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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 7

## Synthesis

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## Chapter 7. Synthesis

The aim of this thesis is to better understand several fundamental aspects of cetacean social, vocal, foraging and migratory behaviour. Because marine mammals are traditionally difficult to study, knowledge of their behavioural patterns is often limited, lagging behind that of terrestrial animals (e.g. Janik 2009). These gaps in knowledge limit our ability to mitigate against potential effects of the growing impact of human activities on the marine environment. To aid in the advance of the study of cetacean social behaviour, I developed a new visual group sampling method (*Chapter 2*), which enabled investigation of the social context of long-finned pilot whale (*Globicephala melas*) foraging behaviour, and the socio-behavioural context of their vocalisations (*Chapter 2* and *3*). Then, I set out to study the unknown social structure of Risso's dolphins (*Grampus griseus*; *Chapter 4*) and whether they show behavioural responses to whale-watching activities (*Chapter 5*). Finally, I investigated the migratory behaviour of five species of baleen whales in the North Atlantic Ocean, and its relation to seasonal changes in ocean productivity (*Chapter 6*). In this chapter, I will discuss my key findings and methodological approach, how these have increased our understanding of the behaviour of deep-diving cetaceans and baleen whales, and their implications for the resilience of cetacean populations to disturbance.

### **Sociality and vocal behaviour of long-finned pilot whales**

The opportunity to gain new insights into the social and vocal context of long-finned pilot whale behaviour relied on the combination of group-level observations with data on the foraging dives of individuals tagged with non-invasive digital archival tags (Johnson & Tyack 2003; Fig. 1). We developed a new protocol to study cetacean group behaviour, using a dynamic definition of the group centred around the tagged individual, and an ethogram quantifying visually observable characteristics of the group (*Chapter 2*).

Long-finned pilot whales display a high degree of sociality in their behaviour (*Chapter 2* and *3*). The species often occurs in large aggregations of 60-100 individuals, composed of several groups, which can maintain coordinated movements over the time-scale of at least a day (*Chapter 2*, see also Ottensmeyer & Whitehead 2003, de Stephanis et al. 2008). Group members, on average 10 per group, are preferentially spaced within 3 body lengths apart and pairs can

be highly synchronous in their surfacing and diving behaviour (Chapter 2, Senigaglia & Whitehead 2012, Aoki et al. 2013). Group members also coordinate the timing of their behaviours (Chapter 2). Proximity and behavioural synchrony serve to maintain social cohesion, accomplish coordinated behaviours and potentially aid in defence against predators (Engel & Lamprecht 1997, Sakai et al. 2009, Senigaglia et al. 2012). A similar function is attributed to vocalisations, which serve to mediate cohesion, contact and coordination in an environment with limited use of visual cues (Tyack 2000) and many groups of conspecifics. This functionality was confirmed by the increase in the proportion of time the whales were silent in larger, more coordinated groups, suggesting that higher levels of social cohesion release the function of vocalising in long-finned pilot whales (Chapter 3).

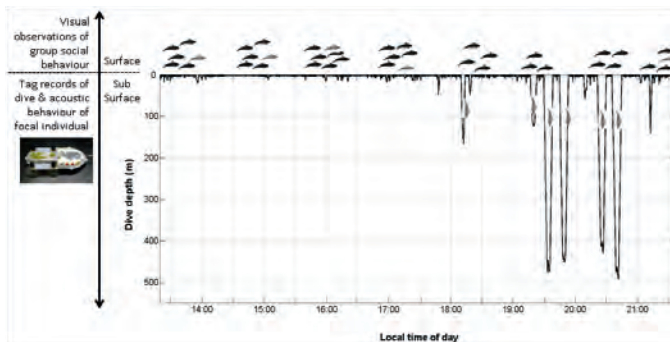


Figure 1. Schematic representation of the behaviour sampling methodology during focal follows of long-finned pilot whale groups: concurrent sampling of group, diving and acoustic behaviour centered around a tagged individual (grey coloured individual).

