

Baseline Behavior of Pilot Whales and their Responses to Playback of Anthropogenic and Natural Sounds

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LONG-TERM GOALS

This project investigated the social ecology and baseline behavior of long-finned pilot whales as part of a broad multi-investigator research program that seeks to understand how cetaceans are affected by mid-frequency sonar and other sources of anthropogenic noise. The study of how noise affects large delphinids is important since results so far have suggested that they have different responses to anthropogenic noise sources compared to beaked whales. However, studies have been hindered by high inherent variability in acoustic and diving behavior and a lack of understanding of the underlying factors shaping this variation. Our goal is to develop new field and analytical methods for studying the baseline behavior and effects of noise on group-living cetaceans, where social responses to noise such as changes in group cohesion likely constitute important predictors of disturbance. We aim to gather data to design, conduct and interpret controlled exposure experiments to social delphinids such as pilot whales, with the ultimate goal of understanding responses to naval sonar and improving Navy environmental analyses.

OBJECTIVES

The primary objectives of this project were to: a) test the feasibility of instrumenting groups of pilot whales with acoustic and movement logging tags which makes it possible to investigate social dynamics and social cohesion mechanisms within pilot whale social groups, and b) develop and field test a stereo camera system for measuring the position of individual whales over time and obtaining accurate estimates of group cohesion. Both of these objectives have been met.

APPROACH

This project included a two-month field expedition to the Strait of Gibraltar, Spain, in collaboration with CIRCE (Conservación, Información y Estudio sobre Cetáceos). This field site is unique in that the year-round resident population of pilot whales (de Stephanis et al., 2008a) is relatively small, less than 200 individuals (Verborgh et al., 2009), and with well-known social structure (de Stephanis et al., 2008c). Field work is concentrated on selectively tagging closely associated pilot whales with acoustic and movement recording DTAGs (Johnson and Tyack, 2003). ARGOS location tags were deployed on

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two individuals within different groups to monitor long-term movement throughout the field season. After tagging, animals are followed by the research vessel while visual observations are conducted. Tags are retrieved when dislodged from the animal using a radio beacon. To quantify movement and surface group cohesion, we will develop and field test a stereo camera system that allows for accurate positioning of animals during focal follow. Finally, playback experiments will be conducted to a subset of the tagged animals when conditions are favourable.

WORK COMPLETED

Fieldwork was completed between July 2nd and August 31st, 2012. This expedition was highly successful, providing us with 33 DTAG deployments and a total of 184 hours of data, including a playback of killer whale and pseudorandom noise stimuli to 3 simultaneously tagged animals. Two long-term satellite tags were deployed on groups within the strait, and reported movement of both groups over the ARGOS network throughout several months. In 2013, additional funding from the Danish Council for Independent Research allowed us to complete additional fieldwork in the Strait of Gibraltar. These combined field cruises have resulted in a total of 63 tags deployed on long-finned pilot whales in the area, including 7 highly cohesive groups of animals with 3 to 5 simultaneously tagged animals. All tagged individuals were identified and linked to previous observations and information from social association studies (de Stephanis et al., 2008c) and studies of foraging ecology using stable isotopes (de Stephanis et al., 2008b). This remarkable identification of animals and high resighting rate gave us a great flexibility in choosing the right animals at the right moment for tagging, and demonstrates clearly that simultaneous tagging of entire social units of pilot whales is feasible in the Strait of Gibraltar. The small population size and large number of animals tagged within this population also makes it very likely that we will be able to find and retag the same animals across field seasons, which is important to understand how representative a short tagging period is for the behavior of the animal and how behavior changes over time. Additionally, a working stereo camera has been designed and tested in the field through 2012 and 2013, both with pilot whales and subsequently with bottlenose dolphins. This system allows us to accurately measure individual positions of animals and quantify important metrics such as surface cohesion.

Table 1: Summary of tag data collected from long-finned pilot whales in the Strait of Gibraltar.

