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Moving in concert: Social and migratory behaviour of dolphins and whales in the North Atlantic Ocean

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Chapter 1

General introduction

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Chapter 1. General introduction

Marine mammals have adapted to their environment using a multitude of behavioural strategies. Many toothed whales form highly cohesive societies that cooperate throughout many aspects of their behaviour, extending to babysitting, cooperative hunting and social defence from predators (Mann et al. 2000). With the limited visual range in their underwater habitat, cetaceans have developed sophisticated vocal repertoires that function in long-distance communication, detection and capture of prey and social interaction (Tyack 2000). Baleen whales have responded to seasonal variation in feeding opportunities and weather conditions by undertaking long-distance migrations between polar regions and the subtropics (Kellogg 1929).

Surprisingly little is known, however, about many aspects of cetacean behaviour and social organisation. For example, the migratory routes of the world's largest animal, the blue whale (*Balaenoptera musculus*), have not been resolved and we do not know to what extent deep-diving cetaceans coordinate to hunt prey. These are questions which have become increasingly important in the light of current global changes in the environment and the growing impact of human activities on marine ecosystems. Our lack of knowledge stems largely from the difficulty of studying animals that perform a large part of their behaviour out of sight of human observers, by diving under water, or by performing extensive movements across the vastness of the oceans.

This thesis aims to investigate behavioural patterns of deep-diving toothed whales and baleen whales in the North Atlantic Ocean using newly developed observational methods and recent advances in technology that allow underwater recordings of whale behaviour, investigation of the social context of individual behaviour and monitoring of large-scale ocean dynamics. Ultimately, this will help us to gain a better understanding of the interactions between cetaceans and their environment, and how cetacean populations will respond to human disturbances and changes in their habitat.

Social behaviour of deep-diving cetaceans

Deep-diving cetaceans dive to extreme depths in pursuit of their prey, deep-sea squid, fish or octopus (Pauly et al. 1998). Many species of deep divers inhabit the North Atlantic Ocean, including members of the Delphinidae, Physeteridae, Kogiidae and Ziphiidae (Perrin et al. 2009). A unifying characteristic of deep-

diving cetaceans is their sociality (Fig. 1). Those species for which the social structure has been unravelled show highly cohesive social organisations, with long-term stable bonds between individuals (Ottensmeyer & Whitehead 2003, Whitehead 2003, McSweeney et al. 2007). Sperm whales (*Physeter macrocephalus*) and long-finned pilot whales (*Globicephala melas*) have matriarchal societies, in which females and their offspring form matrilineal groups which stay together over multiple decades. The adult males separate from their natal pods (e.g. Letteval et al. 2002, De Stephanis et al. 2008). The need for deep foraging dives may form an important driver for the formation of these cohesive family groups (Best 1979, Riedman 1982, Gowans et al. 2001). Performing long, deep dives is challenging for air-breathing mammals and young calves may not be physically able to follow adults in pursuit of prey. Solitary calves are highly vulnerable to predation, by sharks or killer whales (*Orcinus orca*; Best et al. 1984). In sperm whales, this may have led to the evolution of babysitting, in which related females alternately dive and stay with the young at the surface (Whitehead 1996).

The dependency of deep divers on conspecifics for food acquisition, reproduction and protection from predators (Whitehead 1996, Pitman et al. 2001, Curé et al. 2012, 2013) implies that their social behaviour can have major consequences for individual fitness. These social behaviours often require a high degree of coordination among group members. Sperm whales, for example, are known to forage in rank formation, which could function to avoid mutual interference (Whitehead 1989) and individuals rapidly congregate at the surface when exposed to sounds of their potential predators, killer whales, as a social defence strategy (Curé et al. 2013). Coordination in activity is mediated by proximity and synchrony in behaviour (Senigaglia & Whitehead 2012, Senigaglia et al. 2012), and by vocalisations (Palombit 1992, Tyack 2000). Deep-diving delphinids, Risso's dolphins (*Grampus griseus*) and pilot whales, have complex vocal repertoires including clicks, tonal calls and pulsed calls (Taruski 1979, Corkeron & van Parijs 2001, Sayigh et al. 2012). Clicks are mainly used for echolocation, to find prey, whereas tonal and pulsed calls predominantly function in social communication (e.g. Soto et al. 2008, Tyack 2000). The short-finned pilot whale (*Globicephala macrorhynchus*) produces social sounds down to depths of 800 m. These calls may function to signal their presence to group members at the water surface, serving to maintain social cohesion (Jensen et al. 2011). Species from the other families predominantly produce clicks. Next to their function in

bio-sonar based foraging, specific sequences (codas) or the timing of clicks are likely to function in social communication (Whitehead & Weilgart 2000, Dunn et al. 2013). Hence, for deep-diving cetaceans, social and vocal behaviours can be strong drivers of population health and constitute important factors for the understanding of the effects of anthropogenic disturbance.

