Universidade dos Açores

Departamento de Oceanografia e Pescas

Behavioural ecology of the sperm whale (*Physeter macrocephalus*) in the North Atlantic Ocean

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Dissertação apresentada à Universidade dos Açores para obtenção do Grau de Doutor no Ramo de Ciências do Mar, Especialidade em Ecologia Marinha

Horta, Junho 2014

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This PhD was supported by:

FCT Fundação para a Ciência e a Tecnologia
MINISTÉRIO DA CIÊNCIA, TECNOLOGIA E ENSINO SUPERIOR

PhD fellowship to Cláudia Oliveira (SFRH/BD/37668/2007)

TRACE

Research project TRACE-PTDC/MAR/74071/2006

MAPCET

Research project MAPCET-M2.1.2/F/012/2011

QUADRO DE REFERÊNCIA ESTRATÉGICO NACIONAL PORTUGAL 2007-2013
COMPETE PROGRAMA OPERACIONAL FACTORES DE COMPETITIVIDADE
Governo dos Açores
PROCONVERGENCIA AÇORES CONSTRUIR O FUTURO
SRCTE SECRETARIA REGIONAL DA CIÊNCIA, TECNOLOGIA E EQUIPAMENTOS
FRC FUNDO REGIONAL PARA A CIÊNCIA

DOP DEPARTAMENTO DE OCEANOGRAFIA E PESCAS UNIVERSIDADE DOS AÇORES
imar Centro do UNIVERSIDADE DOS AÇORES
UNIVERSITY OF SOUTHERN DENMARK

Acknowledgements

My PhD project and path was only possible due to the contribution of innumerous people to whom I would like to express my profound gratitude.

First of all I would like to thank my supervisors Mónica Silva, Magnus Wahlberg and João Gonçalves. They always believed in this project and supported me. Their supervision was of extreme importance and they were very efficient on "putting me back on track".

I would like to acknowledge DOP's directors, Ricardo Serrão Santos and Helder Marques da Silva for hosting me and supporting my PhD.

During the PhD, I was very fortunate on having extra non-official supervisors, Peter Madsen and Rui Prieto that supported me during field work, data analysis and writing the dissertation.

I am very grateful to Lisa Steiner for her help and for kindly providing her photo-id data set.

Also, I am extremely grateful to Mark Johnson who allowed the use of Dtags during this study and was always available to help with the Matlab Dtag tools and providing new ideas.

Field work off Andenes involved many people and I would like to acknowledge: the crew of R/V Narhvalen, S. Spjelkavik, Hisnakul, Whale Safari Andenes, A. Svensson and his crew on Iolaire, and T. Sletten with crew on Reine.

Field work at the Azores occurred due to the contribution of so many people. I would like to thank them all: Mónica Silva, Magnus Wahlberg, Rui Prieto, Peter Madsen, Mark Johnson, Irma Cascão, João Medeiros, Maria João Cruz, Tiago Sá, Yves Cuenot, Paulo Martins, Vítor Rosa, Franz Hutschenreuter, Sérgio Bairos, Bertel Møhl, Asger Hansen, Danuta Wisniewska, Andrea Fais, Rasmus Buchanan, Anders Heerfordt, Anders Lund, Fritz Vollrath, Christian Mølhave, Pedro Amaral, Mafalda Freitas, Jacobo Marrero Pérez, Natacha Aguilar Soto, Michael Hansen, Rikke Buchholz, Nina Iversen, Kim Lundgreen, Sara Green, João Decq Mota, Hélio Bicho, Pedro Alves, Norberto Serpa, Jorge Fontes, Doutor Humberto Lopes, Luís Pires, Fátima Mendes, Nelson Campino, Marco Ávila, Pedro Filipe, Sr. Manuel Fernandes and Michael Leandro.

I also would like to express my gratitude to the local "vigias" (Martins, Sr. Antero, Carlos, Sr. Vargas, Chico) and all the whale watching companies of Faial and Pico Islands that contributed to the success of field work.

While in Denmark, I received the support of the University of Southern Denmark to which I am very grateful. Many friends and colleagues (Magnus, Henriette, Peter, Nina, Danuta, Anne, Meike, Kim, Sara, Jacob, Danish, Ali, Nana, Lucas and Frantz) contributed for such a good time in Denmark. Thank you very much!

During the data analysis and writing up this dissertation, besides the help and ideas of my supervisors Mónica and Magnus, and non-official supervisors Peter and Rui, I had a substantial contribution from Ricardo Antunes, to whom I would like to express my profound gratitude. He was "always there" during data analysis and writing, provided Matlab tools and gave a set of ideas that were extremely helpful.

Along the data analysis and elaboration of the dissertation I received contributes from several people in different ways to which I am very grateful: Danuta Wisniewska, Andrea Fais, Ricardo Medeiros, Filipa Samarra, Christopher Kim Pham, David Janiger, Roberto Silva, Paula Lourinho, Sandra Andrade, Sandra Silva, José António, Joana Maciel, Paulo Castro and Alierta Pereira.

At the Azores, my friends and colleagues were very important during the whole path: Mónica, Rui, Maria João, Ricardo, Hugo, Sofia, Irma, Marta, Pitta, Renata, Sara, Carla, manos bANdARRA, Inês, Patrícia, Ângela, Rogério, Anabela, Daphne, Fred, Joana, Adriana, Xana R., Vanessa, Dário, Vera, Paulo, Roberto, Xana G., Sandra, Paulinha, Ana Marisa and the "Frozen Community" that was so good in keeping up the mood!

I am profoundly grateful to Sr. Fernando, D. Rosa, Paulo, Natália, Pedro, Paula e Ana for all their support.

To my family, especially my parents and my sister, they are my foundation and always will be. For that and all the support they always gave and continue giving, thank you, with all my heart!

And finally, my uppermost acknowledgement goes to Marco and Margarida, who supported me in so many ways and always were my haven. I dedicate this dissertation to them, my own M&M's.

I would like to acknowledge the funding from Fundação para a Ciência e Tecnologia (FCT) through my PhD fellowship SFRH/BD/37668/2007 and the research project TRACE-PTDC/MAR/74071/2006, Fundo Regional da Ciência, Tecnologia (FRCT) for funding the research project MAPCET-M2.1.2/F/012/2011 [FEDER, the Competitiveness Factors Operational (COMPETE), QREN European Social Fund, and Proconvergencia Açores/EU Program], Danish Research Council, the Carlsberg Foundation, and the support from Department of Oceanography and Fisheries (University of the Azores), Centro do IMAR da Universidade dos Açores, University of Southern Denmark, Aarhus University, Woods Hole Oceanographic Institution, and University of La Laguna. I also acknowledge funds provided by FCT to LARSyS Associated Laboratory & IMAR-University of the Azores/the Thematic Area D & E of the Strategic Project PEst-OE/EEI/LA0009/2011-1012 and 2013-2014 (OE & Compete) and by the FRCT – Government of the Azores pluriannual funding.

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Abstract

Sperm whales (*Physeter macrocephalus*) rely on sound for the majority of their activities. They produce different click types for echolocation and communication. Usual clicks and buzzes have been related with foraging contexts. Among social units coda clicks have been associated with communication and group (clan) recognition. Besides being able to communicate by "vocal" emissions, sperm whales frequently exhibit aerial displays that were hypothesized to have several functions, including intraspecific communication. The function of slow clicks is not very well understood, but apparently they are only produced by males either at higher latitudes or while in breeding grounds when in search for a female to mate.

The Azores and the Andøya Canyon (off Andenes, northern Norway) are known habitats for sperm whales. The former is a breeding and foraging ground, characterized by the presence of groups of females, immatures and calves, where mature males occur occasionally. The second location is a high latitude foraging ground where mature males spend the majority of their time feeding.

In the present study we used different types of tags (time-depth recorders and digital acoustic recording tags) to investigate the foraging, resting and social behaviours of sperm whales both at the Azores and off Andenes, with the ultimate goal of providing new insights into the behavioural ecology of the species.

The results demonstrated that, at the Azores, sperm whales foraged and rested in a highly patterned behaviour. However, individual whales differed in the depths where they started searching for food and ended the foraging phase, possibly as a result of a combination of external factors (e.g. prey vertical distribution) and of individual features related with individual auditory and phonating capabilities, diving ability and efficiency at manoeuvring to capture prey. During a dive descent movements were mainly achieved by stroke and glide. Longer gliding periods were more frequent during ascents, mainly at their final stage. After several foraging dives, sperm whales appeared to rest between 9:00 PM and 7:00 AM in vertical (heads up or down) or horizontal positions. We found individual-specific features in the inter-click intervals, inter-pulse intervals, centroid frequency, root-mean-square bandwidth and inter-pulse decay rate of sperm whale codas, which may contribute to individual identification within a social group. Additionally, our study revealed that sperm whales produced different coda types in different phases of their foraging dive cycle. This provides the first indication that coda production may also be influenced by the environmental or behavioural context of the animals. We therefore suggest that codas are used by sperm whales to convey individual information within a social group to a larger extent than has been previously assumed.

