Behavioral Responses of Odontocetes to Playback of Anthropogenic and Natural Sounds

Peter L. Tyack Woods Hole Oceanographic Institution 266 Woods Hole Road, MS #50 Woods Hole MA 02543

phone: (508) 289-2818 fax: (508) 457-2041 email: ptyack@whoi.edu

Award Number: N00014-07-1-0988

LONG-TERM GOALS

The long-term goal of this research project, which was achieved, was to safely study responses of beaked whales to naval sounds in order to understand the causal chain of events leading from sound exposure to risks of stranding and to measure the exposure required to elicit responses that are safe but indicate potential for risk. The project has provided critical information required to develop measures to protect beaked and other whales from risks related to exposure to sonar and other sounds.

OBJECTIVES

A critical objective for understanding possible links between sonar exposure and injury or stranding involves developing techniques to safely study how beaked whales respond to sound. The objective of this project was to establish, test and refine new protocols for studying how beaked and other whales respond to sound using established sound playback experiment paradigms; to define responses of beaked whales and other species of odontocete whales to mid-frequency active (MFA) sonar, to a control noise stimulus with similar timing and bandwidth, and to natural sounds such as those from killer whales; and to measure exposure parameters for sounds that evoke a behavioral response.

APPROACH

The approach for this study involved controlled exposures to tagged whales where the scientific team controls the sound source (Tyack et al. 2003). This research effort has started to quantify the probability and severity of behavioral change as a consequence of sonar exposure and has developed methods to test what factors affect the probability of behavioral effects (e.g. received level at the animal, distance of the source, sound propagation conditions, waveform of the sound signal, behavioral state of the animal). Our experimental approach has given us the ability to study the causal relationship between sonar exposure and behavioral responses, to compare differences between species and stimuli, and to test for other factors that may affect behavioral responses.

Field efforts were conducted at the Atlantic Undersea Test and Evaluation Center (AUTEC) on Andros Island, Bahamas, adjacent to the deep canyon of the Tongue of the Ocean (TOTO). AUTEC has a 600 square mile, permanent range of 82 bottom-mounted hydrophones, which can be used for detecting and

maintaining the data needed, and c including suggestions for reducing	lection of information is estimated to ompleting and reviewing the collect this burden, to Washington Headqu uld be aware that notwithstanding an DMB control number.	ion of information. Send comments arters Services, Directorate for Info	s regarding this burden estimate ormation Operations and Reports	or any other aspect of the s, 1215 Jefferson Davis	nis collection of information, Highway, Suite 1204, Arlington	
1. REPORT DATE 30 SEP 2011		2. REPORT TYPE		3. DATES COVE 00-00-2011	red I to 00-00-2011	
4. TITLE AND SUBTITLE					5a. CONTRACT NUMBER	
Behavioral Responses of Odontocetes to Playback of Anthropogenic and Natural Sounds					5b. GRANT NUMBER	
					5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S)				5d. PROJECT NUMBER		
					5e. TASK NUMBER	
					5f. WORK UNIT NUMBER	
	ZATION NAME(S) AND AE cographic Institution (A,02543		Road, MS	8. PERFORMING REPORT NUMB	G ORGANIZATION ER	
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)					10. SPONSOR/MONITOR'S ACRONYM(S)	
					11. SPONSOR/MONITOR'S REPORT NUMBER(S)	
12. DISTRIBUTION/AVAIL Approved for publ	ABILITY STATEMENT ic release; distributi	on unlimited				
13. SUPPLEMENTARY NO	OTES					
14. ABSTRACT						
15. SUBJECT TERMS						
16. SECURITY CLASSIFIC		17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON		
a. REPORT unclassified	b. ABSTRACT unclassified	c. THIS PAGE unclassified	Same as Report (SAR)	13		