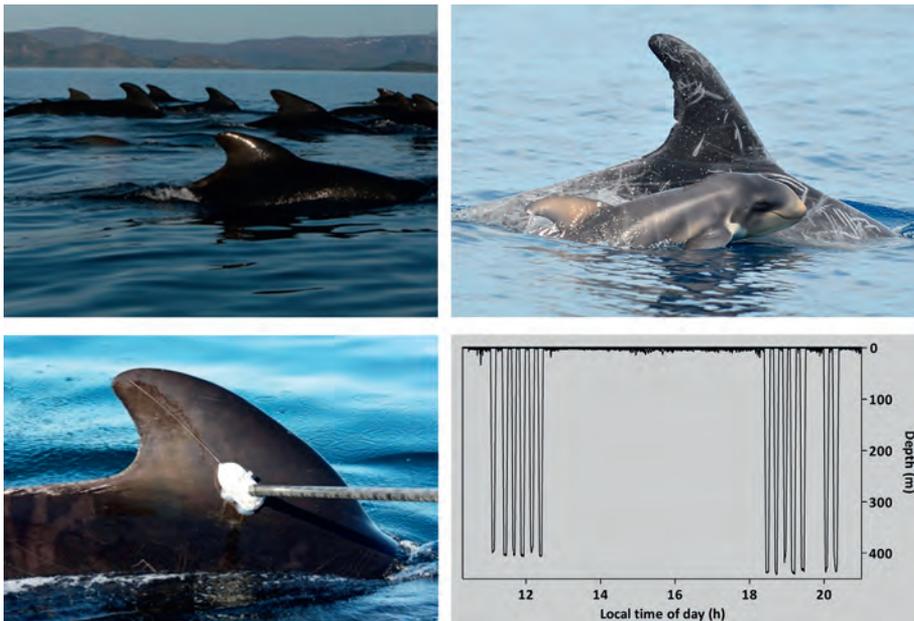


Figure 1. Top left: Social cohesion in a group of long-finned pilot whales (*Globicephala melas*). Top right: close association between a Risso's dolphin (*Grampus griseus*) female and newborn calf. Bottom left: Deployment of a DTAG on an adult long-finned pilot whale. The tag is attached with suction cups, using a pole. Bottom right: the dive profile of the tagged adult pilot whale, showing periods with deep dives, up to 430 m depth, alternated with periods of shallow diving. Pictures: Pilot whales: F.I.P. Samarra, Risso's dolphin: R. N. Antunes.

Our knowledge on the social behaviour of deep-diving cetaceans is generally lagging behind our knowledge of terrestrial social mammals, such as elephants or apes (e.g. de Waal 1982, Janik 2009). Observations of cetacean social behaviour rely largely on what can be observed when the animals are present at the surface. The complex interplay between sociality, behaviour and context, and the distances over which behaviours and interactions can be maintained, further complicate our understanding. However, the recent development of non-invasive tags that can record the underwater behaviours of tagged animals has represented a major advance in the study of the behaviour of deep-diving

cetaceans. The tags can record dive depth, vocalisations, movements, or body contact with conspecifics (Johnson & Tyack 2003, Aoki et al. 2012; Fig. 1). Data from these tags have convincingly proven the use of echolocation and sprints to capture prey during foraging at great depths (e.g. Johnson et al. 2004, Soto et al. 2008). The ability to link the underwater behaviour of one or several individuals to their surface behaviour represents an unprecedented opportunity to study the sociality of deep-diving cetaceans.

Anthropogenic effects on cetacean behaviour

Human activities have a growing impact on the marine environment. A major current concern is the increase of anthropogenic noise in the oceans (Richardson et al. 1995, Nowacek et al. 2007). Anthropogenic sources of sound in the sea have strongly increased over the last decades, due to commercial shipping, (offshore) construction activities for oil and gas exploration or renewable energies, airguns and military sonars, pleasure boats and whale-watching activities (Fig. 2). In the eastern Pacific, for example, intensified commercial shipping has resulted in a 10 dB increase in the levels of background noise in 33 years (Andrew et al. 2002).