Breaching is believed to be an energetically demanding behaviour but previous investigations of this display were based solely on surface observations. This study is the first to describe the underwater movements associated with breaching behaviour of sperm whales. Before breaching, sperm whales perform V-shaped dives to 11-41 m depth, significantly less than previously assumed. During the descent, whales interspersed fluke strokes with periods of gliding. In contrast, whales glided through most of their ascent movement prior to breaching. Their velocity and acceleration during the ascent phase appears to be a product of the velocity and acceleration attained during descent and of their natural buoyancy. We also found that sperm whales rotate during the dives that precede breaches possibly to gain speed to leap out of the water. Mature male sperm whales at the Andøya Canyon produced slow clicks mainly at the surface and while ascending from a foraging dive, contradicting earlier suggestions that these signals could be used during foraging to debilitate prey. Further, some slow clicks were emitted in apparent repetitive temporal patterns. These findings supported the hypothesis that slow clicks' function is long range communication between males at higher latitudes and they may encode information on individual identity or behavioural states.

Within the whole dissertation the results suggested influence of individual specific features on sperm whale acoustic behaviour while foraging, their position while resting, the production of coda clicks and different coda types, some aspects of the dive before breaching, and on the possible temporal patterns of slow clicks. Thus, individual physical features may influence their capacity to move, capture prey, and rest possibly due to differences on their body weight and mass, hearing and acoustic emission capabilities. Moreover, the information encoded in coda and slow clicks may extend the notion of communication within social units and among male sperm whales at higher latitudes.

Resumo

Os cachalotes (*Physeter macrocephalus*) dependem do som na maior parte das suas actividades. Eles produzem diferentes tipos de cliques para eco-localização e comunicação. Os "usual clicks" e os "buzzes" têm sido relacionados com a alimentação. Nas unidades sociais, as "codas" têm sido associadas a comunicação e ao reconhecimento de grupo (clã). Para além de poderem comunicar por emissões "vocais", os cachalotes efectuam exibições aéreas com alguma frequência e este tipo de comportamento tem sido atribuído a diversas funções, nomeadamente a comunicação intra-específica. A função dos "slow clicks" ainda não está totalmente compreendida, mas aparentemente estas "vocalizações" são emitidas somente por machos, tanto em latitudes altas como em zonas de reprodução, quando os machos estão à procura de fêmeas para acasalar.

Os Açores e o Canhão de Andøya (ao largo de Andenes no norte da Noruega) são habitats para os cachalotes. Os Açores são uma zona de reprodução e alimentação que é caracterizada pela presença de cachalotes fêmea, juvenis e crias e, ocasionalmente, machos adultos. O Canhão de Andøya é uma zona de alimentação em latitudes elevadas, onde os machos de grande porte passam a maior parte do seu tempo em alimentação.

Neste estudo utilizaram-se diferentes tipos de marcas (computadores de mergulho, "TDRs"; e marcas digitais acústicas, "Dtags") para estudar o comportamento alimentar, de repouso e social dos cachalotes nos Açores e ao largo de Andenes. Desta forma, pretendeu-se fornecer novos contributos para o conhecimento da ecologia comportamental desta espécie.

Os resultados obtidos demostraram que, nos Açores, os cachalotes alimentaram-se e repousaram de forma padronizada. No entanto, detectaram-se diferenças individuais nas profundidades onde os cachalotes iniciaram a fase de procura e terminaram a fase de alimentação. Isto poderá dever-se à combinação de factores externos (como a distribuição vertical de presas) e de características individuais relacionadas com a sua capacidade auditiva e de emissão de sons, capacidade de mergulho e eficiência na captura de presas. O movimento durante as fases descendentes do mergulho foi essencialmente efectuado pelo tipo "batimento caudal e deslize". Os "deslizes" de duração superior foram mais frequentes nas fases ascendentes e ocorreram essencialmente durante a parte final das subidas. Após vários mergulhos de alimentação os cachalotes aparentaram estar em repouso em posição vertical (cabeças para cima ou para baixo) ou horizontal, entre as 21:00 e 7:00. Foram detectadas características individuais nos intervalos entre cliques, intervalos entre pulsos dos cliques, no centróide de frequências, na raiz quadrada da média da largura de banda e na taxa de decaimento entre os pulsos dos cliques, o que poderá contribuir para o reconhecimento individual dentro de um grupo social. Além disso, os resultados sugerem que os cachalotes produzem

diferentes tipos de “codas” em fases distintas de um ciclo de mergulho de alimentação. Este resultado é uma primeira indicação que a produção de “codas” poderá ser influenciada pelo contexto ambiental ou comportamental dos animais. Assim, sugere-se que as “codas” são usadas pelos cachalotes para transmitir informação individual dentro de um grupo social, o que estende a própria noção de grupo social estabelecida até ao momento. Os saltos fora de água (“breachings”) têm sido classificados como um comportamento energeticamente exigente, mas até agora só foram estudados a partir de observações efectuadas na superfície. Este estudo é o primeiro a descrever os movimentos debaixo de água associados aos “breachings” dos cachalotes. Antes de saltar fora de água os cachalotes efectuaram mergulhos em forma de V até aos 11-41m de profundidade, o que é significativamente inferior ao que se encontrava descrito para estes movimentos. Durante a descida, os cachalotes intercalaram os “batimentos caudais” com períodos de “deslize”. Na subida, os períodos de “deslize” foram mais frequentes. A velocidade e aceleração durante a subida pareceram ser fruto da combinação da velocidade e aceleração obtidas durante a descida, e da flutuabilidade natural dos cachalotes. Adicionalmente, os cachalotes rodam o seu corpo durante os mergulhos, possivelmente para atingir maior velocidade para saltar fora de água. Os machos adultos no Canhão de Andøya produziram “slow clicks” essencialmente na superfície e durante as subidas de mergulhos de alimentação, contrariando o que havia sido sugerido sobre estes sinais acústicos poderem ser usados na debilitação de presas. Além disso, estas “vocalizações” foram emitidas em aparentes padrões repetitivos. Estes resultados corroboram a hipótese que a função dos “slow clicks” é comunicação de longo alcance entre os machos em latitudes elevadas e podem conter informação sobre a identidade e comportamento do indivíduo.

Ao longo desta dissertação, os resultados sugeriram a influência de características individuais no comportamento acústico dos cachalotes durante a alimentação, na posição de repouso, na produção das “codas” e nos seus diferentes tipos, em alguns aspectos dos mergulhos que antecedem os “breachings”, e nos possíveis padrões temporais dos “slow clicks”. Assim, as características físicas de cada indivíduo podem influenciar a sua capacidade de locomoção e captura de presas, e na forma como repousam, possivelmente devido ao seu peso e massa corporal e na capacidade auditiva e de emissão acústica. Além disso, a informação presente nas “codas” e nos “slow clicks” poderá estender a noção de comunicação em unidades sociais e entre machos em latitudes mais elevadas.

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Chapter I

General introduction

Marine mammals and cetaceans

Marine mammals (class Mammalia) are animals that live in the aquatic environment, including species of cetaceans, sirenians, pinnipeds, sea otters and the polar bear (Martin and Reeves 2002). Within the order Cetacea there are two suborders, Odontoceti (toothed whales) and Mysticeti (baleen whales) (Reeves et al. 2003). Eighty-six species of whales, dolphins and porpoises are currently recognized (Beasley et al. 2005; Perrin et al. 2009; Hrbek et al. 2014). Cetaceans spend all their lives in water, where they forage, rest, mate, and bear their young. Their distribution is extremely wide, inhabiting in all the oceans, major seas and many of the main rivers of the world, from cold polar waters to the warm tropical areas (Pompa et al. 2011). They occupy very diverse habitats, from shallow coastal and inshore waters to the deepest oceanic areas (Martin and Reeves 2002).

Behavioural ecology in cetaceans

Behavioural ecology consists of two words, ecology and behaviour. *Ecology* is the study of how organisms live and interact with their environment (Chapman and Reiss 1999), or, with specific reference to cetacean ecology, the study of relationships between the animals and their physical and biological environment (Balance 2009). *Behaviour* consists of a combination of topics, such as animal movement, social interaction, cognition and learning (Breed and Moore 2012). The combination of those two words, *behavioural ecology*, is a fast growing scientific field using notions from evolution, ecology and behaviour (Krebs and Davies 1997). Behavioural ecology may, therefore, be defined as the study of how and why the behaviour of organisms evolve and adapt to changes in their environment.

To perceive and interact with their physical environment, conspecifics, predators and prey of terrestrial species depend mostly on a combination of visual, olfactory, auditory and chemical cues. Although cetaceans also use these senses, most species rely heavily on sound to communicate with conspecifics during socializing and reproductive activities, and, as in the case of odontocetes, to forage and explore their environment.