Report Documentation Page

Form Approved OMB No. 0704-0188 locating cetaceans on the range using marine mammal monitoring equipment developed by NUWCNPT (DiMarzio et al. 2008). This capability for real time monitoring was a critical part of our experimental approach, as we used the range to find whales and to determine in real time when they started and stopped producing echolocation clicks during deep foraging dives, responses that were used to control the playbacks (Boyd et al., 2007). The design of these playback experiments called for tagging the subject with a calibrated sound and orientation recording tag (Digital Acoustic Recording Tag – DTAG: Johnson and Tyack 2003), measuring pre-exposure behavioral data, conducting a playback, and then measuring post-exposure behavioral data. For beaked whales, playbacks were started when the whales started producing echolocation clicks during a deep foraging dive, and were stopped when they ceased echolocating. Playbacks to other species had timing similar to those for beaked whales. Working at AUTEC required close collaboration with NUWC and its marine mammal monitoring (M3R) team. Tagging research had already been conducted on this site to establish baseline data and we collaborated with the Bahamas Marine Mammal Research Organisation (BMMRO) for long-term studies of these populations. This project required extensive collaboration with biologists from the Sea Mammal Research Unit (SMRU) at the University of St. Andrews, biological oceanographers from Duke University, and bioacousticians at Cornell University.

WORK COMPLETED

Behavioral response studies were conducted in the Tongue of the Ocean between 11 August and 31 September 2007 and 18 August and 5 October 2008. The general objective was to conduct playbacks of MFA sonar sounds and control sounds to odontocete whales, to measure behavioral responses to these playbacks and to measure the received levels of sound and other elements of exposure required to evoke these responses. The control sounds included a pseudo-random noise (PRN) stimulus with overall timing and bandwidth similar to the MFA stimulus, and recorded calls of killer whales (ORCA). The protocol put the highest priority on conducting playbacks on Blainville's beaked whales, Mesoplodon densirostris, one of two species most frequently reported to mass strand during sonar exercises. In order to conduct this study, it was necessary to apply for and receive scientific research permits from the US and Bahamian governments and for an assurance from Institutional Animal Care and Use Committees from WHOI and the Bahamas Marine Mammal Research Organisation. The WHOI team helped design and plan the study, built, tested and calibrated sound and orientation recording tags (Digital Archival Tag – DTAG: Johnson and Tyack 2003), tagged beaked, pilot, false killer, and melon-headed whales, and has helped to analyze and write up the results, taking the lead on Tyack et al. (2011), a paper describing avoidance responses of beaked whales, and papers on the vocal repertoire and vocal responses of delphinid species tested.

During 2007, data were collected from 10 tag deployments, 6 on Blainville's beaked whales and 4 on pilot whales. A total of 109 hours of data were collected from the tags, 74 hours from beaked whales and 34 hours from pilot whales. The data collected by the tag included sounds produced by the tagged animal, environmental and anthropogenic sounds received by the animal, details of the animal's movements in terms of its diving, swimming speeds, changes in orientation, and swimming actions. Playbacks were performed to three of the tagged whales: 1 beaked whale (MFA and Orca) and 2 pilot whales. A total of 6 playbacks were conducted in 2008 on 4 species of odontocete cetacean that were tagged with Dtags. In addition, observations were made of odontocete vocalizations at a group/population level using the AUTEC hydrophone array during playbacks. Mapping of potential prey and oceanographic parameters in this habitat also provided an insight into the factors that may

affect beaked whale distribution at AUTEC in addition to anthropogenic acoustic activity. The field operations in 2008 were interrupted by a succession of tropical storms and hurricanes that threatened the region during the time of the study. This meant that the number of playbacks achieved was lower than had been expected if weather conditions had been more typical for the time of year. There were a total of 9 playbacks on animals in BRS08, 5 of PRN1 and 4 of MFA1. For each sequence of transmissions, a full ramp up sequence was performed starting at a source level of 160 dB re 1 μPa at 1 m through maximum target source level of 211 dB, increasing the source level by 3 dB every 25 seconds and continuing transmissions for approximately 5 minutes at full power. For beaked whale playbacks, transmissions were ceased when the whales could not longer be heard clicking.