Tarifa 2012-2013 Tag summary

Date (2012)	Dataset	Tagon time	Duration (hours)	Cause of release	Date (2013)	Dataset	Tagon time	Duration (hours)	Cause of release
4th July	gm12_186a	13:08	0.22	Rubbed off	8th January	gm13_008a	12:26	14.57	Programmed
9th July	gm12_191a	13:18	2.40	Rubbed off	8th January	gm13_008b	18:13	8.74	Programmed
25th July	gm12_207a	15:11	13.66	Programmed	10th January	gm13_010a	13:23	8.01	Breach
25th July	gm12_207b	15:34	1.05	Breach	10th January	gm13_010b	15:35	1.13	Breach
25th July	gm12_207c	16:09	7.43	Rubbed off	10th January	gm13_010c	18:08	5.15	Breach
25th July	gm12_207d	16:48	10.06	Programmed	28th January	gm13_028b	10:39	0.18	Fast swim or breach
25th July	gm12_207e	17:06	0.14	Breach	28th January	gm13_028c	11:08	5.87	Foraging sprint
25th July	gm12_207f	17:48	4.45	Rubbed off	28th January	gm13_028d	11:12	7.24	Programmed
29th July	gm12_211a	10:52	1.51	Sprint	28th January	gm13_028e	11:51	0.24	
29th July	gm12_211b	11:14	0.02	Slid off	30th January	gm13_030a	09:24	9.08	Foraging sprint
29th July	gm12_211c	14:07	1.16	Rubbed off	30th January	gm13_030b	09:29	3.17	Foraging sprint
29th July	gm12_211d	14:20	~	Breach	30th January	gm13_030c	10:04	6.62	Fast swim
3rd August	gm12_216a	08:49	4.28	Rubbed off	30th January	gm13_030d	10:24	3.29	Foraging sprint
3rd August	gm12_216b	11:04	0.11	Breach	30th January	gm13_030e	14:47	1.05	Foraging sprint
3rd August	gm12_216c	14:01	0.01	Breach	30th January	gm13_030f	15:28	0.05	Foraging sprint
4th August	gm12_217a	08:15	15.50	Programmed	30th January	gm13_030g	16:26	1.10	Unknown
4th August	gm12_217b	09:00	15.41	Programmed	30th January	gm13_030h	16:41	7.86	Programmed
4th August	gm12_217c	09:13	4.86	Breach	3rd August	gm13_215a	15:59	3.82	Breach
4th August	gm12_217d	09:44	1.64	Rubbed off	6th August	gm13_218a	13:24	0.01	Breach
4th August	gm12_217e	12:17	3.64	Sprint	6th August	gm13_218b	13:43	4.06	Rubbed off
4th August	gm12_217f	17:12	7.26	Programmed	6th August	gm13_218c	13:59	0.03	Rubbed off
11th August	gm12_224a	09:51	4.36	Fast swim	8th August	gm13_220a	12:35	0.10	Breach
11th August	gm12_224b	09:59	4.57	Fast swim	8th August	gm13_220b	12:40	5.68	Programmed
11th August	gm12_224c	10:23	6.96	Foraging sprint	8th August	gm13_220c	12:47	1.46	Foraging dive
11th August	gm12_224d	11:38	14.68	Programmed	8th August	gm13_220d	13:47	4.71	Programmed
16th August	gm12_229a	08:52	11.37	Programmed	8th August	gm13_220e	14:01	4.20	Programmed
16th August	gm12_229b	09:29	10.26	Fast swim	25th August	gm13_237a	20:50	4.72	Rubbed off
16th August	gm12_229c	11:44	8.01	Fast swim	25th August	gm13_237b	21:06	0.54	Fast swim
28th August	gm12_241a	10:06	0.88	Deep dive	26th August	gm13_238a	18:08	0.93	Breach
29th August	gm12_242a	09:13	9.23	Programmed	26th August	gm13_238b	20:46	0.22	Fast swim
29th August	gm12_242b	09:16	8.29	Fast swim					
29th August	gm12_242c	09:56	3.09	Foraging sprint					
29th August	gm12_242d	12:18	1.87	Foraging sprint					