Foraging is intimately related with environmental features and may occur in shallow depths or in very deep environments depending on the location of their prey (Schreer and Kovacs 1997; Tyack et al. 2006; Aguilar Soto et al. 2008; Arranz et al. 2011). Some species have easily identifiable dive patterns while others have more variable dives, and they can change depending on the tidal state or

the time of the day (Gregory and Rowden 2001; Baird et al. 2002, 2008). Most often, cetaceans forage in areas or at depths where light is scarce. Like bats, toothed whales echolocate to locate and capture prey as well as to navigate (Johnson et al. 2004; Miller et al. 2004a; Aguilar Soto et al. 2008; Au and Hastings 2008). "Echolocation is the process in which an animal obtains an assessment of its environment by emitting sounds and listening to echoes as the sound waves reflect off different objects in the environment" (Au 2009). To echolocate, cetaceans usually produce several types of pulsed sounds (clicks) with distinct strength and inter-click intervals (ICIs), depending on the distance to and the type of target (Benoit-Bird and Au 2001; Jaquet et al. 2001; Madsen et al. 2002a, b; Zimmer et al. 2003; Johnson et al. 2006).

Cetacean communication is mainly associated with social, mating and foraging contexts. Intraspecific acoustic communication in whales may be used while cooperating in foraging events (Pitman et al. 2001; Benoit-Bird and Au 2009) and may convey individual information (Caldwell and Caldwell 1965; Sayigh et al. 1990; Gordon and Tyack, 2001) or group identity (Rendell and Whitehead 2003a), that may be essential to survival and reproduction (Winn and Winn 1978; Darling and Bérubé 2001; Acevedo-Gutiérrez 2009). The ability to communicate with conspecifics is critical to the maintenance of social bonds in group living animals like cetaceans. For most cetacean species, benefits arising from living with conspecifics (e. g. reduction of predation risk, communal care of the young and defense of resources) may translate into increased survival and reproductive success (Acevedo-Gutiérrez 2009).

There are mainly three ways to communicate among cetaceans: visually, acoustically and by tactile sensing (Bradbury and Vehrencamp 1998; Perrin et al. 2009). Whereas tactile and vision only works at very close ranges, whales can communicate over vast distances (tens, or even hundreds of kilometers) using acoustics. All cetaceans studied so far have sensitive hearing (Gordon and Tyack 2001) and a great part of their communication is performed acoustically, by producing different types of sound emissions (e.g. clicks, whistles, moans and songs). Clicks are short, pulsed sounds that are frequently broadband. Whistles are continuous, narrow-band tonal sounds that often have a rich harmonic content. Moans are low frequency pure-tone sounds or more complex tones with a strong harmonic structure and may last up to 30 s. Songs are possibly the most well-known type of vocalization of baleen whales. They are only produced by males and are probably related with attracting mates for reproduction purposes (Dudzinski et al. 2002).

"Non-vocal" sounds may also be important for communication among conspecifics, mainly at or near the surface. These sounds can be produced by flukes, flippers, teeth, jaws, bubbles, respirations and also by striking the body (completely or partially) against the water surface (Herman and Tavolga, 1980; Perrin et al. 2009). Examples where such "non-vocal" communication sounds occur

are the aerial displays of spinner dolphins (*Stenella longirostris*) and the breaching of humpback whales (*Megaptera novaeangliae*).

Tagging tools and deployments for cetacean studies

During the last decades, cetacean studies relied mostly on data collected from surface observations, depth sounders and hydrophone arrays. In order to obtain a better insight into their underwater lives, several new types of tags (e.g. time-depth recorders, bioacoustic probes, A-tags and digital acoustic recording tags) have recently been developed, that collect underwater data on their movement, acoustic emissions and some environmental parameters (Burgess 2000; Akamatsu et al 2005; Johnson and Tyack 2003). These tags brought a new perspective into studies of the diving behaviour of cetaceans.

In the work presented in this thesis, two tags were used to study several aspects of the behavioural ecology of the sperm whale (*Physeter macrocephalus*): time-depth recorders (TDRs, Wildlife Computers, Redmond, WA) and digital acoustic recording tags (Dtags, Johnson and Tyack 2003). TDRs are small size devices that record time, depth, temperature and light levels data and may be incorporated into a custom-built housing. Frequently the housing also has a VHF radio transmitter that allows animal tracking and the device recovery. Often TDRs are attached to the animals either with suction cups or barbs/hooks (Hooker and Baird 2001). TDRs have been successfully used in several studies on the diving behaviour of cetacean species (e.g. Hooker and Baird 1999; Watkins et al. 2002; Amano and Yoshioka 2003; Baird et al. 2008). The Dtag is a small, lightweight, non-invasive tag that records pressure and three-dimensional movement data from the tagged individual, water temperature data, and acoustic data from the tagged animal and its surroundings (either sounds from conspecifics or from other biological or non-biological sources). There are several versions of this device. The versions used here (known as Dtag2 and Dtag3) have four suction cups, and their release from the animal is controlled within a pre-programmed period after which an electric conductor penetrating the suction cup is burnt off and thereby causes the suction cups to be released from the whale after which the tag is ascending to the surface due to positive buoyancy. Dtags have a VHF radio transmitter that allows animal tracking and tag recovery while at the surface. In the last decade, Dtags have been widely used to study different aspects of the diving, foraging, acoustic and three-dimensional behaviour of several cetaceans (e.g. Tyack et al. 2006; Aguilar Soto et al. 2008; Arranz et al. 2011).

Tagging is usually performed with long poles, guns or crossbows, depending on the type of tag and species behaviour at the sea surface (Watkins and Tyack 1991; Madsen et al. 2002b; Amano and Yoshioka 2003). Usually, the target animal is approached from behind or laterally, with the boat speed depending on the behaviour of the target species. When using a pole (hand-pole or cantilevered pole), the attachment is usually made with suction-cups and at short distances from the animals (as for sperm whales; Madsen et al. 2002b; Teloni et al. 2008). Guns (air-guns, launchers or modified spear guns) and crossbows are employed on faster species (Watkins and Tyack 1991; Panigada et al. 2003) and when boats cannot approach the animals at close range.

The sperm whale

Morphology

The sperm whale is the largest of the toothed whales and has the largest brain of any animal. A prominent feature of this species is the squarish nose of the head containing the spermaceti organ (Berzin 1972; Whitehead 2003). This species is the most sexually dimorphic of all cetaceans – maximum length of females and males is about 12 (ca. 15 tons) and 18 m (ca. 45 tons), respectively (Berzin 1972; Best et al. 1984; Gosho et al. 1984).

The sperm whale body is dark brown-grey with a lighter belly. The Y-shaped lower jaw has about 20 teeth and has a white coloration (Berzin 1972; Gosho et al. 1984; Rice 1989). The white colour has been proposed to serve to lure prey while foraging (Fristrup and Harbison 2002).

The head of the sperm whales is about one-quarter to one-third of the body size (Berzin 1972; Gosho et al. 1984). It contains the spermaceti organ which is involved in sound production (Norris and Harvey 1972; Møhl 2001). The blowhole is located at the tip of the head on the left side and when the animals are at the surface they project a blow which is directed forward and to the left side (Berzin 1972). The dorsal fin of sperm whales is thick, rounded and quite low, the flippers are broad and rounded and the fluke is triangular (Rice 1989).

Distribution, movements and life history

Sperm whales have a cosmopolitan distribution that is mainly related to food availability (Gosho et al. 1984; Rice 1989). Even though this species can be found in any deep waters of the world, they

tend to aggregate in some areas (called “grounds” by whalers; Townsend 1935). Adult females, juveniles and calves of both genders live in long-term stable social units in lower latitudes and perform nomadic movements within tropical and temperate waters (Berzin 1972; Whitehead 2003). Between the age of 3 and 15, young males are observed in loose groups of males of the same age (called bachelor groups), and at a higher age they move to colder waters at higher latitudes (Gosho et al. 1984; Whitehead 2003). There, the groups become smaller. As the whales get older, they move to the ice-edges living more solitary lives (Whitehead 2003). Males become migratory when they are in their late twenties, moving between low latitudes used for mating and high latitudes for foraging (Gosho et al. 1984; Whitehead 2003).

Sperm whales may live at least until 50 years of age (Whitehead 2009). Females may conceive at 9 years of age and their gestation period is about 15-16 months (Best et al 1984; Whitehead 2003). The newborns, with a length of around 4 m and a weight of about 1 ton, receive care not only from their mothers but also from other females and/or juveniles of both sexes in the social group. The care from these helpers is called “alloparental care” (Best et al. 1984; Whitehead 2003).

Sound production mechanism and sound types

Many marine mammals, such as seals and probably also baleen whales, produce sounds in the vocal folds of the larynx, whereas odontocetes produce both clicks and whistles in the nasal passages, in a pair of structures called the “monkey lips”. In sperm whales the sound production mechanism is unique and more complex (Cranford et al. 1996; Møhl 2001; Reidenberg and Laitman 2007). The barrel shaped head is composed of several structures, such as two air sacs, the so-called “junk” (which is composed of connective tissue that contains a longitudinal stacked series of lens-shaped bodies of spermaceti), two nasal passages, the “museau de singe” and the spermaceti organ (Cranford 1999; Møhl et al. 2000) (Fig. I.1). In the past, the spermaceti organ was thought of having a hydrostactic or buoyancy regulation function (Clarke 1978a, b). Nowadays, the sound generation function (Norris and Harvey 1972; Cranford 1999; Møhl et al. 2000; Madsen et al. 2002b) has been completely accepted.