Distance to other whales, either within the group or to the nearest other group in the aggregation, is an important determinant of the pilot whale soundscape (Chapter 3, Taruski 1979, Weilgart & Whitehead 1990). Interestingly, the social function of vocalisations may not be limited to the tonal calls (whistles). Echolocation clicks were recorded during 24% of time spent in shallow diving periods, potentially serving to gain information on the location of conspecifics at lower degrees of social cohesion (Chapter 3). Simple social calls were used constantly throughout the behavioural spectrum, suggesting that these call types may function to signal presence, irrespective of behavioural context. Simpler calls more easily maintain their spectral characteristics, and can serve

to broadcast species' identity information over larger distances than would be possible for complex sounds (Brenowitz 1982). In pilot whales they could serve to signal group-specific cues between dispersed group members (Jensen et al. 2011, Chapter 3). The soundscape of deep-diving long-finned pilot whales remains filled with communication and echolocation sounds throughout the depth spectrum (Chapter 3). Social call production becomes more difficult at larger depths, due to pressure-induced limitations and a dwindling air-supply (Jensen et al. 2011). In short-finned pilot whales, this results in a reduction of the length and amplitude of social calls with increasing depth (Jensen et al. 2011). We observed a similar pattern in long-finned pilot whales, for which complex calls are nearly lost from the soundscape below 350 m depth, whereas simple calls are maintained to the maximum dive depth (620 m; Chapter 3).

### **Social foraging strategies of long-finned pilot whales**

Marine mammals have developed intricate cooperative behaviours to herd their prey. Humpback whales make bubble nets to concentrate prey (*e.g.* Wiley et al. 2011), spinner dolphin (*Stenella longirostris*) groups break up into pairs to circle and concentrate schools of fish (Benoit-Bird and Au 2009) and killer whales employ a technique called wave-washing, where they synchronise their swimming to create a wave which washes a seal off an ice floe (Pitman & Durban 2012). The prey is shared among group members. How social foraging is organised within deep-diving cetaceans is less clear. Evidence from foraging sperm whales and short-finned pilot whales suggests that, at depth, these species forage individually or in small groups (Whitehead 1989, Soto 2006).

We found that long-finned pilot whales employ a coordinated foraging strategy, where individuals synchronise the overall timing of their foraging periods, although the exact timing of the foraging dives may differ between individuals (Chapter 2). Periods of active foraging are characterised by a distinct signal in the group behaviour at the surface. During foraging, groups break up into smaller and more widely spaced units with a reduced degree of coordinated swimming (Chapter 2). Concordantly, vocal activity increases (Chapter 3). Most notably, the production of echolocation clicks strongly increases during foraging. However, we also found evidence for increased occurrence of complex social calls during foraging behaviour. Complex calls are relatively long communication calls with three or more frequency inflections (Weilgart & Whitehead 1990, Chapter 3). These calls allow for more distant

and extended information transfer than their simple, shorter counterparts (Jensen et al. 2011). Increased complexity of social calls would point towards intensified and more complex social communication. This could function to compensate for increased distance between group members, or to increase or alter the information content of social calls during foraging (Chapter 3). Thus, vocalisations can have an important role in maintaining social cohesion when group members are dispersed between the surface and several hundred metres depth, and may serve to signal feeding conditions (Chapter 2 and 3).

Combined, our results indicate that individuals coordinate their overall foraging behaviour but pursue prey individually or in small groups at depth. We found evidence that long-finned pilot whales may cooperate during foraging, although they probably do not herd their prey. As pilot whales forage on patchy prey fields, which change their distribution over the water column throughout the day (Shane 1995, Baird et al. 2002), signalling of good feeding opportunities can strongly improve foraging efficiency of the group. Alternatively, joint foraging in small groups may have the benefit of confusing prey items, as postulated for sperm whales (Whitehead 1989).

### **Risso's dolphin social structure**

Group stability in odontocetes shows a positive correlation with body size (Bräger 1999). Risso's dolphin size falls between that of the bottlenose dolphin (*Tursiops truncatus*) and the pilot whale (Perrin et al. 2009). Bottlenose dolphins have a fission-fusion society, where individuals form many loose associations, with long-term stable alliances between pairs and trios of males (Connor et al. 1992, 2000). Pilot whales form long-term stable bonds between individuals, organised in matriline (Ottensmeyer & Whitehead 2003). Given that Risso's dolphins are deep divers, their social structure is expected to more closely resemble that of pilot whales, than of the non-deep-diving bottlenose dolphins. Hence, we expected their social organization to be characterised by stable bonds, potentially organised in matriline (but see Gowans et al. 2001).