Table 1. Summary of BRS 08 playbacks

Date	Waveform Sequence	Tagged Species	
	MFA1, MFA2,		
17-Aug-07	ORCA	Short finned pilot whale	
17-Aug-07	MFA1, ORCA	Short finned pilot whale	
		Blainville's beaked	
2-Sep-07	MFA1, ORCA	whale	
22-Sep-08	PRN1, MFA1	Short finned pilot whale	
26-Sep-08	PRN1, MFA2	False killer whale	
		Blainville's beaked	
27-Sep-08	PRN1	whale	
28-Sep-08	MFA1, PRN1	False killer whale	
29-Sep-08	PRN1, MFA1	Short finned pilot whale	
29-Sep-08	PRN1, MFA2	Melon headed whale	

This integrated data set provides a significant advance in our understanding of the responses of dontocetes, and beaked whales in particular, to MFA sonar and control signals such as a noise stimulus (PRN) with the same timing and bandwidth as the MFA stimulus, and the sounds of killer whales. A series of vessel noise exposures were also conducted during 2008 to groups of Blainville's beaked whales that were detected clicking during deep foraging dives.

The primary work for this project after 2008 involved analysis of data from the BRS 07 and 08 experiments, writing up the results for primary journal articles and also for review articles. The analyses focused on effects of playbacks of sonar and other sound on beaked and other whales, and on calls of pilot whales and clicks of beaked whales. Our analyses of recordings from tagged pilot whales showed problems with previous analyses (Taruski 1979, Weilgart and Whitehead 1990), requiring a new categorization of calls. Recordings of echolocation clicks of beaked whales that were made as part of this project have also been analyzed to define the probability that the detection cue of an echolocation click could be heard. With support from the DECAF project, this new analysis of these data have formed the basis for an important new method using passive acoustic monitoring to define the abundance and density of cetaceans (Marques et al. 2008).

RESULTS

Table 2 summarizes the results of the playbacks to beaked whales, along with the results of Aguilar et al. (2006), which reported a similar response of a Ziphius to the noise of a ship. This small sample of preliminary results suggests that beaked whales silence and show avoidance responses to anthropogenic sounds in a surprisingly narrow range from 136-140 dB re 1 μ Pa (Table 2). A similar but more intense response was seen in response to the killer whale playback, which was elicited by an exposure just barely above the ambient noise at 102 dB re 1 μ Pa. After the killer whale playback, the beaked whale had a prolonged post-dive avoidance response. Nevertheless there remains an ambiguity in the interpretation of the killer whale playback; since the killer whale playback was the second in a series on the same animal, it is possible that the prolonged response was a consequence of the second exposure rather than the killer whale waveform. This suggests that carrying out additional playbacks of sonar and of killer whale should be a priority for future work with beaked whales to resolve this uncertainty. While the playback results are drawn from just two individual beaked whales exposed to playback, this pattern of behavior has been measured against dives on control animals that were not exposed to a playback of any sound. The baseline tagged whales greatly strengthen the power of our statistical analyses.

Table 2. Summary of received sound pressure levels at which beaked whales respond to anthropogenic sounds. The MFA stimulus is mid-frequency active naval sonar, PRN is a pseudorandom noise stimulus with the same overall timing and bandwidth as the MFA stimulus, and Orca is recordings of the calls of killer whales, a known beaked whale predator.

		Received	
Species	Stimulus	Level	Source
			Aguilar et al. (2006)
		136-140 dB re	Marine Mammal
Ziphius	ship	1μPa rms	Science, 22(3): 690-
cavirostris	propulsion	broadband	699
Mesoplodon			
densirostris			
2	PRN		BRS08
Mesoplodon			
densirostris			
1	MFA		BRS07
Mesoplodon		~102 dB re	
densirostris		1μPa rms	
1	Orca	broadband	BRS07

Responses to the playbacks to non-beaked whales were more variable than to beaked whales, but in many cases, the subjects neither silenced nor showed avoidance reactions. Figure 1 shows the plot of two playbacks to a tagged pilot whale within a group. The segments of ship and whale tracks marked in blue indicate a MFA playback, those in magenta indicate a killer whale playback. The whales did

not move away during either playback, and during the killer whale playback, the group became more cohesive. Figure 2 illustrates the calling rates recorded on the tagged whale. There was a first MFA playback before the track illustrated in Figure 1. The calling rate of pilot whales oscillates under baseline conditions due to unknown factors. The tag on the whale certainly did not register silencing after the first MFA playback. The whales did silence during the first 5 minutes of the second MFA playback, then vocalized during the latter part of the playback. After a long silent interval, the whales increased their calling rate as they formed a more cohesive group during the killer whale playback.