RESULTS

The research expeditions to the Strait of Gibraltar have been highly successful, with two ARGOS satellite tag deployments and a total of 63 DTAG deployments, including 7 tightly associated units sampled simultaneously. Although the geography of the Strait often results in more severe weather conditions compared to our previous research site in the Alboran sea, the shorter search time to find pilot whales in the area combined with the smaller average group size makes it ideal for studying the social dynamics of this gregarious delphinid.

The resident pilot whales in the Strait are known from visual surveys in the area to have a very small home range (de Stephanis et al. 2008a). The two deployed ARGOS satellite tags confirm that both groups of tagged animals normally remain in a small part of the Strait that is very similar to the visually estimated home range (Fig. 1). However, these tracking data also revealed an interesting short-term excursion (2-3 days duration) from their normal home range to a deep canyon off the east coast of Morocco. Such excursions might be related to foraging during a period of sparse prey in the Strait, but occasional excursions might also be associated with socio-ecological activities such as seeking out other pods of pilot whales for mating outside the natal pod.

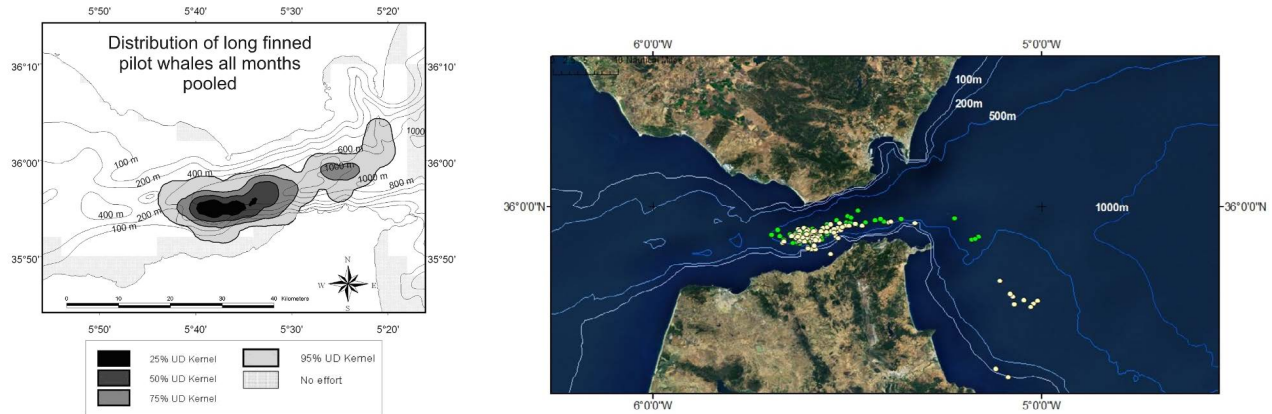


Fig. 1: Left: The annual distribution of long-finned pilot whales (shaded area - Darker shades represent higher probability of occurrence) recorded by visual observers in the Strait of Gibraltar (de Stephanis et al., 2008a). Right: High-quality positions transmitted by ARGOS satellite tags deployed on two long-finned pilot whales in separate groups tagged during summer 2012 expedition. During most of the study period, animals remained within their expected home range, but both groups of animals spent several days moving to and from Ceuta Canyon to the east of Morocco.

Over the past three years, we have developed powerful techniques to study the social dynamics and baseline behavior of highly social cetaceans. These techniques range from field approaches to optimize simultaneous tagging of multiple animals within the same tight social group, to analytical techniques that allow us to identify signals produced by tagged individuals and quantify social interactions, individual and group vocal rates, and information flow through social groups. The questions that we are trying to answer with these methods are (1) how animals mediate changes in group cohesion across varying spatiotemporal scales, (2) whether and how animals within a group coordinate movement and foraging behaviors, and (3) how these dynamics are affected by anthropogenic noise.