We discovered that Risso's dolphin social structure is indeed based on long-term stable associations between individuals, organised in distinct clusters (Chapter 4). However, unlike in pilot whales and sperm whales, these clusters do not represent matriline. Instead, we observed long-term stable clusters of 3 – 11 individuals, of which the large majority are males (Fig. 2). Females also form stable clusters, of 6 -12 individuals, but our results indicate that these are

largely dependent on the presence of nursing calves (Chapter 4). Seemingly, females with nursing calves form stable groups, which may later disassociate. This is not the case for the clusters with adult males, which remain closely associated irrespective of the behavioural context.



Figure 2 Highly synchronous surfacing behaviour of seven Risso's dolphins, likely all males. Picture F. Visser.

Hence, Risso's dolphin social structure, characterised both by fission-fusion (sub-adults) and by long-term stable associations (male groups, female and calf groups), deviates from any cetacean social organisation described to date. The formation of stable bonds between females with nursing calves confirms the need for deep-diving odontocetes to provide parental and social care for their young, until the sub-adults have become independent. Our results also support the hypothesis that deep-diving cetaceans do not necessarily require a social structure built on matriline (Gowans et al. 2001). Just like the deep-diving Northern bottlenose whales (*Hyperoodon ampullatus*; Gowans et al. 2001), Risso's dolphins likely do not form (long-term stable) matriline, whereas some non-deep-diving species, such as the killer whale, do (Bigg et al. 1990).

Why do Risso's dolphin males form long-term stable pods? Male group members coordinate the timing and location of their foraging behaviour (F. Visser, pers. obs.) and cooperate for access to females (Chapter 4). Hence, group formation could have both foraging and reproductive benefits, although the latter would be largely dependent on the genetic relatedness of the males. The male groups are generally larger than alliances of male bottlenose dolphins which cooperate to herd females (size = 2 or 3 individuals; Connor 1992), but smaller than long-finned pilot whale pods (average size = 10 individuals;



Chapter 2). We hypothesize that male pod size represents a trade-off between the benefits of cooperative foraging for deep-diving cetaceans, the potential for habitat defence in populations with high site-fidelity and a reduction of reproductive benefits, in larger groups (Chapter 4). Future studies investigating Risso's dolphin social structure would strongly benefit from a genetic component, to elucidate the relatedness between individuals within and outside of stable clusters, in relation to age- and sex-class and the degree of site-fidelity.

### **Effects of background noise on social cetaceans**

Our results show the importance of simple social sounds for long-finned pilot whales, throughout the behavioural spectrum (*Chapter 3*). These relatively short and weak vocalisations are easily prone to masking by background noise, especially at larger distances between group members. Moreover, cetacean vocal responses to counteract masking, such as increased length or amplitude of calls (Foote et al. 2004, Scheifele et al. 2005), may not be physically possible at depth, during the foraging dives (Jensen et al. 2011). Hence, it is likely that increased levels of background noise may have a significant impact on the ability of long-finned pilot whales to communicate with group members during foraging.

While we did not investigate vocalisations of Risso's dolphin groups, our results from the long-finned pilot whales suggest that foraging Risso's dolphin mother groups may be particularly vulnerable for increased levels of background noise. The formation of stable groups by females with dependent calves indicates that these individuals require a higher degree of social cohesion during this period. Risso's dolphins are also very vocal, in particular when foraging (Neves 2013) and they may employ similar vocal strategies to those used by the pilot whales to maintain contact with group members. If this is impeded by background noise, this may limit the ability of mothers to rejoin or maintain contact with their calves and female associates at the surface during periods of deep diving. To investigate these hypotheses, detailed studies on the potential effects of background noise on Risso's dolphin, pilot whales and other deep-diving cetaceans seem warranted.