Our ignorance of the social and other factors influencing call rate in pilot whales hinders analysis of response to playback, but it is clear that their response is very different from that of the beaked whales. The pattern of alarm calling and forming a more cohesive group under threat is a classic behavior that is often interpreted as a social defense against a threat such as a predator. When wildlife respond to human disturbance, they may invoke species-typical anti-predator responses (Frid and Dill 2002). Morisaka and Connor (2008) point out that some odontocetes seem to have a cryptic silencing response to predators, while others may use social calls as part of a social defense against predation. Morisaka and Connor (2008) focus on whistling vs non-whistling species, but our data also suggest the possibility that beaked whales may have more of a silencing and avoidance response to disturbance, while the social delphinids studied here had more of a social response to disturbance. If the avoidance response involves a higher probability that deep-diving beaked whales swim out of their normal habitat, then it may represent a risk factor for stranding. This interpretation emphasizes the importance of understanding social responses to threats, and we have focused our analyses of responses of the delphinids on this topic.

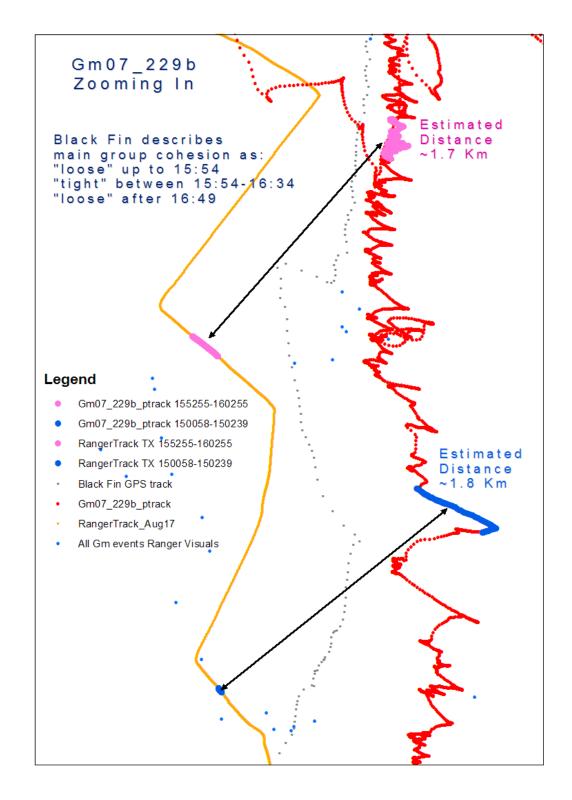


Figure 1. Plot of tracks of ship and tagged pilot whale (Gm229b) during the second MFA playback (in blue) and a killer whale playback in magenta.

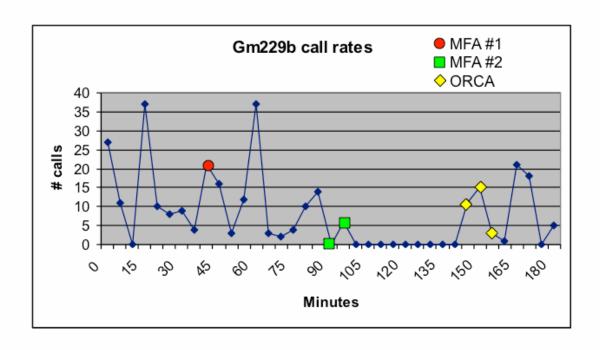


Figure 2. Calling rates of pilot whales recorded on Gm229b during MFA and killer whale playbacks.