An example of the behavior and acoustic activity for a unit of three closely associated individuals recorded in the end of August, 2012, is shown in figure 2. In this example, four tagged animals are shown, three (a,b,c) in the same subgroup. Most of the dives of these social delphinids are synchronized in time, demonstrating that animals often coordinate dive and foraging behavior within a social group, and these patterns are visible across many of the datasets that we have collected so far. During these coordinated dives, most communication sounds produced are short click series at high repetition rates, often called rasps (Aguilar Soto et al., 2012). These sounds seem to be important for short-range coordination whereas more tonal calls seem to be more important for mediating a variety of surface behaviors and when animals become separated during asynchronous foraging dives. With the aid of these unique datasets of simultaneously tagged close associates, we are now able to test how these different communication signals work in mediating cohesion over varying spatial scales.

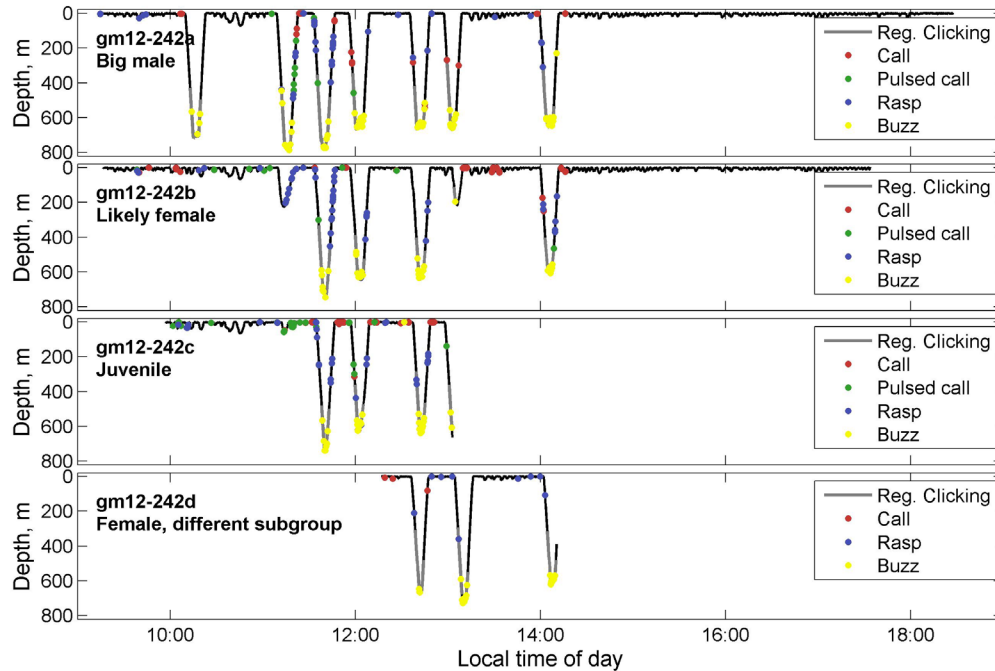


Fig. 2: Annotated dive profiles of a social subgroup of pilot whales (top three plots) and an associated individual within the same group but in a different subgroup (bottom plot). The dive behavior of individuals from tagging to tag release is shown in black. Regular clicking activity during biosonar-based foraging is shown in grey, and foraging attempts are shown in yellow. Three kinds of communication signals varying from purely tonal (calls) across burst-pulse calls to rapid series of pulses are shown as well.