### **Whale-watching effects on social cetaceans**

Cetaceans commonly respond to whale-watching activities, often with a change in behaviour that may negatively affect the build-up of energy reserves or reproductive success (Lusseau 2003, 2004, Bejder et al. 2006, Stensland &

Berggren 2007). The high site-fidelity of the Risso's dolphin population, their inshore distribution and regular presence of mother pods at the Azores (*Chapter 4*) therefore raises some concern about the potential impacts of whale-watching activities in the area. We found that, during the high season of whale watching, Risso's dolphins rested and socialised less. Moreover, they changed the timing of their resting behaviour to periods with the lowest number of vessels (lunch break; *Chapter 5*). Reduced rates of resting and socialising behaviour may have fitness consequences for animal populations (*e.g.* Ricklefs et al. 1996, Frid & Dill 2002). Moreover, social species such as Risso's dolphins rely on cohesion and coordination to structure their behaviour and profit from the benefits of group living (Mann et al. 2000; *Chapter 2-4*). Whale-watching vessels can interfere with these functions by the production of vessel noise that may mask whale vocalisations and other sounds, and by close vessel approaches that may be perceived as a potential threat (Erbe 2002, Williams et al. 2002, Nowacek et al. 2007). Risso's dolphin surface resting behaviour is comparable to that of the long-finned pilot whales (*Chapter 2 and 5*), characterised by a high degree of social cohesion that may entail the group being silent (*Chapter 4*; Neves 2013). This form of resting would require a silent environment in which individuals can move predictably and slowly to avoid loss of cohesion, which would be adversely affected by the presence of a vessel near the group.

The strongest effects, both on the timing and rates of Risso's dolphin behaviour, were observed when larger numbers of vessels were present (*Chapter 5*). This indicates the potential for mitigation against these effects by regulation of the number of vessels in the area. Our results suggest that, if whale-watching vessel presence is regulated to maximally five vessels in the research area per day, of which maximally two vessels are present at the same time (*Chapter 5*), this could reduce the effects on Risso's dolphin activity budget. The number of vessels is also a determinant of the severity and type of behavioural response to whale-watching activities for other cetacean species (*e.g.* bottlenose dolphins, killer whales; Constantine et al. 2004, Williams and Ashe 2007). Hence, regulation of the numbers of active whale-watching vessels in an area could also benefit other targeted cetacean species in the Azores.

### **Baleen whales forage during spring migration**

The trans-Atlantic migration of baleen whales is matched in magnitude by those of several species of birds, turtles and fish (*e.g.* Doyle et al. 2008, Gore et

al. 2008, Egevang et al. 2010). With some exceptions, these extensive migrations reflect strong seasonal fluctuations in food availability and weather conditions. The migratory phase of the cycle is often thought to be associated with high energetic costs, the benefit to be obtained at the end of the journey (Alerstam et al. 2003). However, some species forage during migration, benefitting from areas with locally enhanced productivity. Leatherback turtles (*Dermochelys coriacea*), for example, can locate offshore mesoscale eddies that aggregate prey, and the species with the longest documented routes thus far, the Arctic tern (*Sterna paradisaea*), targets several oceanic high productivity areas during migration (Doyle et al. 2008, Egevang et al. 2010).

We discovered that baleen whales also forage during migration (Chapter 6). Blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), sei whales (*B. borealis*) and humpback whales (*Megaptera novaeangliae*) use the Azorean archipelago in the central North Atlantic Ocean as a foraging area during spring migration to the northerly feeding grounds. Our results identify the Azores as the first documented mid-latitude feeding area for baleen whales in the North Atlantic Ocean, targeted during migration (Chapter 6). Our finding was confirmed by later research, which also showed that satellite tracked blue whales and fin whales suspend their spring migration to forage at the Azores (Silva et al. 2013).

Annual peak abundances of baleen whales at the Azores match the onset of the spring bloom, with a mean time lag of 3 to 4 months (Chapter 2). Several zooplankton species, including favourite prey species like the northern krill (*Meganyctiphanes norvegica*), fine tune egg-development and hatching to the onset of the spring bloom (e.g. Astthorsson 1990, Koeller et al. 2009, Tarling 2010). After about 3 months, the juvenile krill have matured to a size class and density suitable for foraging baleen whales (Labat & Cuzin-Roudy 1996, Tarling & Cuzin-Roudy 2003, Tarling 2010). Thus, the onset of the bloom precedes good feeding conditions for baleen whales with a predictable time lag. What if baleen whales utilise this pattern to track the onset of the spring bloom along their entire trajectory north? This could not only have energetic benefits during migration, but also ensure that the timing of arrival at the feeding grounds matches seasonally enhanced prey abundance in the area. Given the baleen whales' energetic requirement for large quantities of prey (Goldbogen et al. 2011), could the latitudinal advance of the spring bloom possibly be a driver of their migratory cycle? While limited in the number of individuals tagged,