Four short-finned pilot whales were recorded with DTAGs in August 2007 and other delphinids were tagged and subjected to playback as part of the Behavioral Response Study (BRS) in AUTEC. In order to assess possible vocal responses of pilot whales to playbacks, it was first necessary to characterize the pilot whale vocal repertoire. Calls were visually classified into categories, and no attempt was made to distinguish between pulsed and tonal calls. We analyzed approximately 30 hours of acoustic data from 4 tagged whales. Tag durations were as follows: tag 229a: 12 hours and 43 minutes; tag 229b: 3 hours and 56 minutes; tag 259a: 12 hours and 7 minutes; tag 260a: 1 hour and 36 minutes. Tags sampled audio at 96 kHz. Using Adobe Audition, all calls were excised to produce 3,202 files, some containing multiple calls, for a total of 4,090 calls. Spectrograms of all files were produced with the same time and frequency scaling, and these were printed and then mixed so that information regarding sequential ordering of calls was unavailable. Spectrograms were then independently categorized into call types by three auditors.

Of the total of 4090 calls, 1,734 (42%) were placed into 174 call types, which was defined as any call that occurred two or more times. The remainder consisted of short calls (27%), distinctive but unclassifiable calls (7%), long pulsed calls (3%), and calls that were unclassifiable due to poor signal/noise (21%). Of the 174 call types, 51 contained a minimum of 10 calls (mean = 24), and

comprised 70% of the categorized calls. These calls that were detected at least 10 times are referred to as predominant call types (PCT's). PCT's accounted for 38% of all calls with sufficient signal/noise for categorization. Predominant call types tended to occur in sequences of the same call. Of 1,168 transitions between PCT's, significantly more (760 or 65%) occurred within 30 seconds of another PCT of the same type than over greater time periods (407 or 35%; paired t test, p<0.001). In most cases, these tightly timed sequences appeared to be produced by a single animal, based on consistency in amplitude and lack of overlap. However, in several cases we observed apparent exchanges, consisting of adjacent or overlapping calls of the same type. In some of these cases calls had quite different amplitudes, suggesting that they were produced by different whales. Further evidence for call types being produced by multiple whales comes from the result that 10 of 51 PCT's (20%) were recorded on two tags.

Our data clearly illustrate that pilot whales produce shared, stereotyped calls, some of which consist of overlapping tonal and pulsed components, and that these calls comprise a large portion of their vocal repertoire. These calls share similarities with the stereotyped calls of killer whales, which are thought to function to maintain group cohesion (Ford 1989). The data also suggest the possibility that pilot whales may produce individually distinctive call types in addition to shared call types. Overall, these data indicate that rough counts of calls may mix very different kinds of signals, and the data emphasize the importance of categorizing calls before attempting to draw conclusions about call usage and possible effects of sonar on vocal behavior. In contrast to beaked whales, many delphinid species are highly social. They live in relatively large groups, making frequent use of sound to communicate in both affiliative and agonistic contexts, and use group or individual-specific calls to maintain social cohesion. Now that we have been able to categorize the calls, we are completing our analysis of variation in overall calling rates and rates of PCT's as a function of playback condition.

Unlike beaked whales, which appear to silence and flee from predators, delphinids may rely in some contexts on social defenses against predators or conspecific competitors (Tyack 2000). Initial examination of the BRS DTAG sound recordings revealed several instances in which false killer whales (*Pseudorca crassidens*) produced whistles similar to the MFA signal just after its reception. We therefore conducted a quantitative analysis to test whether false killer whales and the other delphinid species exposed to simulated MFA signals (pilot whales *Globicephala macrorhynchus* and melonheaded whales *Peponocephala electra*) responded to MFA by increasing whistle production rate and by mimicking the MFA sound. An index of similarity between each whistle contour and the MFA signal contour was calculated using a dynamic time warping (DTW) metric (Buck and Tyack 1993).

To test for a correlation between whistle and MFA similarity and the time since the last MFA reception, we fitted a straight line to the DTW score data and applied a rotation test (DeRuiter and Solow 2008), using the line's slope as the test statistic. We tested the hypothesis that DTW score increases (i.e., whistles become less similar to the MFA signal) with increasing time since last MFA reception by comparing the observed slope of the DTW data with those obtained in 100,000 rotations of the dataset. We also applied a point-process time series model (Truccolo et al. 2005) to quantify whistle production rate and relate it to time since the last MFA reception, time since the first MFA reception, and number of whistles occurring in the preceding interval. One group of false killer whales (pc08_270a) and one group of pilot whales (gm08_273a) produced very few whistles during the MFA exposure (4-5 whistles total per group). No clustering or autocorrelation of whistle times was detected for those groups, although the power of the tests was limited by the very small sample size. For all