The greater part of sound emissions made by the sperm whales are clicks with frequency content between 2 and 25 kHz (Madsen et al. 2002a, b; Whitehead 2009). Clicks are produced by forcing the air from the right naris through the “museau de singe” in the distal part of the head, producing the sound pulse. The majority of the energy of the click is directed backwards along the spermaceti organ. Then it is reflected in the frontal air sac and part of this signal is redirected by the junk into the water. The rest of the signal is reflected back in the distal air sac and again in the frontal air sac,

creating a second pulse that is equally redirected to the water by the junk (Cranford 1999; Madsen et al. 2002b). Successive reflections back and forth explain the multi-pulsed structure of sperm whale clicks, where each inter-pulse interval (IPI) is proportional to the size of the spermaceti organ. Based on this relationship, Gordon (1991a) and Rhinelander and Dawson (2004) developed methods to calculate the body length of sperm whales through the use of the IPI.

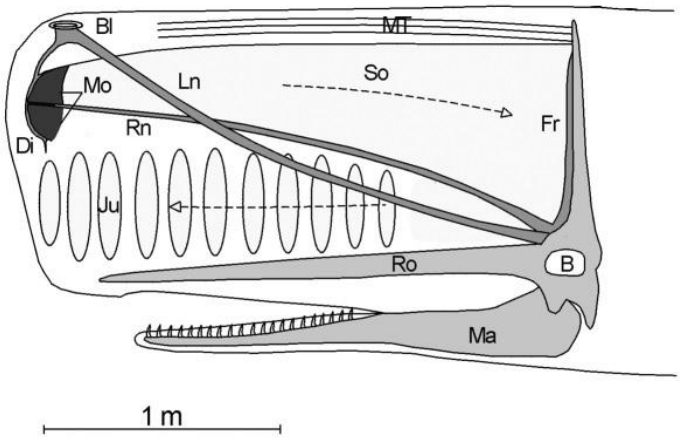

Figure I. 1 – Cross section of the head of a sperm whale, showing anatomical structures relevant for sound production. B, brain; Bl, blow hole; Di, distal air sac; Fr, frontal air sac; Ju, junk; Ln, left naris; Ma, mandible; Mo, monkey lips/museau de singe; MT, muscle/tendon layer; Ro, rostrum; Rn, right naris; So, spermaceti organ (adapted from Madsen et al. 2002b).

Sperm whales produce at least four click types (usual clicks, buzzes, codas, and slow clicks; Fig. I.2) and occasional tonal sounds (e.g. trumpets, squeals, and pips) (Goold 1999; Whitehead 2003; Teloni 2005). Clicks are sharp-onset broadband pulses with their main energy centred between 2 and 25 kHz (Madsen et al. 2002a, b). Usual clicks are highly directional (Møhl et al. 2000), have regularly spaced intervals of 0.5-1.0 s which change with depth (Madsen et al. 2002a; Thode et al. 2002). Buzzes are a rapid series of clicks with short ICIs of 15–100 ms (Whitehead 2003), and occur within a foraging context (Jaquet et al. 2001). Codas are stereotyped patterns of 3 to 20 clicks, having a duration of 0.2–5 s (Watkins and Schevill 1977b) and are mostly produced within social units (Weilgart and Whitehead 1993). Slow clicks have a distinctive metallic sound, longer ICIs (5-8 s) and are apparently only produced by males (Mullins et al. 1988; Weilgart and Whitehead 1988; Jaquet et al. 2001; Madsen et al. 2002a).

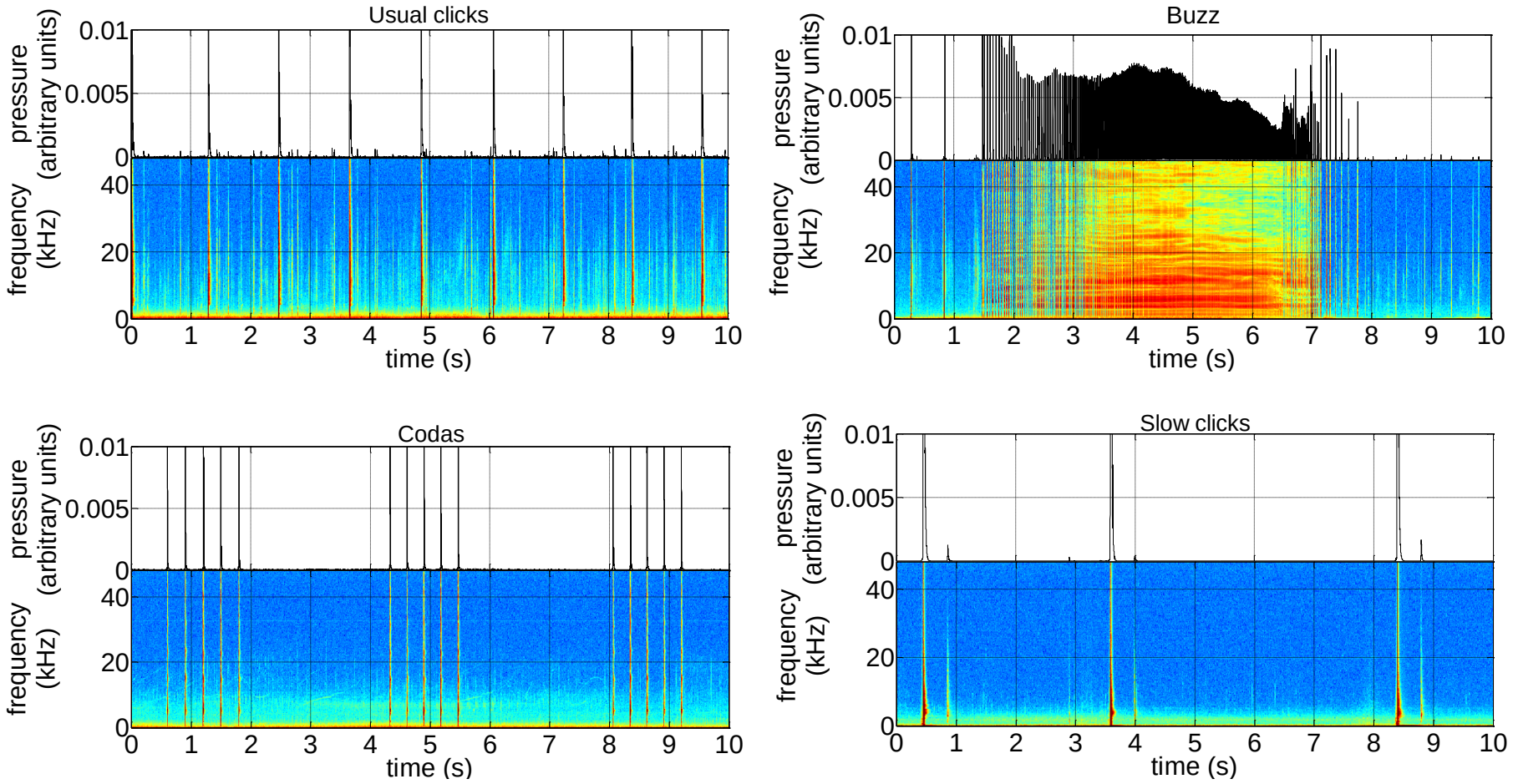

Figure I. 2 – Waveform and spectrogram (512 FFT block size with 10 s segments, 5 Hz sampling rate) of usual clicks, buzz, codas and slow clicks.

Diet, foraging and resting

The diet of sperm whales is mainly comprised of deep water prey items - cephalopods (Gosho et al. 1984) and also fish (teleosts and occasionally elasmobranchs; Berzin 1972). Sometimes other animals are also ingested, such as tunicates, crustaceans, sponges, starfish, sea cucumbers and ascidians (Berzin 1972). The prey items found in sperm whale stomachs during the whaling era were related to the geographical area where the animals were caught. For example, large males in high latitudes seemed to consume much more fish than females in low latitudes, due to the greater abundance of fish at their foraging depths (Whitehead 2003).

In order to search and capture prey items, sperm whales generally perform deep dives and use acoustic emissions (usual clicks and buzzes; Watwood et al. 2006). In lower latitudes, sperm whales usually perform 30-45 min dives to a maximum depth of 1200 m (Amano and Yoshioka 2003; Watwood et al. 2006) but in colder waters males explore a wider range of water depths (100-1900 m depth) (Teloni et al. 2008). For sperm whales who are part of social units (mainly females and juvenile males), usually start emitting usual clicks (meaning they started searching for food) around 100-220 m depth, and the foraging phase (the period between the first and last buzzes within a dive) start at about 500-640 m and last around 29 min (Watwood et al. 2006). Buzzes have been related with prey capture events (Miller et al. 2004a) and the bursts of speed observed in the dive data may indicate the capture of more powerful prey (Amano and Yoshioka 2003; Aoki et al. 2012). Sperm whale usual clicks and buzzes seem therefore related with long- and short-range echolocation, respectively (Jaquet et al. 2001; Madsen et al. 2002a).

