing their call production patterns in response to the MFA sound, but that the increased similarity of the two sounds was coincidental. Previous work has observed that bottlenose dolphin whistle rates increase and whistle modulation decreases when they are under stress (Caldwell *et al.* 1970, Esch *et al.* 2009), when ambient noise is high (Morisaka *et al.* 2005), or as vessels approach (Buckstaff 2004). This type of reaction could explain our results if false killer whales respond to stress and/or noise as dolphins do, and if such changes occur and then decline over periods as short as the 25 second intervals studied here.

The observed whistle response of false killer whales to MFA clearly differs from some commonly discussed reactions to anthropogenic noise, such as avoidance responses and silencing (although we did see a very subtle silencing effect in the melon-headed whale dataset). For highly social delphinid species that communicate extensively using sound and rely on group defenses rather than acoustic or behavioral crypsis to guard against predation and other threats, vocal responses and changes in group cohesion or group behavior may be the dominant type of reaction to such stimuli. The methods presented here, which allow detailed quantitative analysis of call rates including the effects of clustering and external covariates, offer a promising avenue toward greater understanding of delphinid social-acoustic behavior in the presence and absence of anthropogenic sounds.

ACKNOWLEDGEMENTS

The authors are extremely grateful to the science party and crew of BRS 07-08 and collaborators at AUTEC, and sincerely thank everyone who contributed to this large team effort. John Buck and Erik Siggelkoe provided Matlab code for dynamic time warping (used in a previous version of this paper). Andy Solow provided statistical advice on an early version of this analysis, and multiple anonymous reviewers provided comments on earlier versions of the paper. This research was funded by the US Office of Naval Research, the US Strategic Environmental Research and Development Program, the Environmental Readiness Division of the US Navy, the US Chief of Naval Operations Submarine Warfare Division (Undersea Surveillance), the US National Oceanic and Atmospheric Administration (National Marine Fisheries Service, Office of Science and Technology) and the Joint Industry Program on Sound and Marine Life of the International Association of Oil and Gas Producers. The research permits were issued to J. Boreman and B. Southall (US NMFS 1121-1900), P. Tyack (US NMFS 981-1578), Bahamas Marine Mammal Research Organisation (Bahamas permit #01/09) and I. Boyd (Bahamas permit

#02/07 and #02/08). Experiments were approved by the WHOI and BMMRO Institutional Animal Care and Use Committees.

LITERATURE CITED

Aguilar Soto, N., M. P. Johnson, P. T. Madsen, P. L. Tyack, A. Bocconcelli, and J. F. Borsani. 2006. Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*)? Marine Mammal Science 22:690-699.

Arak, A. 1983. Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorhinus* (Rhacophoridae). Animal Behaviour 31:292-302.

Balcomb, K. C. III, and D. E. Claridge. 2001. A mass stranding of cetaceans caused by naval sonar in the Bahamas. Bahamas Journal of Science 8:1-12.

Barber, J. R., and W. E. Conner. 2007. Acoustic mimicry in a predator-prey interaction. Proceedings of the National Academy of Sciences 104: 9331-9334.

Barlow, J., and G. A. Cameron. 2003. Field experiments show that acoustic pingers reduce marine mammal bycatch in the California drift gill net fishery. Marine Mammal Science 19:265-283.

Boyd, I. L., D. E. Claridge, C. Clark, B. L. Southall, and P. L. Tyack. 2008. Behavioral Response Study-2007 (BRS-07) Cruise Report (unpublished). Available online at www.sea-inc.net/resources/brs_07finalcruisereport.pdf (accessed 5/11/2011).

Buckstaff, K. C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 20:709-725.

Caldwell, D. K., and M. C. Caldwell. 1972. Vocal mimicry in the whistle mode in the Atlantic bottlenosed dolphin. Cetology 9:1-8.

Caldwell, M. C., D. K. Caldwell, and R. H. Turner. 1970. Statistical analysis of the signature whistle of an Atlantic bottlenosed dolphin with correlations between vocal changes and level of arousal. Los Angeles County Museum of Natural History Foundation, Technical Report no. 8. 31 pp.

Carretta, J. V., J. Barlow, and L. Enriquez. 2008. Acoustic pingers eliminate beaked whale bycatch in a gill net fishery. Marine Mammal Science 24:956-961.

Chu, M. 2001. Vocal mimicry in distress calls of *Phainopepla*s. The Condor 103:389-395.