Noise can affect cetacean populations by masking of their vocalisations, inducing shifts in behaviour, causing (temporary) hearing-loss, physical injury or, in the extreme case, death (Richardson et al. 1995, Nowacek et al. 2007). Masking occurs if background noise overshadows cetacean calls. Cetaceans rely heavily on acoustic signals for communication, foraging and orientation (Tyack 2000). The importance of information transfer through calling becomes apparent from the observed changes in frequency, amplitude, length and duration of call types across a wide range of cetaceans, which function to compensate for increased levels of background noise (Miller et al. 2000, Foote et al. 2004, Scheifele et al. 2005, Parks et al. 2007). Physical damage, such as hearing loss, or death can result from exposure to powerful or prolonged sound sources (Richardson et al. 1995). Over the last decade, atypical lethal strandings of cetaceans, mostly beaked whales (Ziphiidae), have coincided with military sonar exercises (Parsons et al. 2008). These strandings are most likely started by an avoidance response to the powerful sonar, which may result in an alteration of their dive pattern. Beaked whales can dive to extreme depths, >1000 m, and often have very regular dive cycles. Alterations of their dive pattern may result in injuries related to bubble formation in tissues and organs through decompression, resulting in stranding (Cox et al. 2006, Jepson et al. 2009, Tyack et al. 2011).

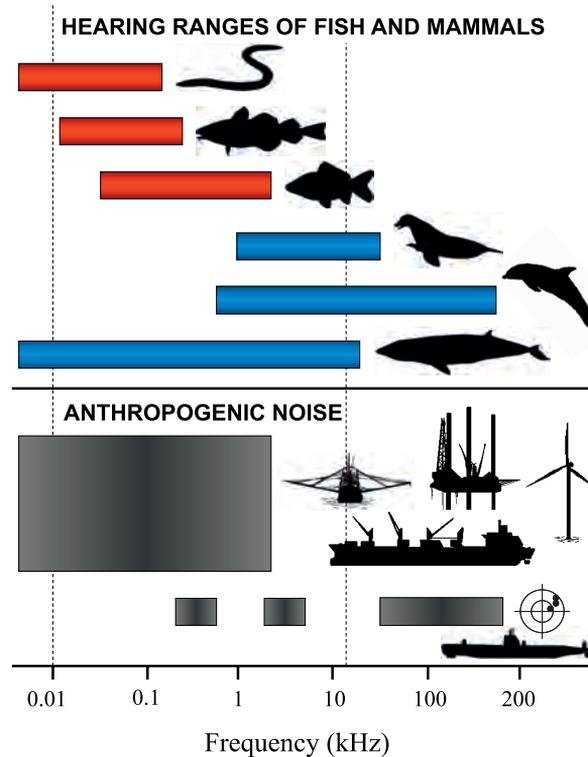


Figure 2. A selection of anthropogenic sound sources within the hearing ranges of marine mammals and fish. Reprinted from Slabbekoorn et al. (2010) with permission from Elsevier.

The growing industry of marine ecotourism activities may also affect cetacean populations (Duffus & Dearden 1990, Lusseau et al. 2006). For many tourists, whale-watching trips offer a unique opportunity to learn more about dolphins and whales (Fig. 3). As such, whale watching contributes to public awareness, and generates support for the conservation of their habitat. Yet, whale watching also exposes cetaceans to vessel noise combined with close vessel approaches, and can have an array of short- and long-term effects on behaviour, comparable to predator-avoidance responses (e.g. Lusseau 2003). The type and the severity of the behavioural response depend on the perception of the disturbance, its characteristics and environmental context and the social and behavioural state of the exposed individuals (e.g. Nowacek et al. 2007, Southall et al. 2007). For example, whether killer whales respond to the presence of whale-watching vessels with a more directional or a more tortuous travel path, depends on the number of vessels (Williams & Ashe 2007). Furthermore, male and female bottlenose dolphins (*Tursiops truncatus*) may differ strongly in the timing of

their avoidance response to close vessel approaches (Lusseau 2003). Strong avoidance responses to whale-watching vessels or other shifts in behaviour that reduce the potential for foraging and reproduction may negatively affect population health (e.g. Bejder et al. 2006, Nowacek et al. 2007).

Cetaceans in European waters are protected under a series of management measures, and all species are included in Annex IV of EU habitat directive 92/43/EEC. Under this directive, regular assessments are to be made of the abundance and distribution of each species, and of the pressures and threats experienced. A main limitation in our understanding of the severity and long-term consequences of pressures and threats for social deep-diver populations, however, is the general lack of knowledge on their natural patterns of behaviour (Southall et al. 2007). Why do some species respond strongly to a disturbance, but others seem unaffected? Does the behavioural change represent a response to a sound source or is it a natural transition in behaviour that would also have occurred in undisturbed conditions? Does a reduction in feeding opportunity impact survival or will they easily find prey elsewhere? To mitigate against potential negative effects, it is therefore essential to i) gain more information on the natural patterns of the behaviour of social, deep-diving cetaceans and ii) to investigate behavioural responses to potential threats.