The tight but dynamic coordination of dive activity shown in this example seems to be characteristic of long-finned pilot whale social units, and may play a role in increasing the foraging success of individuals in the social group. The foraging activity of the animals is readily identified through recordings of echolocation clicks and foraging buzzes (e.g. Aguilar Soto et al., 2008; Madsen et al., 2013). Foraging buzzes reveal prey capture attempts (here shown in yellow), so these data show how long-finned pilot whales in the same unit target similar prey layers at 500-800 meters of depth. However, from this data alone, it is impossible to determine the reason for dive coordination. To study the ecological function of dive coordination, we need information about how animals are moving relative to one another. This could be done by reconstructing the dive track of each animal based on information measured by inertial sensors in each tag. However, this approach would be sensitive to currents, which in the Strait can be quite significant, and small errors in the inertial measurements would accumulate over time and result in large errors in absolute position over each dive. An alternative approach is to estimate clock offset and separation distance from the round-trip travel time between animal pairs (e.g. Aguilar Soto, 2006, Johnson et al. in prep). To do this, we use the biosonar clicks produced by each tagged animal and recorded on other nearby tags. Periods where both animals are producing echolocation clicks are then used to estimate the instantaneous clock offset and used to fit a model of clock offset over time. Once the clock offset is known, the time delay for each echolocation period can be converted into an estimate of separation distance. Figure 3 shows the pairwise separation distance for a trio of long-finned pilot whales. The trio exhibits a strong degree of dive synchronization similar to the group shown in figure 2, but from the estimates of separation distance, it

is evident that individuals spread out during these foraging dives and then rejoin during or following the ascent. While this level of analysis is somewhat time consuming and more data still needs to be processed, this does suggest that dive synchronization does not result in cooperative foraging, but may have other social benefits such as perhaps protection from predators when at the surface.