Cox, T. M., T. J. Ragen, A. J. Read, *et al*. 2006. Understanding the impacts of anthropogenic sound on beaked whales. Journal of Cetacean Research and Management 7:177-187.

DeRuiter, S. L., and A. R. Solow. 2008. A rotation test for behavioural point-process data. Animal Behaviour 76:1429-1434.

Esch, H. C., L. S. Sayigh, J. E. Blum, and R. S. Wells. 2009. Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). Journal of Mammalogy 90:638–650.

Evans, D.L. and G. R. England. 2001. Joint Interim Report, Bahamas marine mammal stranding event of 14 – 16 March 2000. Unpublished report released by the U.S. Department of Commerce and the Secretary of the Navy, vi + 59 pp. Available from: http://www.nmfs.noaa.gov/pr/acoustics/reports.htm

Fernández, A., J. F. Edwards, F. Rodríguez, A. Espinosa de los Monteros, P. Herráez, P. Castro, J. R. Jaber, V. Martín, and M. Arbelo. 2005. “Gas and fat embolic syndrome” involving a mass stranding of beaked whales (Family Ziphiidae) exposed to anthropogenic sonar signals. Veterinary Pathology 42:446-457.

Filadelfo, R., J. Mintz, E. Michlovich, A. D. D'Amico, P. L. Tyack, and D. R. Ketten. 2009. Correlating military sonar use with beaked whale mass strandings: what do these historical data show? Aquatic Mammals 35:435-444.

Frantzis, A. 1998. Does acoustic testing strand whales? Nature 392:29.

Fripp, D., C. Owen, E. Quintana-Rizzo, A. Shapiro, K. Buckstaff, K. Jankowski, R. Wells, and P. L. Tyack. 2005. Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. Animal Cognition 8:17-26.

Goodale, E., and S. W. Kotagama. 2006. Context-dependent vocal mimicry in a passerine bird. Proceedings of the Royal Society B - Biological Sciences 273:875-880.

Greenwood, M. 1946. The statistical study of infectious diseases. Journal of the Royal Statistical Society 109:85-110.

Herman, L. M. 1980. Cognitive characteristics of dolphins. Pages 363-429 *in* Cetacean Behavior: Mechanisms and functions (L.M. Herman, Ed.). New York, NY: Wiley Interscience.

Hager, C. A. 2008. Assessment of the performance of the nearbottom hydrophones of the U.S. Navy Southern California offshore range in detecting, localizing and reconstructing 10-20 kHz odontocete whistles. PhD Thesis, Naval Postgraduate School, Monterey, CA. 81 pp.

Hildebrand, J. A. 2005. Impacts of Anthropogenic Sound. Pages 101-124 i*n* J. E. I. Reynolds, W. F. Perrin, R. R. Reeves, S. Montgomery, and T. J. Ragen, eds. Marine mammal research: Conservation beyond crisis. Johns Hopkins University Press, Baltimore, MD.

Houser, D. S., R. Howard, and S. Ridgway. 2001. Can diving-induced tissue nitrogen supersaturation increase the chance of acoustically driven bubble growth in marine mammals? Journal of Theoretical Biology 213:183-195.

Janik, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289:1355-1357.

Janik, V. M., and P. J. B. Slater. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56:829-838.

Johnson, M. P., P. T. Madsen, W. M. X. Zimmer, N. Aguilar de Soto, and P. L. Tyack. 2006. Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. Journal of Experimental Biology 209:5038-5050.

Johnson, M. P., P. T. Madsen, W. M. X. Zimmer, N. Aguilar de Soto, and P. L. Tyack. 2004. Beaked whales echolocate on prey. Biology Letters 271:S383-S386.

Johnson, M. P., and P. L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE Journal of Oceanic Engineering 28:3-12.

Krebs, J. R., R. Ashcroft, and K. V. Orsdol. 1981. Song matching in the great tit *Parus major* L. Animal Behaviour 29:918-923.

Krebs, J. R., and D. E. Kroodsma. 1980. Repertoires and geographical variation in bird song. Pages 143-177 *in* J. S. Rosenblatt, ed. Advances in the study of behavior. Academic Press, New York, NY.