Overall, it seems that sperm whales exhibit a highly patterned foraging behaviour (Watwood et al. 2006). However, it remains to be shown if the patterned foraging behaviour may be influenced by other aspects, such as food availability or individual specific features. Additionally, sperm whales do not seem to cooperate while foraging, rather they seem to forage independently (Whitehead 2003) and avoid interfering with each other through the choice of different prey patches. Synchronous dives and surfacings were documented from visual observations at the surface (Whitehead 2003) but the underwater movements of synchronous diving whales remain unknown and could provide a novel perspective of the intraspecific relation while foraging.

Frequently after a foraging period, sperm whale groups are observed socializing or staying quiet at the surface, apparently resting (Whitehead and Weilgart 1991; Watkins et al. 1999). Often their heads or flukes break the surface with the animal in a vertical position (Gordon 1991b; Miller et al. 2008). Large males in higher latitudes seem to rest for longer periods but less often than females and immature at lower latitudes (Whitehead et al. 1992).

Social behaviour and communication

As mentioned above, females, immatures and calves of both sexes live in *social units*. These units have a mean of about 11 individuals that live and travel together for several years (Christal et al. 1998). However, sperm whales also socialize and gather with other conspecifics that do not belong to their social unit. There are several terminologies among scientists studying sperm whale social behaviour. Here we follow the commonly accepted nomenclature of Whitehead (2003). Sperm whales may be observed in: *groups* of about 20-30 animals that move together in a coordinated fashion over periods of at least hours; *aggregations* of several animals within a certain area of a few kilometers at a particular time; *clusters* of various animals separated by a few body lengths that swim side by side in a coordinated manner; and *clans* of animals that use a similar coda repertoire.

Long-term relationships bring advantages to sperm whales - reduction of predation risk, "babysitting" or alloparental care and, perhaps also an increased foraging success (Whitehead 2003). Reduction of predation risk from killer whales benefits adults, immatures and calves. Frequently, sperm whales dispose themselves in a "marguerite formation" to protect against predators: the animals form a circle with or without a protecting target (that may be a young or injured animal) in the middle, and may react with their flukes or jaws against the aggressors (Arnbom et al. 1987; Pitman et al. 2001). The communal care of the young is beneficial to both calf and mother. The first one receives protection and sometimes also milk from other lactating females (allosuckling) and the mother may continue foraging at great depths (Best et al. 1984; Gordon 1987a; Whitehead 1996). Increased foraging success may be accomplished by avoiding interfering with other sperm whales foraging in the area, or by eavesdropping at other conspecifics to find good places for foraging (Whitehead 1989).

Therefore, group recognition and individual recognition may be of extreme importance. For group or individual recognition sperm whales use acoustic communication and their social behaviour is intimately related to the production of coda clicks. Codas have been related with the reinforcement of group cohesion (Weilgart and Whitehead 1993; Whitehead 2003). Distinct groups of sperm whales that share different coda types constitute the "vocal clans" (Weilgart and Whitehead 1997; Rendell and Whitehead 2003a). Additionally, there is a proposed clan signature function that would convey a cultural identity to its members, which may be very important for their reproduction and survival (Rendell and Whitehead 2003a). A recent study performed with hydrophone arrays recognized that there were individual-specific features in 5Reg codas (Antunes et al. 2011). If confirmed, the possibility of individual recognition in coda clicks may be of extreme importance among conspecifics within social units, like mother-calf pairs, and it would bring a new insight into the function of codas.

Male sperm whales that live in higher latitudes have been described to possess a weak social organization (Whitehead et al. 1992; Whitehead 2003) with no preferred companionship (Letteval et al. 2002). However, there is an occasional tendency to form clusters and seek the company of other conspecifics (Letteval et al. 2002). Slow clicks may have a communication purpose among mature males in cold feeding grounds (Madsen et al. 2002a). Yet, the way they communicate within this apparent low interaction rate is still poorly understood.

Sperm whales perform several surface activities – spyhopping, lobtailing, breaching, fluking-up, sidefluking – that have been observed with a lot of enthusiasm by humans. Breaching, i.e. jumping out of the water, has been related with several purposes, but the mostly accepted ones are related to communication, parasite removal, excitement and disturbance (Beale 1839; Whitehead 1985a, 2002, 2003). Apparently, sperm whales have the tendency to breach in sequences and frequently splashing into the water by falling on the same body side (Gordon 1987b; Waters and Whitehead 1990; Whitehead 2003). Mature males have not been observed to breach frequently (Waters and Whitehead 1990), so breaching may have a strong social component within social units. Until now, the breaching behaviour of sperm whales has only been described from surface observations and its function is not yet well understood (Whitehead 1985b, 2002; Waters and Whitehead 1990). Underwater movements before breaching have not been described yet and they may contribute to the determination of the function of this behaviour.

Study area

This work was conducted at two study sites: the Azores archipelago, Portugal, and the Andøya Canyon, off Andenes, northern Norway (Fig. I.3). In the Azores, sperm whale data were collected during July and August, 2010, and at the Norwegian site, data were collected in July, 2005, and May, 2010.

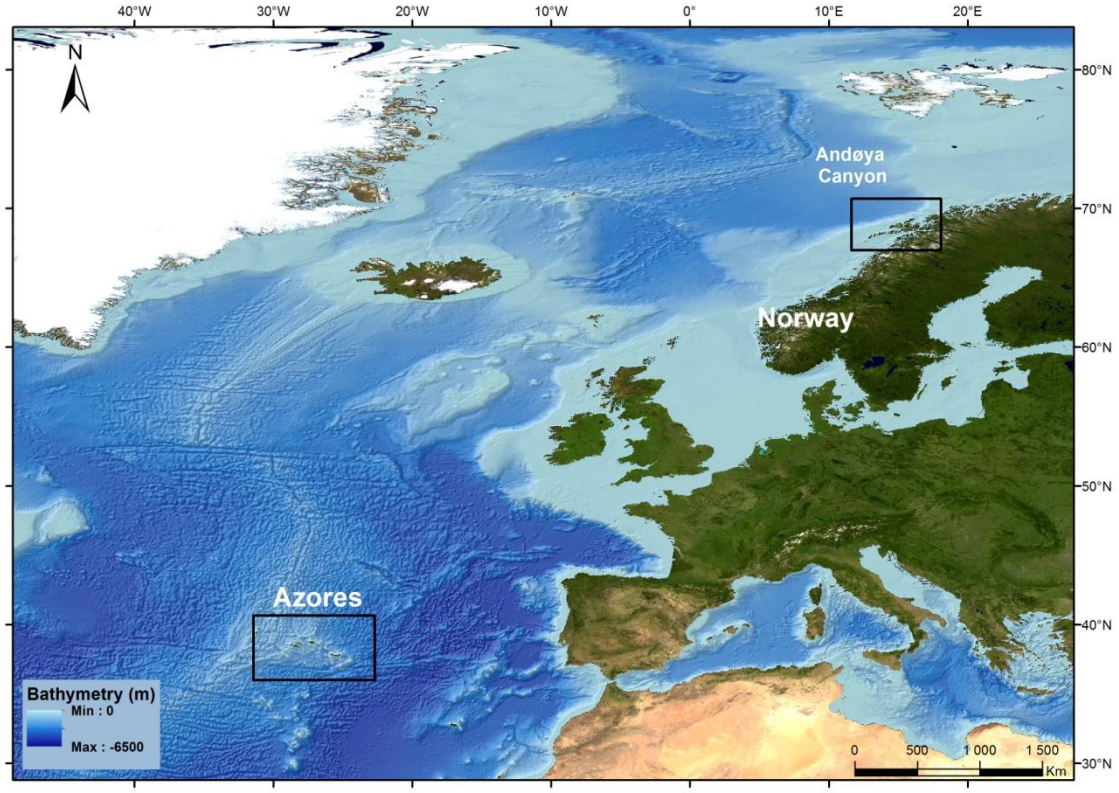

Figure I. 3 – Study sites in the Azores archipelago (Portugal) and in the Andøya Canyon, off Andenes (Norway). R.Medeiros©ImagDOP.

The Azores

The Azores is a volcanic archipelago with nine islands divided into three groups (eastern, central and western groups), that extends for more than 600 km between 37 and 40° N and 25 and 32° W in the Atlantic Ocean (Fig. I.4; Santos et al. 1995). The Azores delimitates the triple junction of three major lithospheric plates in the Mid-Atlantic Ridge: the American Plate, the African Plate and the Eurasian Plate (Morton et al. 1998). The Azorean sea floor is very deep close to the coast which favours the proximity of oceanic species to the islands. The area is indirectly influenced by the Gulf Stream. This stream splits in the North Atlantic Current and the Azores Current both having some influence in the local oceanography (Santos et al. 1995).