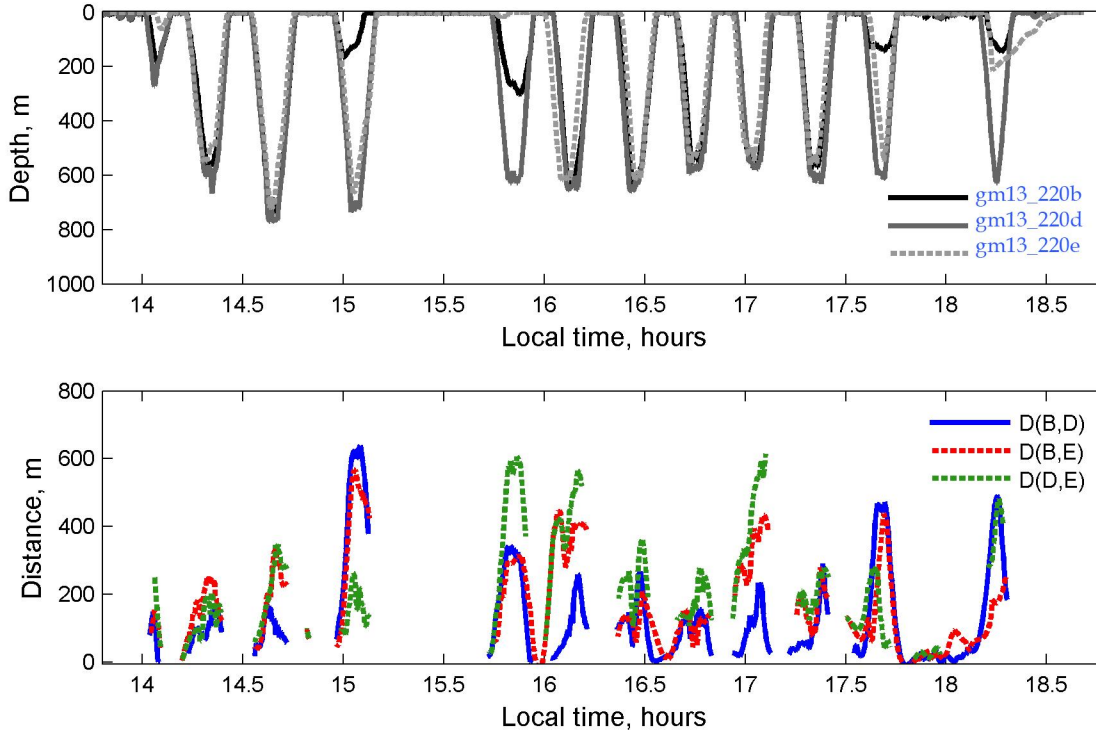


Fig. 3: Simultaneous dive profiles (top) and pair-wise separation distances interpolated with a two-state Kalman filter (bottom) for a unit of three long-finned pilot whales tagged during 2013 expedition. The dive profiles are recorded by individual tags and show highly synchronized deep diving activity that might be interpreted to suggest that animals remain close during diving. However, estimated separation distance clearly shows how animals spread out during foraging activity and then rejoin during or after the ascent.

Estimating pair-wise separation distance with this method only works for periods where animals are producing sound. For surface periods where animals are unlikely to echolocate, and where call activity can be highly varied, different means of estimating position and separation distance between group members are needed. This is especially important for understanding potential responses to anthropogenic noise since delphinids appear to have developed a social defense strategy to protect against potential predators. We have therefore developed a stereo camera system for quantifying surface group movement and social cohesion of cetaceans that works well under relatively calm sea states (Figure 4). Figure 5 shows a brief (20 minute) plot of the movement of 6 animals within the same group. We are now refining different methods for modelling the position of animals between surfacings, giving us a higher time resolution of the 2D location of animals, interanimal distances and mean group dispersion (Fig. 5), and more reliable estimates of speed-over-ground and animal orientation than have been available previously.



Figure 4: The current stereo geocoding system for 3D localization of whales and quantification of social group cohesion. Left: Example of stereo camera system used in August 2012 field cruise, sampling at 4 Hz. Center: Image of 3 pilot whales similar to what is captured by a single of the two cameras. Images from both cameras are analysed to find a distance to different whales using the known aperture and calibration values, and then combined with the GPS position and pointing vector of the camera to calculate georeferenced positions. Right: Conceptual illustration of geocoded position estimates of the three animals shown on image in the bottom left. An initial RMS measure of social group cohesion could be derived as the root-mean-squared distance from each whale (dorsal fin location shown in blue circles) to the mean group position (red circle), for a mean group spread of 4.05 m in this example, and with individual distances between animals noted on figure. Range resolution for the current system is better than $\pm 1m$ at 50 meters distance.