Kvadsheim, P., F.-P. Lam, P. J. O. Miller, *et al*. 2009. Cetaceans and naval sonar - the 3S-2009 cruise report. Forsvarets forskningsinstitutt, Kjeller, Norway. 133 pp. Available online at http://rapporter.ffi.no/rapporter/2009/01140.pdf (accessed 5/11/2011).

Lesage, V., C. Barrette, M. C. S. Kingsley, and B. Sjare. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. Marine Mammal Science 15:65-84.

Madsen, P. T., D. A. Carder, K. Beedholm, and S. H. Ridgway. 2005*a*. Porpoise clicks from a sperm whale nose - Convergent evolution of 130 kHz pulses in toothed whale sonars? Bioacoustics 15:195-206.

Madsen, P. T., M. P. Johnson, N. Aguilar de Soto, W. M. X. Zimmer, and P. L. Tyack. 2005*b*. Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). Journal of Experimental Biology 208:181-194.

Marshall, D. C., and K. B. Hill. 2009. Versatile aggressive mimicry of cicadas by an Australian predatory katydid. PLoS ONE 4:e4185.

Miksis, J. L., P. L. Tyack, and J. R. Buck. 2002. Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. Journal of the Acoustical Society of America 112:728-739.

Miller, P. J. O., A. D. Shapiro, P. L. Tyack, and A. R. Solow. 2004. Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. Animal Behaviour 67:1099-1107.

Morisaka, T., and R. C. Connor. 2007. Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. Journal of Evolutionary Biology 20:1439-1458.

Morisaka, T., M. Shinohara, F. Nakahara, and T. Akamatsu. 2005. Effects of ambient noise on the whistles of Indo-Pacific bottlenose dolphin populations. Journal of Mammalogy 86:541-546.

National Research Council. 2005. Marine mammal populations and ocean noise: Determining when noise causes biologically significant effects. Committee on Characterizing Biologically Significant Marine Mammal Behavior, Ocean Studies Board, Division on Earth and Life Studies, National Research Council, The National Academies Press, Washington, DC.142 pp.

Parsons, E. C. M., S. J. Dolman, A. J. Wright, N. A. Rose, and W. C. G. Burns. 2008. Navy sonar and cetaceans: Just how much does the gun need to smoke before we act? Marine Pollution Bulletin 56:1248-1257.

Quick, N. J., and V. M. Janik. 2008. Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): Influences of group size and behavior. Journal of Comparative Psychology 122:305-311.

Reiss, D., and B. McCowan. 1993. Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. Journal of Comparative Psychology 107:301-312.

Rendell, L. E., and J. C. D. Gordon. 1999. Vocal response of long-finned pilot whales (*Globicephala melas*) to military sonar in the Ligurian Sea. Marine Mammal Science 15:198-204.

Richards, D. G., J. P. Wolz, and L. M. Herman. 1984. Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*, Journal of Comparative Psychology 98:10-28.

Rowe, M. P., R. G. Coss, and D. H. Owings. 1986. Rattlesnake rattles and burrowing owl lines: a case of acoustic Batesian mimicry. Ethology 72:53-71.

Sayigh, L. S., Quick, N. J., Hastie, G., Janik, V. M., Boyd, I. L., Claridge, D. E., Clark, C., Moretti, David J., Southall, Brandon L., and Tyack, Peter L. (in press). Repeated calls in short-finned pilot whales, *Globicephala macrorhynchus*. Marine Mammal Science (in press).

Searcy, W. A., and M. D. Beecher. 2009. Song as an aggressive signal in songbirds. Animal Behaviour 78:1281-1292.

Simmonds, M. P., and L. F. Lopez-Jurado. 1991. Whales and the military. Nature 337:448.

Southall, B. L., A. E. Bowles, W. T. Ellison, *et al*. 2007. Marine mammal noise exposure criteria: Initial scientific recommendations. Aquatic Mammals 33:411-521.

Taruski, A. G. 1979. The whistle repertoire of the north Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. Pages 345-367 *in* H. E. Winn and B. L. Olla, eds. Behavior of marine animals. Plenum, New York, NY.

Taylor, C. K., and Saayman, G. (1973). Imitative behavior by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour*, *44*, 286-298.

Truccolo, W., U. T. Eden, M. R. Fellows, J. P. Donoghue, and E. N. Brown. 2005. A point process framework for relating neural spiking activity to spiking history, neural ensemble, and extrinsic covariate effects. Journal of Neurophysiology 93:1074-1089.

Tyack, P. 1986. Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry of signature whistles? Behavioral Ecology and Sociobiology 18:251-257.