Figure 3. A whale-watching vessel observing a group of Risso's dolphins close to the coast of Terceira Island, Azores. Picture: F. Visser.

Migratory behaviour of baleen whales

Six species of rorqual baleen whales (Balaenopteridae) inhabit the North Atlantic Ocean, ranging in adult size from 7 m in length (minke whale *Balaenoptera acutorostrata*) to 30 m (blue whale) (Perrin et al. 2009). Individuals of most species migrate between mid- to high latitude feeding grounds in summer and subtropical breeding grounds during winter (Kellogg 1929, Norris 1967). While migratory baleen whales aggregate at the feeding grounds, they mostly occur solitarily or in small groups during migration (Brown & Corkeron 1995). To communicate with their distant conspecifics, and potentially for navigation, baleen whales produce long, low frequency calls (e.g. with a duration of 10 – 30 s at 10 - 40 Hz for blue whales), which can be heard over distances of several hundreds of kilometres (Cummings & Thompson 1971, Payne & Webb 1971). For most species, we have little information on their migratory routes and breeding grounds. Moreover, not all populations may adhere to the general pattern of annual north-south migrations (Simon et al. 2010).

It is, however, evident that seasonal presence of baleen whales at the summer feeding grounds coincides with increased food availability in these waters (e.g. Croll et al. 2005). Due to their large size baleen whales need dense aggregations of their prey (krill or fish) to enable efficient foraging (Whitehead & Carscadden 1985, Friedlaender et al. 2006, Goldbogen et al. 2011). Capture of exceptional numbers of prey is accomplished using a unique feeding strategy, lunge feeding, where an individual speeds forward to engulf a large volume of prey-laden water (Fig. 4). Blue whales can engulf a water mass equivalent to 125% of their body weight in one lunge, holding several hundred kilograms of krill (Goldbogen et al. 2011). Lunges are energetically costly, and prey abundances show strong spatio-temporal variability (Valdés et al. 2007, Dakos et al. 2009). Baleen whales are therefore particularly skilled to locate their patchily distributed prey, allowing them to feed on the patches with highest densities and largest prey items (Croll et al. 2005, Doniol-Volcroze et al. 2007, Goldbogen et al. 2011).

The search for maximum densities of prey is reliant on predictable patterns of seasonal abundance. Baleen whales are thought to fast during migration, relying on energy reserves obtained in the northerly feeding grounds during the preceding summer (Bowen & Siniff 1999). In the North Atlantic Ocean, however, the annual phytoplankton spring bloom offers a conspicuous wave of enhanced primary productivity, which propagates northwards from subtropical latitudes

to subarctic waters over spring and summer (Siegel et al. 2002, Behrenfeld 2010). The spring bloom is likely to fuel secondary production by zooplankton including krill, important prey items of many baleen whales. If it is shown that baleen whales feed on krill during spring migration, tracking areas with enhanced productivity en route, this would represent a fundamental change in our understanding of baleen whale foraging and migratory behaviour, and their energetic requirements.

Modern technology, using satellite remote sensing of the colour of the ocean, can accurately determine patterns of surface phytoplankton production of entire ocean basins (e.g. NASA Ocean Color website <http://oceancolor.gsfc.nasa.gov/>), including the phytoplankton spring bloom (Fig. 4). This provides essential information on changes in seasonal and geographical patterns of ocean surface productivity, which can then be matched to observations of species that migrate over vast ocean areas in search of prey.

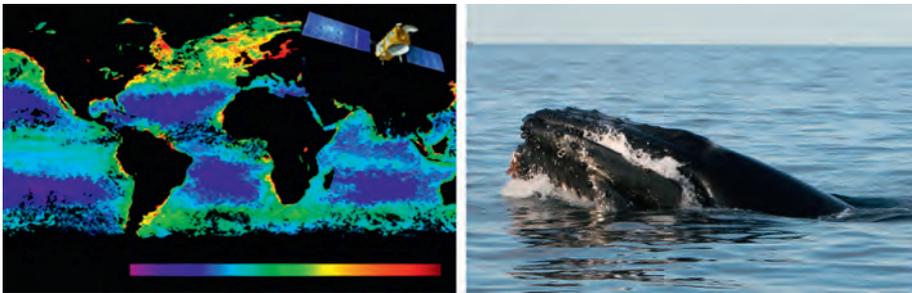


Figure 4. Left: Satellite remote sensing of ocean chlorophyll *a* concentration in June 2006 (mg m^{-3} ; NASA Ocean Color website <http://oceancolor.gsfc.nasa.gov/>). Right: Humpback whale (*Megaptera novaeangliae*) surfacing at the end of a lunge off northern Norway. Picture: F.I.P. Samarra for the 3S Project.