and lacking direct observations of foraging behaviour, the study of Silva et al. (2013) suggests that satellite tracked blue and fin whales do not utilise other feeding areas than the Azores during migration to the high-latitude feeding grounds. However, a sei whale tagged at the Azores did forage at a second, more northerly area of enhanced productivity during its spring migration, the Charlie Gibbs Fracture Zone (Olsen et al. 2009). Hence, further studies are needed to reveal whether migratory baleen whales in the North Atlantic only benefit from foraging at the Azores, or may also utilise other areas for foraging during migration.

Abiotic cues, such as the seasonal increase in light and temperature, trigger long-distance migration in several migratory taxa, including birds and insects (Malcolm 1987, Gwinner 1996). Baleen whales can locate fronts (Croll et al. 2005). Hence, it is possible that they respond to the same abiotic factors to fine-tune the timing of their migration, *e.g.* changes in light availability and temperature stratification, that trigger the onset of the phytoplankton spring bloom (Sverdrup 1953, Huisman et al. 1999, Siegel et al. 2002). Alternatively, baleen whales might not use abiotic cues, but might simply track large-scale gradients in prey abundance resulting from the seasonal advance of the spring bloom.

Irrespective of the mechanism, the observation that baleen whales track the phytoplankton spring bloom to forage on high abundances of krill, suggests possible implications of climate change for migratory baleen whales. Warming of ocean surface waters can result in an enhanced temperature stratification, which suppresses phytoplankton growth by reducing the upward flux of nutrient into the surface layers (Behrenfeld et al. 2006, Huisman et al. 2006). In the case of the Azores, the area could become incorporated in the expanding permanently stratified and extremely oligotrophic North Atlantic Subtropical Gyre (Sarmiento et al. 2004, Polovina et al. 2008). This would suppress the phytoplankton spring bloom at the Azores, potentially resulting in the loss of a foraging area at the early stages of migration, potentially with major implications for the capability of baleen whales to build up energy reserves in spring.

### Future challenges

While we have provided novel insights into the behaviour of deep-diving cetaceans, many open questions remain. Future work on the social foraging strategies of deep-diving cetaceans would greatly benefit from studies in

which the majority of the individuals in the group are tagged. These studies could help to elucidate the coordination between group members at depth by investigation of the extent of their horizontal and vertical dispersal from each other, and how this is related to the production of social and echolocation calls by individuals, and to their soundscape.

Our results point to previously unrecognised interactions between long-finned pilot whale socio-behavioural contexts and their vocalisations, and provide improved understanding of their call types (Chapter 3). It remains challenging, however, to move beyond the generally recognised broad functions of deep-diver social communication. The complexity, fluidity and near-constant 'chatter' of the whales suggests a functionality of the vocal repertoire beyond maintaining contact and cohesion. Moreover, call rates do not simply increase with larger numbers of whales (Chapter 3). Taruski (1979) suggests that call-complexity may serve to communicate the level of arousal, or behavioural state. This is confirmed by the increased complexity of calls during more complex behaviours (Weilgart & Whitehead 1990; Chapter 3). Future studies could build on our methodology, combining vocal, dive and social behaviour data associated with one focal individual, extending the categorisation of the call types. For instance, simple calls could be subdivided into upsweep and downsweep calls, which may have different propagation properties and potentially serve different functions in cetacean repertoires (Weilgart & Whitehead 1990, McCowan & Reiss 2001). It would also be valuable to assign vocalisations to the individual who made the call; in our case, the tagged individual. This is possible based on analysis of the low-frequency content, received level and the angles of arrival of the call on the two hydrophones of the DTAG (*e.g.* Johnson et al. 2009, Jensen et al. 2011). This would greatly aid in our understanding of social calling, as it identifies the relation between the vocal behaviour of individuals and nearby vocalising conspecifics.