other groups, whistle times were clustered and auto-correlated. The point-process model took such clustering into account by allowing for dependence on whistle production rates in the preceding interval. This clustering parameter was significant (p<0.05) in all cases except when sample size was very small (under 10 whistles). For the false killer whale group (pc08_272a), the rotation test indicated a correlation between DTW score and time since last MFA reception: whistle-MFA similarity was highest immediately following each MFA reception. 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 related to time since last MFA reception. The results of these analyses support the hypothesis that one false killer whale group responded to MFA by mimicking the MFA signal: the group whistled more immediately following each MFA reception, and whistle-MFA similarity decreased with time since the last reception. We did not observe mimicry or vocal response to the MFA signal by any of the other four delphinid groups we studied; in fact, the melon-headed whales had lower whistle rates immediately after individual MFA receptions.

Other data used for preliminary description of possible responses in the 2007 and 2008 playbacks come from dive records on the tag and observations of the visual observers on the vessels near the whales. Although reactions to sonar sounds and control sounds were observed in some of the playbacks to delphinids, there was little consistency in the responses observed. By contrast, the beaked whales showed premature silencing and surfacing to all 3 playbacks, along with prolonged avoidance to the killer whale playback. The delphinids tested showed much more variable responses in dive behavior and vocal and avoidance behavior. While some delphinids did swim away from the sound source during playback, there was no prolonged avoidance behavior of the sort observed with the beaked whale exposed to killer whale calls. During some playbacks to delphinids, the visual observers described the whales as increasing their rate of travel during the playback, but during other playbacks, the whales slowed down and increased group cohesion. While these responses of delphinids to playback were varied, they all were clearly different from the responses of beaked whales to playback of the same sound stimuli, and many are consistent with social defense against a threat.

To summarize our results, the beaked whale exposed to killer whale playback responded at $\sim \! 100$ dB re 1 μPa with the longest and slowest ascent observed. Response to MFA sonar at $\sim \! 139$ dB re 1 μPa was the second longest and slowest ascent in our dataset. After MFA and Orca exposure, this beaked whale continued to swim steadily away from the exposure location for > 10 hours and ~ 20 km. This silencing and avoidance response is similar in timing and spatial scale to responses of beaked whales to actual sonar exercises on the AUTEC range (Tyack et al. 2011). While the response data are outliers from baseline, there is no suggestion that response posed a risk to the whale.

This BRS project has developed a safe method to define behavioral disruption in beaked and other whales, along with the exposure required to disrupt behavior. Beaked whales showed consistent disruption of behavior to all three anthropogenic sounds at exposures considerably lower than pilot whales and delphinids (supports conclusions of particular sensitivity of beaked whales to anthropogenic sounds). A beaked whale exposed to killer whale sounds showed a prolonged avoidance response, but other species seemed to have social defenses against predation and were less likely to flee. This observation suggests that some modes of anti-predator behavior may be a risk factor for strandings. More tests are needed to confirm these preliminary results, especially in an area where beaked whales hear less sonar

IMPACT/APPLICATIONS

This study aims to reduce risks to whales from naval sonar and to foster the development of mitigation measures by defining the mechanisms by which beaked whales and other species are affected by sonars. The results will have immediate applications for regulators and for the Navy. These data are consistent with the conclusion that, similar to harbor porpoises (Southall et al. 2008), beaked whales are particularly sensitive in terms of behavioral responses to acoustic exposure. If delphinids rely less upon flight and more upon social defense against a threat, this may put them at less risk of stranding. In the US, regulators have a separate exposure criterion for harbor porpoise than other cetaceans. Regulators predict that any exposure above 120 dB SPL will disturb behavior in porpoises, while a variety of higher criteria are used for other species (Southall et al. 2008). Our results support a similar criterion of about 140 dB SPL for beaked whale exposure to mid-frequency sounds. Our results do support a lower acoustic threshold of disturbance for beaked whales than is currently applied in the US. However, more data from beaked whales are required to finalize a dose:response function, and analyses of similar experiments with different species are required to support the interpretation that other species may be less sensitive or less at risk than beaked whales. The research described here has pioneered the techniques that will be required to complete the understanding of how beaked and other whales respond to sonar and other sounds, and to define the function relating acoustic dosage and behavioral response.