Outline of this thesis

This thesis focuses on behavioural patterns of deep-diving toothed whales, and of baleen whales, in the North Atlantic Ocean. It addresses functional aspects of their social, vocal and migratory behaviour. Our approach combines shore- and vessel-based visual observations of the behaviour of individuals and groups with tagging, photographic and remote sensing technology. We develop new methodology and a novel definition of animal groups to quantitatively record cetacean social behaviour using visual observations. These approaches allow us to investigate the diving behaviour, social organisation and foraging behaviour

of social cetaceans, as well as the migratory behaviour of baleen whales in relation to the distribution of prey en route. In addition, we applied these approaches to evaluate behavioural responses of cetaceans to anthropogenic disturbances, such as the impact of whale watching on the behaviour of social cetaceans and the potential effects of climate change on the migratory routes of baleen whales.

The work presented in this thesis combines results obtained from two research projects. The first project, based in the Azores, allowed for shore- and vessel-based observations of six species of baleen whales and of a range of deep-diving cetaceans. Four years of dedicated baleen-whale observations at the Azores provided the basis for our study of the migratory behaviour of baleen whales in relation to the North Atlantic spring bloom. For our study of the behaviour of social deep-diving cetaceans, we focussed on Risso's dolphin (*Grampus griseus*). Thus far, Risso's dolphin social organisation and patterns of behaviour have received little study. The species is commonly present in the inshore waters off the Azores, and is a regular target of whale-watching activities in the area. This generated an excellent opportunity to study the sociality and behaviour of this social deep diver, and its behavioural response to a potential source of disturbance. The second project, based in Norway, was the 3S Project. The 3S Project investigated the baseline behaviour and behavioural response of long-finned pilot whales, killer whales and sperm whales to military sounds (Miller et al. 2011). The experimental approach of the 3S Project, using non-invasive tags to study underwater behaviour, allowed us to generate a new protocol for the sampling of surface group behaviour of social cetaceans. Using this protocol, we studied behavioural patterns of one of the target species of the 3S Project, the social, deep-diving long-finned pilot whale.

In Chapters 2 to 5 we investigate functional aspects of the behaviour and social organisation of the two species of deep-diving cetaceans, long-finned pilot whales and Risso's dolphins. Chapter 2 addresses current limitations in the analysis of group-level behaviour in social cetaceans by the development and testing of a novel sampling protocol describing the social context of individual behaviour. The protocol is based on a new definition of the group, centred around a focal individual, and quantitative records describing characteristics of the group. Using this protocol, we investigate the relation between the behaviour of long-finned pilot whale groups observed at the surface and the deep-diving foraging behaviour of focal individuals monitored by tag data.

In deep-diving cetaceans, social cohesion and coordination of the group are thought to be mediated by their vocal behaviour (Tyack 2000). In Chapter 3 we test this theory by investigating the relation between long-finned pilot whale calls and the socio-behavioural context in which they are produced. Again, a key aspect of our approach, allowing assessment of the functionality of the pilot whale calls, is the selection of a focal individual that forms the central point of recordings of the group-level behaviour and the soundscape.

In Chapters 4 and 5, we shift our focus to a second species of deep divers, Risso's dolphins. Thus far, the social organisation and behaviour of Risso's dolphins have received very little study. First insights into their social structure indicate the presence of stable associations between individuals, comparable to other deep-diving species such as pilot whales and sperm whales. Social behaviour is of vital importance for deep-diving species. Its form and function are regulated by the stability and duration of associations between individuals in the society (Mann et al. 2000). Thus, to gain insight into Risso's dolphin behaviour, knowledge on their social structure is essential. Do Risso's dolphins form long-term stable social units, and are they also organised in matrilineal groups? These questions are investigated in Chapter 4, by social network analysis of the associations between Risso's dolphins in the Azores.

The Azores have seen a growing whale watching industry, with limited regulation (Magalhães et al. 2002). Whale-watching activity may be particularly strong in the summer months. The inshore presence and site-fidelity of Risso's dolphin groups (Chapter 4) suggests that individuals may be regular targets of whale-watching vessels, and could regularly be exposed to vessel noise at close range and by multiple vessels. In Chapter 5 we investigate whether these whale-watching activities affect their behaviour. We use shore-based observation methods to avoid the potentially disturbing presence of a research vessel near the group. In particular, we are interested in how cetacean behaviour may depend on the intensity of whale watching, and propose regulation of whale-watching activities to mitigate negative effects.