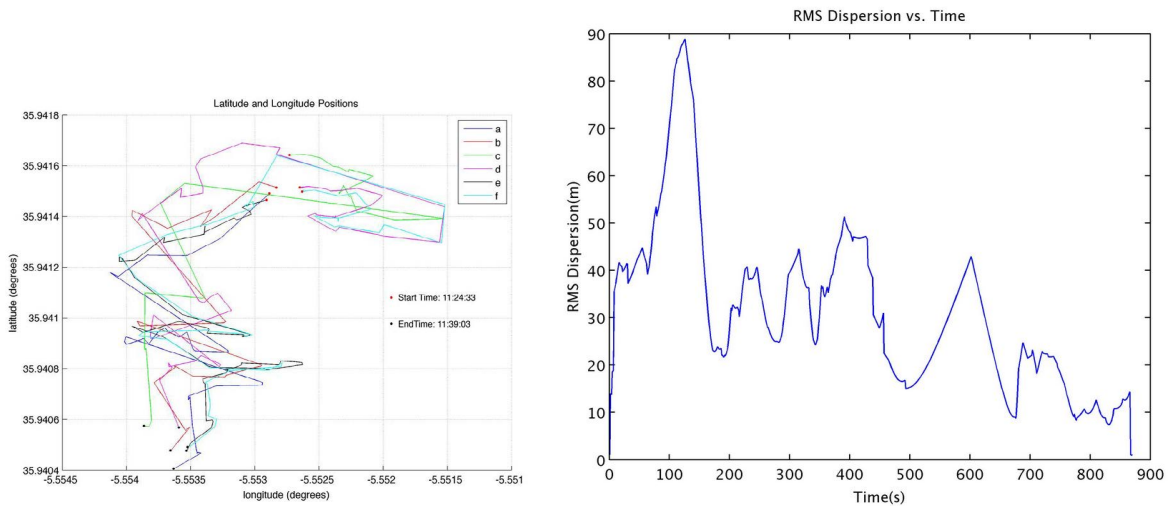


Figure 5: Movement and cohesion of a group of six long-finned pilot whales measured with a stereo camera system. Left: Individual positions (latitude and longitude) measured for all six animals over the course of 20 minutes. Right: RMS group dispersion over time for the six animals tracked with the stereo camera, representing the mean of the distances from the centre of the group to each individual.

IMPACT/APPLICATIONS

An important research topic for the ONR Marine Mammals and Biology program is to study the responses of beaked whales and other whales to naval and anthropogenic sounds. This study is important for this on several levels: First, an increased understanding of the behavior and acoustic

signalling during different degrees of social group separation provides an important baseline for interpreting and designing controlled exposure experiments to pilot whales. For these and other gregarious cetaceans, the group composition, spatial distribution and foraging activity presumably modulate the likelihood of response of individuals exposed to playbacks. Second, an important response variable for social delphinids exposed to disturbance is acoustic activity (DeRuiter et al., 2012) and data on individual and group social communication during different behavioral states may help us better interpret the importance of changes in social signalling. Third, an important variable for responses is changes in orientation and movement (Pirotta et al., 2012; Tyack et al., 2011) and directional approach or avoidance responses (Curé et al., 2012). The stereo camera system under development as part of this project is capable of measuring orientation and speed of animals, as well as quantifying changes in group cohesion that might be part of a possible defensive response to a disturbance. We hope that this system can help provide more quantitative estimates of these important response metrics rather than relying on visual scoring of these metrics by observers.

RELATED PROJECTS

P. L. Tyack and A. Bocconcelli: Tagging and Playback studies of toothed whales (N000140910528) preceded this project with previous work on long-finned pilot whales in the Alboran Sea.
F. H. Jensen and P. L. Tyack: Social ecology and group cohesion in pilot whales and their responses to playback of anthropogenic and natural sounds (N000141410410) continues this project with a new field season in 2015 to retag some of the previously tagged pilot whale groups, and increase playback sample size with a redesigned playback protocol.

REFERENCES

- Aguilar Soto, N.** (2006). Acoustic and diving behaviour of pilot whales (*Globicephala macrorhynchus*) and Blainville's beaked whales (*Mesoplodon densirostris*) off the Canary Islands, with implications for effects of man-made noise and ship strikes. Ph.D. thesis: La Laguna University, Tenerife.
- Aguilar Soto, N., Johnson, M. P., Madsen, P. T., Diaz, F., Dominguez, I., Brito, A. and Tyack, P.** (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *Journal of Animal Ecology* **77**, 936-47.
- Aguilar Soto, N., Madsen, P. T., Tyack, P., Arranz, P., Marrero, J., Fais, A., Revelli, E. and Johnson, M.** (2012). No shallow talk: Cryptic strategy in the vocal communication of Blainville's beaked whales. *Marine Mammal Science* **28**, E75-E92.
- Curé, C., Antunes, R., Samarra, F., Alves, A. C., Visser, F., Kvadsheim, P. H. and Miller, P. J. O.** (2012). Pilot Whales Attracted to Killer Whale Sounds: Acoustically-Mediated Interspecific Interactions in Cetaceans. *PLoS ONE* **7**, e52201.
- de Stephanis, R., Cornulier, T., Verborgh, P., Salazar Sierra, J., Gimeno, N. P. and Guinet, C.** (2008a). Summer spatial distribution of cetaceans in the Strait of Gibraltar in relation to the oceanographic context. *Marine Ecology Progress Series* **353**, 275-288.
- de Stephanis, R., García-Tíscar, S., Verborgh, P., Esteban-Pavo, R., Pérez, S., Minvielle-Sebastia, L. and Guinet, C.** (2008b). Diet of the social groups of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Marine Biology* **154**, 603-612.