Our understanding of cetacean social behaviour and the potential for mitigation against anthropogenic impacts that affect cetacean populations would benefit from a consensus on the sampling protocols and validated and quantitative measurements of functional behaviours (*e.g.* foraging). For example, in the comprehensive study of Weilgart and Whitehead (1990) on the relationship between long-finned pilot whale behaviours and their vocalisations off Newfoundland, foraging appeared to occur at the surface, during highly active, coordinated behaviour. Interestingly, the patterns of vocal behaviour

observed during these probable foraging events matched our results for the Norwegian pilot whales, while the patterns of social and diving behaviour were entirely opposite (Weilgart & Whitehead 1990; Chapter 4). In the study of Weilgart & Whitehead (1990), foraging was characterised by coordinated surface active behaviour. This and similar cases represent open challenges in the study of cetacean behaviour. Here, the use of concurrent observations of surface and underwater behaviour may strongly increase our ability to quantify functional behaviours such as foraging, and will allow comparison of these behaviours between different populations and different contexts.

The potential ocean-wide scale at which baleen whales may benefit from the spring bloom and the implications of this finding for baleen whale energy budgets call for additional studies on baleen whale migration. Based on our results, we suggest that these should focus on the following questions: (i) What are the energetic implications of the loss of a foraging area during early stage of migration for baleen whales? (ii) To what extent can baleen whales adjust the timing and trajectory of their spring migration to avoid a mismatch with the availability of suitable prey (Learmonth et al. 2006)? Future work could combine satellite tagging of individual whales at the Azores, with the use of digital archival tags, capable of recording high-resolution data on prey-capture and energy expenditure of foraging baleen whales.

## References

- Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. *Oikos* 103:247–260.
- Aoki K, Sakai M, Miller, PJO, Visser F & Sato K (2013). Body contact and synchronous diving in long-finned pilot whales. *Behavioural Processes* 99:12-20.
- Astthorsson OS (1990) Ecology of the euphausiids *Thysanoessa raschi*, *T. inermis* and *Meganyctiphanes norvegica* in Ísafjord-deep, northwest-Iceland. *Marine Biology* 107:147-157.
- Baird RW, Borsani JF, Hanson MB, Tyack PL (2002). Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. *Marine Ecology Progress Series* 237:301-305.
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, Feldman GC, Milligan AJ, Falkowski PG, Letelier RM, Boss ES (2006) Climate-driven trends in contemporary ocean productivity. *Nature* 444:752-755.
- 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.
- Benoit-Bird KJ, WWL Au (2009) Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *Journal of the Acoustical Society of America* 125:125-137.
- Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report to the International Whaling Commission Special Issue 12: 383-405.

- Bräger S (1999) Association patterns in three populations of Hector's dolphin, *Cephalorhynchus hectori*. Canadian Journal of Zoology 77:13-18.
- Brenowitz EA (1982) Long-range communication of species identity by song in the red-winged blackbird. Behavioural Ecology and Sociobiology 10:29-38.
- Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among bottlenose dolphins (*Tursiops* spp.). Proceedings of the National Academy of Sciences of the USA 89: 987-990.
- Connor RC, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin, social relationships in a fission-fusion society. In Mann J, Connor RC, Whitehead H, editors. Cetacean societies. Field studies of dolphins and whales. The University of Chicago Press, Chicago and London. pp. 91-126.
- Constantine R, Brunton DH, Todd D (2004) Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation 117:299-307.
- 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.
- 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.
- Doyle TK, Houghton JDR, O'Súilleabháin PF, Hobson VJ, Marnell F, Davenport J, Hays GC (2008) Leatherback turtles satellite-tagged in European waters. Endangered Species Research 4:23-31.
- Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proceedings of the National Academy of Sciences of the USA 107: 2078-2081.
- Engel J, Lamprecht J (1997) Doing what everybody else does? A procedure for investigating behavioural synchronization. Journal of Theoretical Biology 185:255-262.
- Erbe C (2002) Underwater noise of whale watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. Marine Mammal Science 18:394-418.
- Foote AD, Osborne RW, Hoelzel AR (2004) Whale-call response to masking boat noise. Nature 428:910.
- Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.
- 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.
- Gore MA, Rowat D, Hall J, Gell FR, Ormond RF (2008) Transatlantic migration and deep mid-ocean diving by basking shark. Biology Letters 4:395-398.
- 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.
- Gwinner E (1996) Circannual clocks in avian reproduction and migration. IBIS 138:47-63.
- Huisman J, van Oostveen P, Weissing FJ (1999) Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. Limnology and Oceanography 44:1781-1787.
- 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 London B 278:3017-3025.
- 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 M, de Soto NA, Madsen PT (2009) Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. Marine Ecology Progress Series 395:55-73.
- Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S, Richards A, Ouellet P, Orr D, Skúladóttir U, Wieland K, Savard L, Aschan M (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. Science 324:791-793.
- Labat J Ph, Cuzin-Roudy J (1996) Population dynamics of the krill *Meganyctiphanes norvegica* (M. Sars, 1857) (*Crustacea: Euphausiacea*) in the Ligurian Sea (NW Mediterranean Sea): size structure, growth and mortality modelling. Journal of Plankton Research 18:2295-2312.
- Learmonth JA, MacLeod CD, Santos MB, Pierce GJ, Crick HQP, Robinson RA (2006) Potential effects of climate change on marine mammals. Oceanography and Marine Biology 44:429-456.