In Chapter 6 we investigate the relation between the timing of migratory baleen whales at the Azores and the North Atlantic spring bloom. Six species of baleen whales are known to occur at the Azores, with a strongly seasonal presence. Satellite tracking of individual baleen whales suggests use of the area during spring migration (Olsen et al. 2009). The Azores archipelago is characterized by high ecosystem productivity in spring (Johnson & Stevens

2000, Siegel et al. 2002). Hence, the question is whether migratory baleen whales might use the Azores as a foraging area during their spring migration towards the northern feeding grounds, which would challenge the classic idea that whales fast during migration.

Finally, in Chapter 7, I synthesize the results presented in this thesis. In particular, I discuss our new insights into the foraging strategies, sociality and vocal behaviour of deep-diving toothed whales, the migratory behaviour of baleen whales, the resulting potential implications of anthropogenic disturbance, and directions for future research.

References

- Andrew RK, Howe BM, Mercer JA, Dzieciuch MA (2002) Ocean ambient sound: Comparing the 1960's with the 1990's for a receiver off the California coast. *Acoustics Research Letters Online* 3:65-70, doi: 10.1121/1.1461915.
- Aoki K, Amano M, Mori K, Kourogi A, Kubodera T, Miyazaki N (2012) Active hunting by deep-diving sperm whales: 3D dive profiles and manoeuvres during bursts of speed. *Marine Ecology Progress Series* 444:289-301.
- Behrenfeld MJ (2010) Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. *Ecology* 91: 977–989.
- Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, Watson-Capps J, Flaherty C, Krützen M (2006) Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* 20:1791-1798.
- Best PB (1979). Social organization in sperm whales, *Physeter macrocephalus*. In: Winn HE, Olla BL, editors. *Behavior of Marine Animals*. Vol. 3. Plenum Press, NY. pp 227-289.
- Best PB, Canham PAS, Macleod N (1984) Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Reports of the International Whaling Commission (special issue)* 8:51-79.
- Bowen WD, Siniff DB (1999) Distribution, population biology and feeding ecology of marine mammals. In: Reynolds JE III, Rommel SA, editors. *Biology of marine mammals*. Smithsonian Institution Press, Washington. pp 423-484.
- Brown M, Corkeron P (1995) Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the East Australian coast. *Behaviour* 132:163-179.
- Corkeron PJ, van Parijs SM (2001). Vocalizations of eastern Australian Risso's dolphins, *Grampus griseus*. *Canadian Journal of Zoology* 79:160-164.
- Cox TM, Ragen, TJ, Read AJ, Vos E, Baird RW, Balcomb K, Barlow J, Caldwell J, Cranford T, Crum L, D'Amico A, D'Spain G, Fernandez A, Finneran J, Gentry R, Gerth W, Gulland F, Hildebrand J, Houser D, Hullar T, Jepson PD, Ketten D, MacLeod CD, Miller P, Moore S, Mountain DC, Palka D, Ponganis P, Rommel S, Rowles T, Taylor B, Tyack P, Wartzok D, Gisiner R, Mead J, Benner L (2006) Understanding the impacts of acoustic sound on beaked whales. *Journal of Cetacean Research and Management* 7:177-187.
- Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series* 289: 117–130.
- Cummings WC, Thompson PO (1971). Underwater sounds from the blue whale *Balaenoptera musculus*. *Journal of the Acoustical Society of America* 50: 1193–1198.
- Curé C, Antunes R, Samarra F, Alves AC, Visser F, Kvadsheim PH, PJO Miller (2012). Pilot whales attracted to killer whale sounds: Acoustically mediated interspecific interactions in cetaceans. *PLoS ONE* 7(12): e52201.
- Curé C, Antunes R, Alves AC, Visser F, Kvadsheim PH, PJO Miller (2013) Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: implications for anti-predator strategies. *Scientific Reports* 3: 1579.