- de Stephanis, R., Verborgh, P., Perez, S., Esteban, R., Minvielle-Sebastia, L. and Guinet, C.** (2008c). Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta Ethologica* **11**, 81-94.
- DeRuiter, S. L., Boyd, I. L., Claridge, D. E., Clark, C. W., Gagnon, C., Southall, B. L. and Tyack, P. L.** (2012). Delphinid whistle production and call matching during playback of simulated military sonar. *Marine Mammal Science*, Published online before print: 19 July 2012.
- Johnson, M. P. and Tyack, P. L.** (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *Ieee Journal of Oceanic Engineering* **28**, 3-12.
- Madsen, P. T., de Soto, N. A., Arranz, P. and Johnson, M.** (2013). Echolocation in Blainville's beaked whales (*Mesoplodon densirostris*). *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology* **199**, 451-469.
- Pirotta, E., Milor, R., Quick, N., Moretti, D., Di Marzio, N., Tyack, P., Boyd, I. and Hastie, G.** (2012). Vessel Noise Affects Beaked Whale Behavior: Results of a Dedicated Acoustic Response Study. *PLoS ONE* **7**, e42535.
- Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., Clark, C. W., D'Amico, A., DiMarzio, N., Jarvis, S. et al.** (2011). Beaked Whales Respond to Simulated and Actual Navy Sonar. *PLoS ONE* **6**, e17009.
- Verborgh, P., De Stephanis, R., Pérez, S., Jaget, Y., Barbraud, C. and Guinet, C.** (2009). Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Marine Mammal Science* **25**, 523-536.

PUBLICATIONS

- Macfarlane N. B. W., Howland J., Jensen F. H., Tyack P. L. (submitted): Accurate positioning of animals in space and time using a compact stereo photography system. *Behav. Ecol. Sociobiol.* [submitted, refereed]
- Tyack PL, Janik VM (2013): Effects of noise on acoustic signal production. In *Animal Communication and Noise* (ed. Brumm H.). Springer Verlag, Berlin. [published, refereed]
- Jensen FH, Beedholm K, Wahlberg M, Madsen PT (Submitted): Estimating the biosonar beamwidth and sound production aperture in freeranging Atlantic spotted dolphins (*Stenella frontalis*). *J Exp Biol* [submitted, refereed]
- Fenton BMB, Jensen FH, Kalko EKV, Tyack PL (2014): Sonar Signals of Bats and Toothed Whales. In: *Biosonar* (eds: P. E. Nachtigall, A. M. Surlykke, A. N. Popper, R. R. Fay). Springer, New York (Springer Handbook of Auditory Research) [published, refereed]
- Sayigh L, Quick N, Hastie G, Tyack PL (2013). Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*. *Marine Mammal Science* **29**: 312-324 [published, refereed]
- Shamir L, Yerby C, Simpson R, von Benda-Beckmann A, Tyack PL, Samarra F, Miller P, Wallin J (submitted). Quantitative analysis of killer and pilot whale sounds using Whale FM. *J. Acoust. Soc. Am.* [submitted, refereed]
- Visser F, Miller PJO, Antunes RN, Oudejans MG, Mackenzie ML, Aoki Kagari A, Lam F-Pa, Kvadsheim PH, Huisman J, Tyack PL (2014): The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). *Behaviour* **151**: 1453-77. [published, refereed]