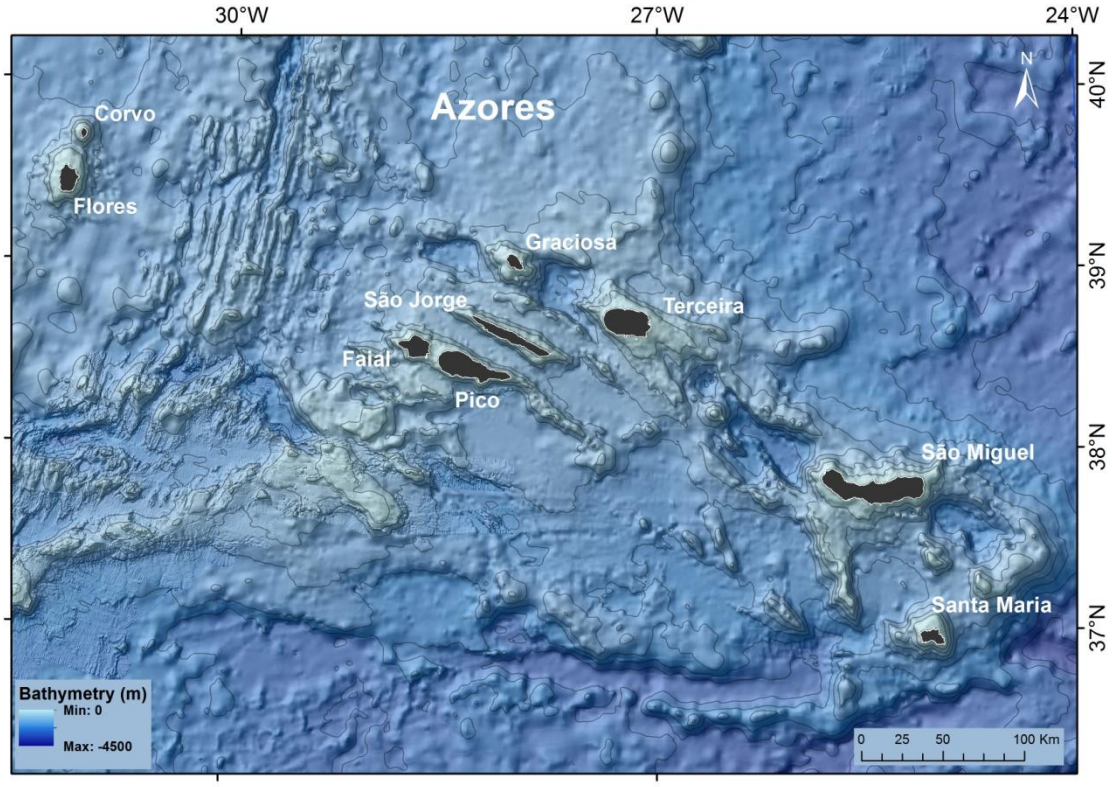

Figure I. 4 – Detail of the Azorean islands in the Mid-Atlantic Ridge. R.Medeiros©ImagDOP.

In the Azores it is possible to find about 27 cetacean species (Silva et al. 2014). Here sperm whales can be found almost daily (weather permitting) year-round (Silva et al. 2014) and relatively near the coast, mainly because of the topography of the Azorean sea floor (Silva et al. 2003). Groups of females, juveniles and calves are commonly observed and mature males are occasionally encountered (Matthews et al. 2001). Sperm whales are one of the main target species of a regional whale watching activity that has been increasing since 1993 (Oliveira et al. 2007).

The Andøya Canyon

The Andøya Canyon is an underwater canyon located in the NE Norwegian-Greenland Sea. It is about 40-50 km long, has a maximum depth of over 2000 m and is located between 69 and 70° N and 15 and 16° E, in the narrowest and steepest part of the northern Norwegian margin (Fig. I.5; Laberg et al. 2000, 2005). There, the Norwegian Current transfers masses of Atlantic water which are the warmest ones in the area (ranging from 2 to 12° C, depending on the season; Kostianoy et al. 2004). In May, the daylight period is about 24h: 22h with the sun visible and about 2h when the sun is not visible, and in July the sun is visible for the entire 24h of the day (http://weatherspark.com).

In the region of the Norwegian Sea that includes the Andøya Canyon it is possible to find several cetacean species and, as in the Azores archipelago, the sperm whale is one of the main target species of the local whale watching operations (Nøttestad and Olsen 2004). Off Andenes, male sperm whales are found in deep waters along the continental slope and they are usually found either foraging or resting, with low interaction rates between conspecifics (Letteval et al. 2002).

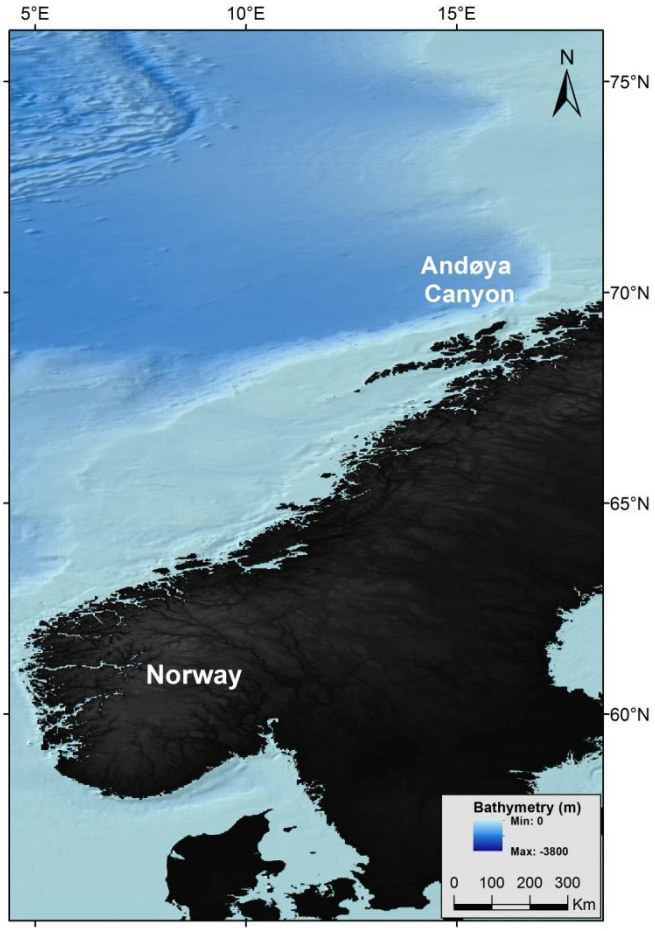

Figure I. 5 – Location of the Andøya Canyon, off Andenes, northern Norway. R.Medeiros©ImagDOP.

Previous research on sperm whales and a link between the study areas

Sperm whales have been studied in the Azores archipelago for some decades. Until 1984 there was a whaling industry in the archipelago and besides the local economical profits it also contributed carcasses to study the diet and some morphological aspects of this species (Clarke 1956; Ávila de Melo 1986; Clarke et al. 1993). Sperm whales studied in the Azores mostly feed on cephalopods, but sometimes they also ingest different species of fish (Clarke 1956).

Using closed capture-recapture models, Matthews et al. (2001) estimated a population of 300-800 female and immature sperm whales between 1987 and 1995 in the central group of islands of the Azores. Open models provided estimates for the same area of 400-700 female and immature whales in 1988-1990 and 1600-2200, in 1991-1994 (Matthews et al. 2001). Silva et al. (2006) reported an annual estimate of about 700 whales using lagged identification rate models. A recent study suggested that a few thousand whales may forage in the Azores every year (Silva et al. 2014). Based on seasonal variations in the observation rates of newborns in the Azores, Silva et al. (2014) estimated a breeding activity between April and June in the area.

The only study on the dive behaviour of sperm whales in the area was based on surface observations and reported that whales take a breath (blow) about every 12 s (females and immature males) and 18 s (large males) and their complete dive cycle lasted on average 52 min (Gordon and Steiner 1992). Sperm whales may be disturbed from whale watching activities in the area, with reports of changes in the swimming speed and increased exhibition of aerial displays (Magalhães et al. 2002).

Male sperm whales have been studied in the Andøya Canyon for several years. Between 1987 and 2000, 365 different animals were photographically identified (Nøttestad and Olsen 2004). As previously referred, several acoustical studies of the sound producing mechanism in sperm whales and their click properties have been conducted in this region (e. g. Møhl et al. 2000; Madsen et al. 2002b). The diving behaviour of male sperm whales was studied with both hydrophone arrays and Dtags, showing that they can forage both at shallow and great depths. In the deeper environments, prey seem to be more densely distributed than in shallower layers (Wahlberg 2002; Teloni et al. 2008).

As previously referred, male sperm whales leave their natal units and migrate to higher latitudes, where they forage and apparently do not interact much with other conspecifics. The link between male sperm whales observed in the Azores and other northern locations has first been made by Martin (1982) that reported a male sperm whale that was captured in Iceland having a harpoon used by an Azorean whaling company from Flores Island. Recently, Steiner et al. (2012) reported three photo-identification matches from sperm whales photographed in 1993, 1999 and 2003 in the Azores and observed in Norway in 2007 and 2008. Thus, even though the Azorean waters and the Andøya Canyon are two very distant and different locations, they are habitat for male sperm whales that use these two sites in distinct seasons and different parts of their life-cycle. Thus, there is a need to better understand and relate the behavioural ecology of the lower latitude social units and the large males in the colder high latitudes.