- Dakos V, Benincà E, van Nes EH, Philippart CJM, Scheffer M, Huisman J (2009) Interannual variability in species composition explained as seasonally entrained chaos. *Proceedings of the Royal Society London B* 276: 2871–2880.
- De Stephanis R, Verborgh P, Pérez S, Esteban R, Minvielle-Sebastia L, Guinet C (2008) Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta Ethologica* 11:81-94.
- De Waal F (1982) Chimpanzee politics: Power and sex among apes. John Hopkins University Press, Baltimore. pp 235.
- Doniol-Valcroze T, Berteaux D, Larouche P, Sears R (2007) Influence of thermal fronts on habitat selection by four baleen whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series* 335: 207–216.
- Duffus DA, Dearden P (1990) Non-consumptive wildlife-oriented recreation: a conceptual framework. *Biology and Conservation* 53:213–231.
- Dunn C, Hickmott L, Talbot D, Boyd I, Rendell L (2013) Mid-frequency broadband sounds of Blainville's beaked whales. *Bioacoustics* 22:153-163, doi: 10.1080/09524622.2012.757540.
- Footo AD, Osborne RW, Hoelzel AR (2004) Whale-call response to masking boat noise. *Nature* 428:910.
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the western Antarctic Peninsula. *Marine Ecology Progress Series* 317: 297–310.
- Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *Journal of Experimental Biology* 214: 131–146.
- Gowans S, Whitehead H, Hooker SK (2001) Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging? *Animal Behaviour* 62:369-377.
- Huisman J, Pham Thi NN, Karl DM, Sommeijer B (2006) Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. *Nature* 439:322-325.
- Janik VM (2009) Acoustic communication in delphinids. In: Naguib M, Zuberbuhler K, Clayton NS, Janik VM, editors. *Advances in the study of behavior*, vol. 40. Elsevier Academic Press, San Diego. pp 123-157.
- Jensen FH, Perez Jm, Johnson M, Soto NA, Madsen PT (2011). Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proceedings of the Royal Society B* 278:3017-3025.
- Jepson PD, Arbelo M, Deaville R, Patterson JAP, Castro P, Baker JR, Degollada E, Ross HM, Herráez P, Pocknell AM, Rodríguez F, Howiell FE, Espinosa A, Reid RJ, Jaber JR, Martin V, Cunningham AA, Fernández A (2003). Gas-bubble lesions in stranded cetaceans. *Nature* 425:575-576.
- Johnson J, Stevens I (2000) A fine resolution model of the eastern North Atlantic between the Azores, the Canary Islands and the Gibraltar Strait. *Deep-Sea Research I* 47:875–899.
- Johnson MP, 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.
- Johnson MP, Madsen PT, Zimmer WMX, Soto NA, Tyack PL (2004) Beaked whales echolocate on prey. *Proceedings of the Royal Society of London B* 271:S383-S386.
- Kellogg R (1929) What is known on the migrations of some of the whalebone whales? *Smithsonian Institution Annual Report No. 1928*. U.S.G.P.O. Washington, DC, p 467–494.
- Lettevall E, Richter C, Jaquet N, Slooten E, Dawson S, Whitehead H, Christal J, McCall Howard P (2002) Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* 80:1189-1196.
- Lusseau D (2003) Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series* 257:267-274.
- Lusseau D, Slooten E, Currey RJC (2006) Unsustainable dolphin-watching tourism in Fiordland, New Zealand. *Tourism and the Marine Environment* 3:173–178.
- Magalhães S, Prieto R, Silva MA, Gonçalves J, Afonso-Dias M, Santos RS (2002). Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale watching vessels in the Azores. *Aquatic Mammals* 28:267-274.
- Mann J, Connor RC, Tyack PL, Whitehead H (2000) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago. pp 433.
- McSweeney DJ, Baird RW, Mahaffy SD (2007). Site fidelity, associations, and movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off Hawai'i. *Marine Mammal Science* 23:666-687.