Tyack, P. L. 1998. Acoustic communication under the sea. Pages 163-220 *in* S. L. Hopp, M. J. Owren, and C. S. Evans, eds. Animal acoustic communication: Sound analysis and research methods. Springer Verlag, New York, NY.

Tyack, P. L. 2000. Functional aspects of cetacean communication. Pages 270-307 *in* J. Mann, R. Connor, P. L. Tyack, and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL.

Tyack, P. L. 2008. Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. Journal of Comparative Psychology 122:319-331.

Tyack, P. L., M. P. Johnson, N. Aguilar de Soto, A. Sturlese, and P. T. Madsen. 2006. Extreme diving of beaked whales. Journal of Experimental Biology 209:4238-4253.

Tyack, P. L., W. M. X. Zimmer, D. Moretti, *et al*. 2011. Beaked whales respond to simulated and actual navy sonar. PloS One 6:e17009.

Watwood, S. L., E. C. G. Owen, P. L. Tyack, and R. S. Wells. 2005. Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 69:1373-1386.

Weilgart, L., and H. Whitehead. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. Behavioral Ecology and Sociobiology 26:399-402.

Zimmer, W. M. X., M. P. Johnson, P. T. Madsen, and P. L. Tyack. 2005. Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). Journal of the Acoustical Society of America 117:3919-3927.

Authors' Final Draft. Published version at DOI: 10.1111/j.1748-7692.2012.00587.x

Zimmer, W. M. X., and P. L. Tyack. 2007. Repetitive shallow dives pose decompression risk in deep-diving beaked whales. Marine Mammal Science 23:888-925.

TABLES

Table 1. Dtag deployments and MFA sonar controlled exposure experiments on delphinids during BRS 07-08.

Tag ID	Species	Date	Time (tag on to tag off, local time)	MFA exposure start-end (local time)	Number of MFA transmissions	Received Level (dB re 1µPa peak)
gm07_229b	Pilot Whales	17 Aug 2007	1415-1728	1458 – 1606*	44	112-129
gm08_273a	Pilot Whales	29 Sept 2008	1022 – 1640	1338 – 1351	30	109-153
pc08_270a	False Killer Whales	26 Sept 2008	0821 – 1319	1254 – 1306	31	122-158
pc08_272a	False Killer Whales	28 Sept 2008	1704 – 2328	1732 – 1744	30	116-161
pe08_273b	Melon-Headed Whales	29 Sept 2008	1333 – 1512	1338 – 1349	30	109-144

*The exposure was suspended from 1502-1552 due to the presence of whales less than 1,000 m from the sound source.

Table 2. Statistical results (model parameter values and p-values). Gray shading indicates results that were not statistically significant at the $p < 0.02$ level. **ΔAIC is the difference between the AIC of the best model and the model with the next-lowest AIC; the subscripted +,-, or 0 indicates that the number of parameters in the next-best model was more, fewer, or the same (i.e., a different value for lag time).**

	gm07_229b	**pc08_272a**	**pe08_273b**
Species	Pilot Whales (*Globicephela macrorhynchus)*	False Killer Whales (*Pseudorca crassidens)*	Melon-headed Whales (*Peponocephala electra)*
Number of whistles (N MFA-like)	173 (114)	466 (96)	53 (11)
SI Correlation/Rotation Test: Fitted Model (P-value)^1	$SI = 2.0 + 0.0010S_k$ (0.58)	$SI = 2.1 - 0.015S_k$ (0.0041)	$SI = 2.1 - 0.0089S_k$ (0.17)
All Whistles: Fitted Point Process Model (parameter P-values) (ΔAIC)	$\lambda(t_k \mid H_k) = \exp\{-6.9 + 0.22(N_k-N_{(k-10/\Delta)})\}$ $(<2x10^{-16}, <2x10^{-16})$ (-2.7_0)	$\lambda(t_k \mid H_k) = \exp\{-5.5 - 0.42S_k + 0.041(N_k-N_{(k-30/\Delta)})\}$ $(<2x10^{-16}, 2.4x10^{-10}, <2x10^{-16})$ (-3.0_0)	$\lambda(t_k \mid H_k) = \exp\{-8.6 + 0.055S_k + 0.19(N_k-N_{(k-40/\Delta)})\}$ $(<2x10^{-16}, 0.0068, 0.00014)$ (-0.8_0)
MFA-like Whistles: Fitted Point Process Model (parameter P-values) (ΔAIC)	$\lambda(t_k \mid H_k) = \exp\{-7.2 + 0.27(N_k-N_{(k-10/\Delta)})\}$ $(<2x10^{-16}, 2.2x10^{-12})$ (-1.4_+)	$\lambda(t_k \mid H_k) = \exp\{-5.3 -0.0015T_k – 0.10S_k + 0.044(N_k-N_{(k-50/\Delta)})\}$ $(<2x10^{-16}, 7.7x10^{-11}, 0.0055)$ (-0.4_0)	$\lambda(t_k \mid H_k) = \exp\{-9.1\}$ $(<2x10^{-16})$ (-0.2_+)