TRANSITIONS

The methods developed by the Behavioral Response Study have been used in three additional studies based on the same methodology: the 3S project, a joint Norwegian-Dutch-St Andrews – WHOI project studying responses of cetaceans to sonar in Norwegian waters, the Med09 project studying responses of toothed whales in the Mediterranean to sonar and killer whales, and the BRS Socal project. The passive acoustic monitoring results from tagging beaked whales on the AUTEC range have provided critical input data for the DECAF project (http://www.creem.st-and.ac.uk/decaf/), leading to the first paper using passive acoustic monitoring to estimate absolute density and abundance of cetaceans (Marques et al. 2008).

RELATED PROJECTS

ONR: Tagging and Playback Studies to Toothed Whales N00014-09-1-0528

ONR: Cetaceans and Naval Sonar: Behavioral Response as a Function of Sonar Frequency N00014-08-1-0661

Naval Postgraduate School: Dtagging and analysis of studies on effects of naval sounds on marine mammals in waters off southern California

SERDP: Acoustic Response and Detection of Marine Mammals on Navy Ranges Using a Digital Acoustic Recording Tag.

Naval Oceanographic Office: Behavioral Response Study (BRS-07) Analysis and Supplemental Funding for BRS08

Marine Mammal Monitoring on Navy Ranges (M3R; David Moretti PI, NUWC-NPT)

REFERENCES

Aguilar de Soto N, Johnson M, Madsen PT, Tyack PL, Bocconcelli A, Borsani JF. 2006. Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*). *Marine Mammal Science*. 22:690-699.

Boyd IL, Claridge D, Clark CW, Southall B, Tyack PL. 2007. Behavioral Response Study 2007 BRS-07 Cruise Report

Buck JR, Tyack PL. 1993. A quantitative measure of similarity for *Tursiops truncatus* signature whistles. *Journal of the Acoustical Society of America*. 94(5):2497-506.

DeRuiter SL, Solow AR. 2008. A rotation test for behavioural point-process data. *Animal Behavior*. 76(4):1429-34.

DiMarzio N, Moretti D, Ward J, Morrissey R, Jarvis S, Izzi AM, Johnson M, Tyack P, Hansen A. 2008. Passive acoustic measurement of dive vocal behavior and group size of Blainville's beaked whale (*Mesoplodon densirostris*) in the Tongue of the Ocean (TOTO). *Canadian Acoustics* 36:166-172

Frid A, Dill LM. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1):11

Ford JKB. 1989. Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67:727-745

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

Marques TA, Thomas L, Ward J, DiMarzio N, Tyack PL 2009. Estimating cetacean population density using fixed passive acoustic sensors: An example with Blainville's beaked whales. *Journal of the Acoustical Society of America* 125:1982-1994.

Morisaka T, Connor RC. (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. doi: 10.1111/j.1420-9101.2007.01336.x

Southall BL, Bowles AE, Ellison WT, Finneran JJ, Gentry RL, Greene Jr. CR, Kastak D, Ketten DR, Miller JH, Nachtigall PE, Richardson WJ, Thomas JA, Tyack PL. 2008. Marine mammal noise exposure criteria: initial scientific recommendations. *Aquatic Mammals* 33:411-521

Taruski AG. 1979. The whistle repertoire of the north Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In Behavior of Marine Animals, Vol. 3: Cetaceans, (Ed. by H. E. Winn & B. C. Olla), pp. 345-368. New York: Plenum Press.

Truccolo W, Eden UT, Fellows MR, Donoghue JP, Brown EN. 2005. A point process framework for relating neural spiking activity to spiking history, neural ensemble, and extrinsic covariate effects. *Journal of Neurophysiology*. 93(2):1074-89.

Tyack PL. 2000. Functional aspects of cetacean communication. In: Mann J, Connor R, Tyack PL, Whitehead H, editors. Cetacean Societies: Field studies of dolphins and whales. Chicago, IL: University of Chicago Press; p. 270-307.