- Lusseau D (2003) Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology* 17:1785-1793.
- Lusseau D (2004) The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. *Ecology and Society* 9:2.
- Malcolm SB (1987) Monarch Butterfly migration in North America: controversy and conservation. *Trends in Ecology and Evolution* 5:135-138.
- Mann J, Connor RC, Tyack PL, Whitehead H (2000) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago. pp 433.
- McCowan B, Reiss D (2001). The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour* 62:1151-1162.
- Neves S (2013) Acoustic behaviour of Risso's dolphins, *Grampus griseus*, in the Canary Islands, Spain. PhD thesis, University of St Andrews, Scotland. pp 162.
- 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.
- Perrin WF, Würsig B, Thewissen JGM (2009) *Encyclopedia of Marine Mammals*. Academic Press, London. pp 1352.
- Pitman RL, Durban JW (2012) Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science* 28:16-36.
- Polovina JJ, Howell EA, Abecassis M (2008) Ocean's least productive waters are expanding. *Geophysical Research Letters* 35: L03618. doi:10.1029/2007GL031745.
- Ricklefs RE, Konarzewski M, Daan S (1996) The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *American Naturalist* 147:1047-1071.
- Sakai M, Morisaka T, Kogi K, Hishii T, Kohshima S (2009) Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behavioural Processes* 83:48-53.
- Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Soldatov V, Spall SA, Stouffer R (2004) Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* 8:GB3003. doi:10.1029/2003GB002134.
- 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.
- Shane SH (1995) Behavior patterns of pilot whales and Risso's dolphins off Santa Catalina Island, California. *Aquatic Mammals* 21:195-197.
- Siegel DA, Doney SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. *Science* 296:730-733.
- Silva MA, Prieto R, Jonsen I, Baumgartner MF, Santos RS (2013) North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? *PLoS ONE* 8: e76507.
- Soto AN (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. PhD thesis, La Laguna University, Tenerife.
- 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.
- Stensland E, Berggren P (2007) Behavioral changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. *Marine Ecology Progress Series* 332:225-234.
- Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. *ICES Journal of Marine Science* 18: 287-295.
- Tarling GA (2010) Population dynamics of northern krill (*Meganyctiphanes norvegica* Sars). *Advances in Marine Biology* 57:59-90.



- Tarling GA, Cuzin-Roudy J (2003) Synchronization in the molting and spawning activity of northern krill (*Meganyctiphanes norvegica*) and its effect on recruitment. *Limnology and Oceanography* 48:2020-2033.
- 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.
- Weilgart LS, Whitehead H (1990) Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behavioural Ecology and Sociobiology* 26:399-402.
- Whitehead H (1989) Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. *Canadian Journal of Zoology* 67:2131-2139.
- Wiley D, Ware C, Bocconcelli A, Cholewiak D, Friedlaender A, Thompson M, Wienrich M (2011) Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour* 148: 575-602.
- Williams R, Ashe E (2007) Killer whale evasive tactics vary with boat number. *Journal of Zoology* 272:390-397.
- Williams R, Trites AW, Bain DE (2002) Behavioral responses of killer whales (*Orcinus orca*) to whale watching boats: Opportunistic observations and experimental approaches. *Journal of Zoology* 256:255-270.