FIGURE LEGENDS

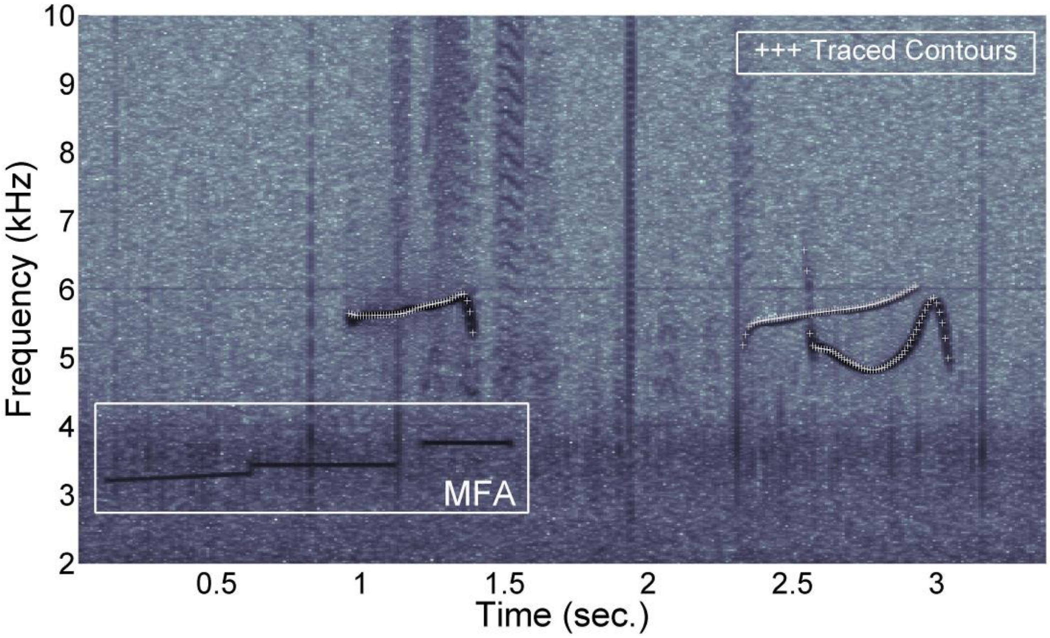

Figure 1. Spectrogram of Dtag acoustic data, showing the MFA signal (inside white box), as well as several false killer whale whistles and their traced contours (white crosses).

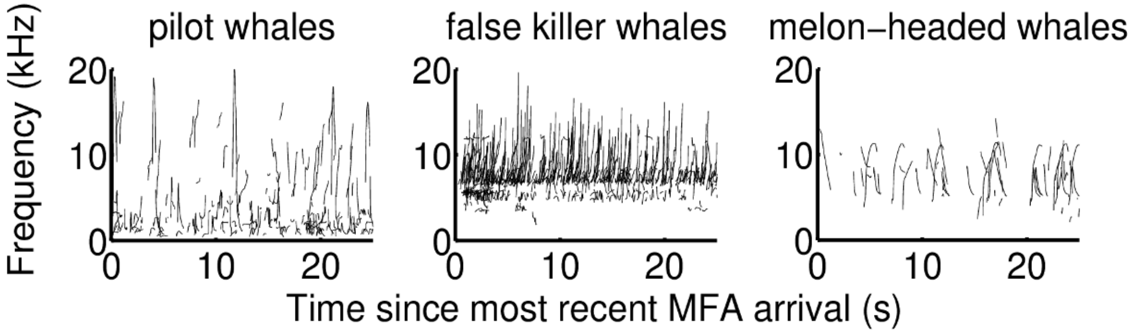

Figure 2. All whistle contours for pilot whales (gm07_229b), false killer whales (pc08_272a), and melon-headed whales (pe08_273b), plotted as a function of time since the most recent MFA arrival.