Motivation of the current study

Cetaceans are presently protected by several legal tools (e.g. the International Whaling Commission, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, EC Habitats Directive). However, noise pollution from various sources (such as whale watching, hydrocarbon and mineral drilling, marine dredging and construction, sonars, explosions and transportation; Richardson et al. 1995) is growing and is believed to be a major threat to several cetaceans. As shown before, sperm whales are highly dependent on sound (to forage, interact with conspecifics and reproduce). Studies on how sperm whales use sound to forage and communicate are of extreme importance to understand the impacts from the increasing noise levels in the ocean and the constant human presence and disturbance of their habitat. Consequently, behavioural ecology studies on sperm whales, both at the individual and population levels, are crucial to contribute to their global conservation and to the reduction of some anthropogenic impacts.

In the current study, acoustic emissions are a major focus, either for foraging or communication purposes, for the sperm whales in the North Atlantic Ocean. Several results obtained in previous studies instigated a set of questions, which I intend to answer in this thesis.

a. The waters of the Azores archipelago are described as oligotrophic, which certainly influences the life of marine predators. However, sperm whales are known to occur on a year-round basis in the region and repeatedly over the years. How do these whales organize their daily activities, namely how do they balance foraging and resting behaviours, to cope with a supposedly lower food supply in the Azores?

b. Codas apparently convey individual information rather than just clan identity (Antunes et al. 2011). Is it possible to find individuality in codas recorded from sperm whales in the Azores archipelago? Which signal features contribute to the individuality of coda clicks?

c. Sperm whale acoustic communication may occur with other “non-vocal” emissions (Perrin et al. 2009). The breaching behaviour is believed to also play a communicative role among cetaceans (Tyack and Miller 2002). Within sperm whale social units, how do they perform the breaching behaviour? Do they need to perform a long dive to be able to jump out of the water?

d. Apparently large males at high latitudes exhibit a low interaction rate (Letteval et al. 2002). Do they lose all their social bonds or do they also interact within a social context? How do they communicate with each other?

Objectives and thesis overview

In the present study, sperm whales were instrumented with TDRs and Dtags to investigate the diving, acoustic and surface behaviour of sperm whales off the Azores archipelago and at the Andøya Canyon, off Andenes.

The current thesis is organized in six chapters: a general introduction reviewing current knowledge on the behavioural ecology of cetaceans and of the sperm whale in particular, identifying several knowledge gaps that are the focus of this work, and describing the study areas; four chapters of research into distinct aspects of the foraging and diving behaviour, and acoustic and non-acoustic communication of the sperm whale; and a general discussion chapter that summarizes the conclusions of each chapter relating them in a broader ecological perspective.

Chapter II centres on the foraging (diving and acoustical) and resting behaviour of the sperm whales tagged with TDRs and Dtags around the Azores archipelago (in preparation for submission).

In Chapter III the individuality of coda clicks is investigated for several different signal parameters using data from tagged sperm whales around the Azores archipelago (in preparation for submission).

Chapter IV explores the underwater movement of the breaching behaviour among sperm whales tagged around the Azores archipelago (in preparation for submission).

Finally, Chapter V focuses on the communication function of slow clicks among males in colder waters (higher latitude habitats) that were tagged in the Andøya Canyon (published in the Journal of the Acoustical Society of America).

Chapter II

Foraging and resting behaviour of the sperm whale in the Azores

The Azores supported a sperm whaling industry for over one century and presently host a growing whale watching industry that mainly targets this species. Despite their low productivity, the waters around the Azores are one of the most important feeding grounds for the species in the North Atlantic. Yet, very little is known about the foraging behaviour of sperm whales in the Azores and about their daily routines in the area. In this study, we deployed 22 tags (11 time depth recorders and 11 digital acoustic recording tags) to sperm whales around the Azores to investigate their foraging, diving and resting behaviours. The mean number of buzzes per dive (14±6), as well as the mean duration of search (34±5 min) and foraging (25±6 min) phases of whales in the Azores were lower than in other world locations. Their estimated foraging efficiency (0.46±0.11) seemed smaller than the one found in other locations, which may be counterbalanced by the type of prey consumed. The foraging behaviour is very likely dependent on prey vertical distribution, which may be related with seafloor depth. Gliding periods were more frequent and of longer duration during ascent than descent phases. The depths at which whales started the search phase and ended the foraging phase varied significantly among individuals, which may be related with specific individual features, such as emission and reception of acoustic signals, efficiency and manoeuvrability to capture prey. The majority of sperm whales at the Azores rested for 11-17% of their tagging time, between 9:00 PM and 7:00 AM. We also found significant differences in resting position among individuals, which may be related with differences in body mass and on buoyancy ability.

In preparation for submission with the following authors:
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Introduction

The sperm whale (*Physeter macrocephalus*), the largest of the toothed whales, performs hour-long dives to depths of more than 500 m in search of deep-sea squid and fish. Despite decades of studies of this species, little is known about many aspects of their foraging behaviour, e.g. how they catch their prey, whether or not they corporate while foraging, and whether there are any different foraging strategies used in different locations.

Studies of foraging and diving behaviour of sperm whales were developed during the past five decades using mainly surface observations, echo depth-sounders and hydrophone arrays (Gaskin 1964; Backus and Schevill 1966; Clarke 1976; Watkins and Schevill 1977a; Mullins et al. 1988; Papastavrou et al. 1989; Whitehead 1989; Lockyer 1997; Wahlberg 2002; Drouot et al. 2004). These studies provided a wealth of information on diving depths and durations, approximate vertical descent rates, depth where sperm whales started producing usual clicks and spatial distribution of the foraging whales. More recently, knowledge of their foraging behaviour has greatly improved with the use of sonar transponders (Watkins et al. 1993), radio and satellite tags (Watkins et al. 2002), time-depth recorders (TDRs; Amano and Yoshioka 2003) and digital acoustic recording tags (Dtags; Johnson and Tyack 2003). TDRs collect depth and temperature data, and increased knowledge of the foraging and diving behaviour of several free ranging cetaceans (Baird 1998; Amano and Yoshioka 2003). Dtags collect acoustic, pressure and orientation data and are more powerful than TDRs to study the behaviour of diving whales (Zimmer et al. 2003; Miller et al. 2004a; Watwood et al. 2006), by combining the information collected from all these sensors.

Sperm whale social units usually forage for about 30-45 min between 400 and 1200 m depth in lower latitudes (Amano and Yoshioka 2003; Watwood et al. 2006). Mature males seem to use distinct food layers at their high-latitude foraging grounds, diving between 100 and 1900 m and for 30-40 min (Teloni et al. 2008). Additionally, buzzes (also called ‘creaks’, consisting of a series of clicks emitted with a high repetition rate) are used for prey capture mostly during the bottom phases of foraging dives (Miller et al. 2004a), where sperm whales swim actively (Miller et al. 2004b). For sperm whales tagged in lower latitudes, the average speed during descent was slower than the average ascent speed, but the ascents had longer periods of gliding (Miller et al. 2004b). Sperm whales also performed bursts of speed that were associated with hunting behaviour (Amano and Yoshioka 2003; Aoki et al. 2012), but not all the buzzes were associated with these bursts of speed, possibly meaning that sperm whales only use them to catch powerful and nutritious prey (Aoki et al. 2012).

The resting behaviour of sperm whales has frequently been associated and interspersed with socializing periods (Whitehead and Weilgart 1991; Watkins et al. 1999). The whales are usually observed quiet at the surface and sometimes take a vertical position while passively drifting (Gordon 1991b; Miller et al. 2008). Such resting events apparently occur mainly between 18:00 and 24:00 (Miller et al. 2008).

The Azores region has been described as an oligotrophic area (Morton et al. 1998). On the other hand, the Azores are known to be a sperm whale breeding and feeding ground where there previously was a large whaling industry dedicated to their capture (Clarke 1954, 1956). Currently, there is a growing whale watching industry that observes sperm whales during the majority of their working season (Oliveira et al. 2007). Research studies in the region have revealed that it is possible to observe sperm whales on a year-round basis (Silva et al. 2014) and several social units are repeatedly seen in the same year and also over the years (Magalhães et al. 2002). These apparently contradicting findings open several questions: why do sperm whales stay in a supposedly oligotrophic area for such a long time and repeatedly over the years? How do they organize their daily routines, and in particularly how do they balance foraging and resting activities, when foraging in areas with distinct food availability? At present, very little is known about the foraging, diving and resting activity of sperm whales in the Azores. Therefore, in order to answer the previous questions, we investigated the underwater foraging and resting behaviour of sperm whales in the Azores, using data collected with TDRs and Dtags.

Methods

Study area

The foraging and resting behaviour of the sperm whales was studied around the central group of islands in the Azores archipelago (38°N, 28°W). Here, females, immatures and calves of both sexes can be found near the coast almost daily, throughout the year (Silva et al. 2014). Mature males are also year-round regular visitors to the area (Silva et al. 2014).

Tagging

Two different tags were used to study the foraging behaviour of the sperm whales: MK9 Time-Depth-Recorders (TDRs, Wildlife Computers, Redmond, WA) and acoustic recording tags (Dtag; Johnson and Tyack 2003).