- Miller PJO, Biassoni N, Samuels A, Tyack PL (2000). Whale songs lengthen in response to sonar. *Nature* 405:903.
- Miller PJO, Antunes RN, Alves AC, Wensveen P, Kvadsheim PH, Kleivane L, Nordlund N, Doksæter L, Lam FPA, Ijsselmuide S, Visser F, Tyack PL (2011). The 35 experiments: studying the behavioral effects of sonar on killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and long-finned pilot whales (*Globicephala melas*) in Norwegian waters. Scottish Ocean Institute Technical Report, SOI-2011-001.
- Norris K (1967) Some observations on the migration and orientation of marine mammals. In: Storm RM (ed) *Animal orientation and navigation*. University of Cal Press, Berkeley, CA, p 320-380.
- Nowacek DP, Thorne LH, Johnston DW, Tyack PL (2007) Responses of cetaceans to anthropogenic noise. *Mammal Review* 37:81-115.
- Olsen E, Budgell WP, Head E, Kleivane L, Nøttestad L, Prieto R, Silva MA, Skov H, Vikingsson GA, Waring G, Øien N (2009) First satellite-tracked long-distance movement of a sei whale (*Balaenoptera borealis*) in the North Atlantic. *Aquatic Mammals* 35:313-318.
- Ottensmeyer CA, Whitehead H (2003) Behavioural evidence for social units in long-finned pilot whales. *Canadian Journal of Zoology* 81:1327-1338.
- Palombit R (1992) A preliminary study of vocal communication in wild long-tailed macaques (*Macaca fascicularis*) II. Potential of calls to regulate intragroup spacing. *International Journal of Primatology* 13:183-207.
- Parks SE, Clark CW, Tyack PL (2007) Short- and long-term changes in right whale calling behaviour: The potential effects of noise on acoustic communication. *Journal of the Acoustical Society of America* 122:3725-3731.
- Parsons ECM, Dolman SJ, Wright AJ, Rose NA, Burns WCG (2008) Navy sonar and cetaceans: Just how much does the gun need to smoke before we act? *Marine Pollution Bulletin* 56:1248-1257.
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55: 467-481.
- Payne RS, Webb D (1971) Orientation by means of long range acoustic signaling in baleen whales. *Annals of the New York Academy of Sciences* 188:110-141.
- Perrin WF, Würsig B, Thewissen JGM (2009) *Encyclopedia of Marine Mammals*. London: Academic Press. pp 1352.
- Pitman RL, Ballance LT, Mesnick SI, Chivers SJ (2001). Killer whale predation on sperm whales: observations and implications. *Marine Mammal Science* 17:494-507.
- Richardson WJ, Greene CR, Malme CI, Thomson DH (1995). *Marine mammals and noise*. Academic Press, Inc., San Diego, CA. p 576.
- Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology* 57:405-435.
- 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.
- Scheifele PM, Andrew S, Cooper RA, Darre M, Musiek FE, Max L (2005). Indication of a Lombard vocal response in the St. Lawrence River beluga. *Journal of the Acoustical Society of America* 117:1486-1492.
- Senigaglia V, Whitehead H (2012) Synchronous breathing by pilot whales. *Marine Mammal Science* 28:213-219.
- Senigaglia V, De Stephanis R, Verborgh P, Lusseau D (2012) The role of synchronized swimming as affiliative and anti-predatory behavior in long-finned pilot whales. *Behavioural Processes* 91:8-14.
- Siegel DA, Doney SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. *Science* 296: 730-733.
- Simon M, Stafford KM, Beedholm K, Lee CM, Madsen PT (2010) Singing behaviour of fin whales in the Davis Strait with implications for mating, migration and foraging. *Journal of the Acoustical Society of America* 128: 3200-3210.
- Slabbekoorn H, Bouton N, van Opzeeland I, Coers A, ten Cate C, Popper AN (2010) A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology and Evolution* 25: 419-427.
- Soto NA, Johnson MP, Madsen PT, Díaz F, Domínguez I, Brito A, Tyack, PL (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *Journal of Animal Ecology* 77:936-947.
- 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 (2007). Marine mammal noise exposure criteria: initial scientific recommendations. *Aquatic Mammals* 33: 411-521.

- Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. *ICES Journal of Marine Science* 18: 287–295.
- Taruski AG (1979) The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In: Winn HE, Olla BL, editors. *Behavior of marine mammals*, vol 3.:Plenum Press, New York. pp 345-368.
- Tyack PL (2000) Functional aspects of cetacean communication. In: Mann J, Connor RC, Tyack PL, Whitehead H, editors. *Cetacean societies: field studies of dolphins and whales*. University of Chicago Press, Chicago. pp. 270-307.
- Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, Durban JW, Clark CW, D'Amico A, DiMarzio N, Jarvis S, McCarthy E, Morissey R, Ward J, Boyd I (2011) Beaked whales respond to simulated and actual navy sonar. *PLoS ONE* 6:e17009.
- Valdés L, López-Urrutia A, Cabal J, Alvarez-Ossorio M and others (2007) A decade of sampling in the Bay of Biscay: what are the zooplankton time series telling us? *Progress in Oceanography* 74: 98–114.
- Whitehead H, Carscadden JE (1985) Predicting inshore whale abundance—whales and capelin off the Newfoundland coast. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 976–981.
- Whitehead H (1989) Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. *Canadian Journal of Zoology* 67:2131-2139.
- Whitehead H (1996) Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology* 38:237-244.
- Whitehead H (2003) Sperm whales: social evolution in the ocean. University of Chicago Press, Chic.
- Whitehead H, Weilgart L (2000) The sperm whale: social females and roving males. In: Mann J, Connor RC, Tyack PL, Whitehead H, editors. *Cetacean societies: field studies of dolphins and whales*. University of Chicago Press, Chicago. pp 154-172.
- Williams R, Ashe E (2007) Killer whale evasive tactics vary with boat number. *Journal of Zoology* 272:390-397.