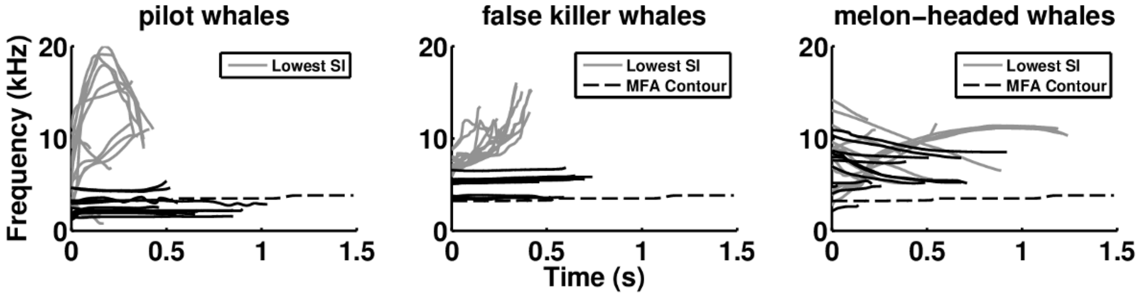

Figure 3. Most and least MFA-like whistle contours produced by pilot whales (gm07_229b), false killer whales (pc08_272a), and melon-headed whales (pe08_273b). Grey traces show the contours with the lowest SI (least MFA-like), and black traces the contours with highest SI (most MFA-like). In each case, 15 traces of each type are plotted, except that only the 11 traces with highest SI were plotted for the melon-headed whales (since only those 11 met the criterion for being “MFA-like”). Dotted lines show the MFA contour.

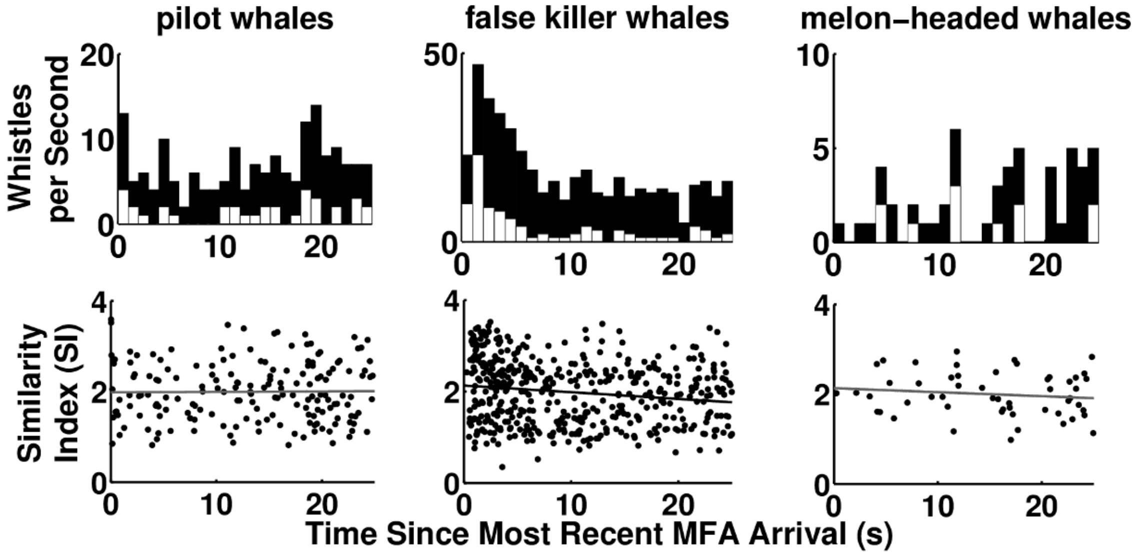

Figure 4. Patterns in whistle production in relation to time since the most recent MFA arrival. Upper panels show whistle rate as a function of time since most recent MFA arrival, with the full whistle dataset in black and only MFA-like whistles in white. Lower panels show Similarity

Index as a function of time since the most recent MFA arrival. Dots show SI values for traced whistle contours, grey lines show regression lines (not significant at the *P* = 0.02 level), and the black line is a regression line (*P* = 0.0041).