Tyack P, Gordon J, Thompson D. 2003. Controlled exposure experiments to determine the effects of noise on large marine mammals. *Marine Technology Society Journal*, 37(4): 41-53.

Weilgart LS, Whitehead H. 1990. Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behav. Ecol. Sociobiol.*, 26:399-402.

PUBLICATIONS

D'Amico AD, Gisiner R, Ketten DR, Hammock JA, Johnson C, Tyack P, Mead J. 2009. Beaked whale strandings and naval exercises. Aquatic Mammals 35:452-472 [published, refereed]

DeRuiter SL, Boyd IL, Claridge DE, Clark CW, Gagnon C, Southall B, Tyack PL. Delphinid whistle production during playback of simulated military sonar. Marine Mammal Science [submitted, refereed]

DiMarzio N, Moretti D, Ward J, Morrissey R, Jarvis S, Izzi AM, Johnson M, Tyack P, Hansen A. 2008. Passive acoustic measurement of dive vocal behavior and group size of Blainville's beaked whale (*Mesoplodon densirostris*) in the Tongue of the Ocean (TOTO). *Canadian Acoustics* 36:166-172

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

Filadelfo R, Davis S, Chase R, Mintz J, Wolfanger J, Tyack P, Ketten DR, D'Amico AD. 2009. Correlating whale strandings with Navy exercises off Southern California. Aquatic Mammals. 35:445-451 [published, refereed]

Hindell MA, Crocker D, Mori Y, Tyack P. 2010. Foraging behaviour. Chapter 11 in Marine Mammal Ecology and Conservation: A handbook of techniques. (Boyd I, Bowen D, Iverson S, eds.) Techniques in Ecology and Conservation Series, Oxford University Press, Oxford. [published]

Jones BA, Stanton TK, Lavery AC, Johnson MP, Madsen PT, Tyack PL. 2008. Classification of broadband echoes from prey of a foraging Blainville's beaked whale. Journal of the Acoustical Society of America 123:1753-1762. [published, refereed]

Marques TA, Thomas L, Ward J, DiMarzio N, Tyack PL 2009. Estimating cetacean population density using fixed passive acoustic sensors: An example with Blainville's beaked whales. Journal of the Acoustical Society of America 125:1982-1994. [published, refereed]

Nowacek DP, Thorne LH, Johnston DW, Tyack PL. 2007. Responses of cetaceans to anthropogenic noise. *Mammal. Review* 37:81-115 [published, refereed]

Pirotta E, Milor R, Quick N, Moretti D, Di Marzio N, Tyack P, Boyd I, Hastie G. submitted. Vessel noise affects beaked whale behavior: results of a dedicated acoustic response study. Biological Conservation [submitted, refereed]

Sayigh L, Quick N, Hastie G, Tyack P. Stereotyped calls in short finned pilot whales, *Globicephala macrorhynchus*. Marine Mammal Science [submitted, refereed]

Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, Durban JW, Clark CW, D'Amico A, DiMarzio N, Jarvis S, McCarthy E, Morrissey R, Ward J, Boyd I. 2011. Beaked whales respond to simulated and actual navy sonar. PLOS One 6(3):e17009 [published, refereed]

Tyack PL. 2009. Effects of human-generated sound on marine mammals. Physics Today. 62:39-44 [published, refereed]

Tyack PL. 2009. Acoustic playback experiments to study behavioral responses of free-ranging marine animals to anthropogenic sound. Marine Ecology Progress Series 395:187-200 [published, refereed]

Tyack P. 2008. Implications for marine mammals of large-scale changes in the marine acoustic environment. *Journal of Mammalogy* 89:549-558 [published, refereed]

Ward J, Morrissey R, Moretti D, DiMarzio N, Jarvis S, Johnson M, Tyack P, White C. 2008. Passive acoustic detection and localization of *Mesoplodon densirostris* (Blainville's beaked whale) vocalizations using distributed bottom-mounted hydrophones in conjunction with a digital tag (DTAG) recording. *Canadian Acoustics* 36:60-66 [published, refereed]