From 2005 to 2009 we attached 11 TDRs to the sperm whales. In 2005, field work was carried out from an 11 m cabined boat and using an inflatable kayak to approach and tag the whales. The kayak had a crew of two rowers and one tagger. The sperm whales were approached from behind at a low speed and the tag was attached to the animal either with a snorkeling gun adapted to launch it or with a short pole. During 2008 and 2009, tags were deployed from a 2 m height platform mounted on the bow of the cabined boat and using a 7 m telescopic hand-pole. TDRs were placed in the dorsal area between the head and the dorsal fin. Whales were detected visually, frequently with the help of local whale watching lookouts ("vigias").

Depth and temperature sensors on TDRs collected data every 1 s with 12 bit resolution. TDRs were incorporated in syntactic-foam housing and were attached to the back of sperm whales with one suction cup. The tag was linked to the suction cup with two galvanic links that corroded after 2-5 hours when immersed in salt water, thereby releasing the tag. Different release times were chosen depending on the time of day, to ensure the TDRs were released during daylight of the tagging day.

During the summer of 2010 we attached 11 Dtags to the sperm whales. Field work was carried out using two boats: a 6 m long rigid-hulled inflatable boat (RHIB) and a 15 m long sailing boat. The RHIB used visual observations and a directional hydrophone (HTI-96-MIN, High Tech, Inc.'s, with a custom-built baffle to add directionality) to localize animals. Visual observations of whales were also supported by the "vigias". The sailing boat was used to detect sperm whales using a towed array and Rainbow Click software (Gillespie 1997), and also to recover the tags.

Dtags record 2 channels of acoustic data (96 kHz sampling frequency, 16 bit resolution) and sample pressure, temperature, and three axes accelerometers and magnetometers at 50 Hz, 16 bit. The Dtag was attached with 4 suction cups and automatically released from the animal after a programmed maximum period of 24 hours. Whales were tagged by carefully approaching them from behind at a low speed (maximum 4 knots) and the tag deployment was made with an 11 meter cantilevered pole. Dtags were attached between the head and the dorsal fin of the whale.
All tagging efforts (both with TDRs and Dtags) were photographed with a Nikon D90 and a Nikkor AF 70-300 mm lens. Sperm whales responded mildly to the Dtag attachment typically performing a dorsal flex. Sometimes they defecated and dived with or without fluking. Sperm whales showed a

stronger response to the TDR attachments, but tended to resume their pre-tagging behaviour after a few minutes. The tagged animals were tracked using the VHF beacon built-in both tags. The VHF transmissions were detected during the whale's surfacings using a 3-element (for the TDRs) and 4-element (for the Dtags) Yagi antennas, attached to a VHF Advanced Telemetry Systems receiver (for the TDRs) and a VHF receiver R1000 (for the Dtags). The time and position of every surfacing of the tagged whale were recorded when possible. Whenever more than one whale was tagged simultaneously, the surfacing positions were noted down only for the whale closest to the boat, except if the telemetry signal of the second tag was detected and the whale was within an approachable distance. After release, TDRs and Dtags were recovered while floating at the surface by radio tracking.

Tagged whales were classified as females when they were close to small calves and suckling behaviour was observed. The lack of suckling behaviour associated with the tagged individual meant that there was no information about the gender of the animal (so it was classified as "unknown").
Field work was performed under permits no. 7/CN/2005, 76/2007/DRA, 20/2009/DRA (for TDR deployments) and no. 49/2010/DRA (for Dtag deployments) issued by the Regional Directorate for Sea Affairs, Autonomous Region of the Azores.

Data analysis

Tagged sperm whales were coded using the first two letters of the Latin species name, the last numbers of the year, the Julian day and a letter indicating the order of tags deployed that day. For example, pm05_181a indicates a sperm whale (***P****hyseter* ***m****acrocephalus*) tagged in 2005, on the 181st Julian day, and it was the first or only tagged individual during that day.

Sperm whales spend their time either foraging at depth or resting at or near the sea surface (Miller et al. 2008). To analyse the foraging data, dive cycles are commonly divided into different phases: descent, bottom, ascent and surface phases (Miller et al. 2004a; Watwood et al. 2006). Here, we defined the surface phase as the interval between dives in which the whale dove deeper than 20 m. Descent was defined as the period since the whale left the surface until the pitch of the whale exceeded 0 degrees (Miller et al. 2004a). Similarly, ascents started when the pitch was consistently greater than 0 degrees until the whale reached the surface. A few brief episodes (duration up to 27.4 s) of downward pitch angle during one ascent of pm10_230a were ignored and the ascent phase was considered until the animal reached the surface. The period between descent and ascent phases was defined as the bottom phase and the search and foraging phases were defined as the periods

between the first and last produced usual clicks and buzzes, respectively (Watwood et al. 2006). Foraging efficiency was calculated as: foraging phase duration/(dive duration + post-surface duration), following Ydenberg and Clark (1989). Gliding periods were calculated between fluke stroke events (see Johnson and Tyack 2003; Miller et al. 2004b). The period between 07:00 AM and 09:00 PM was considered day time hours.

Both complete and partial dives were included in the analysis. For partial dives, only data from descent or descent+bottom phases were included, when the tag detached from the animal during the bottom or ascent phase, respectively. The first foraging dive after tagging was of similar duration of the subsequent dives for all whales, except for pm09_146a and pm09_268a. Thus, for the majority of tagged whales we did not remove the first dive from the analysis.

TDR data were analysed with the Wildlife Computers Instrument Helper, where it was possible to calculate the dive duration (descent + bottom + ascent durations), duration of the different phases of the dive cycle, maximum depth within a dive and descent and ascent velocities. Acoustic and dive depth data collected with the Dtags were analysed in Matlab 7.0 (Mathworks, Inc.) with a custom spectrogram display function (built by Mark Johnson; 512 FFT block size in 15 s segments with 2 s overlap) to identify different click types (usual clicks, buzzes, codas and slow clicks) and other recorded sound emissions. The orientation of the whale was determined by correcting the accelerometer and magnetometer data from a coordinate system with the tag as a reference ('tag frame') to one with the whale as a reference ('whale frame', by Johnson and Tyack 2003).

The angle-of-arrival on both hydrophones on the tag, the received levels and also the depth of the animal were used to assign each click to the tagged whales or to other untagged whales. The angle-of-arrival was calculated from the time-of-arrival-difference between the tag's two hydrophones (Johnson et al. 2006). The clicks that were not clearly assigned to a tagged or untagged individual were removed from the analysis. The onset of coda clicks, first usual click in a descent, last usual click in an ascent, pauses between usual clicks and buzzes, beginning and end of buzzes were marked to investigate the foraging behaviour of the sperm whales.

The resting behaviour of the sperm whales were studied with the pitch, depth profile and velocity of the animals that exhibited resting periods. Data from pm10_227c were not included in this analysis because this animal was tagged with a different version of the Dtag (Dtag3) that requires analysis tools that were not available during this study.

The ocean bottom depth values were extracted from a bathymetric map generated using data from Smith and Sandwell (1997). All the statistical tests were performed in STATISTICA 6.0.

Results

Eleven sperm whales were successfully tagged with TDRs between 2005 and 2009, and another 11 whales were tagged with Dtags in 2010 (Table II.I). However, only 7 of the sperm whales tagged with Dtags performed foraging dives. Of the remaining whales, one started a foraging dive but the Dtag detached 22 min after deployment and the other three spent most of their time resting at or near the surface.

Table II. I – Date, duration of recorded data, sex (F, female or -, unknown) and observations of the sperm whales tagged around the Azores from 2005 to 2010. For Dtags, the duration of recorded data includes simultaneous audio and sensor recordings.

	Animal	Date	Duration of recorded data (hours:minutes)	Sex	Observations
TDRs	pm05_181a	30 Jun 2005	04:32	-	last dive incomplete (tag off)
	pm05_266a	23 Sep 2005	02:41	F	last dive incomplete (tag off)
	pm05_271a	28 Sep 2005	05:15	F	last dive incomplete (tag off)
	pm08_204a	22 Jul 2008	04:07	-	last dive incomplete (tag off)
	pm08_227a	14 Aug 2008	01:35	-	last dive incomplete (tag off)
	pm09_146a	26 May 2009	02:57	-	
	pm09_174a	23 Jun 2009	04:08	-	
	pm09_175a	24 Jun 2009	04:26	-	
	pm09_175b		04:36	F	
	pm09_198a	17 Jul 2009	04:43	-	
	pm09_268a	25 Sep 2009	04:15	-	
Dtags	pm10_211a	30 Jul 2010	-	-	Dtag lost
	pm10_211b		14:44	-	
	pm10_222a		06:14	F	
	pm10_222b	10 Aug 2010	15:08	-	
	pm10_222c		00:23	-	tag off after 22 minutes
	pm10_226a	14 Aug 2010	17:03	F	
	pm10_227a		02:08	-	always at the surface
	pm10_227b	15 Aug 2010	02:58	-	majority of time at the surface
	pm10_227c		05:58	-	majority of time at the surface
	pm10_228a	16 Aug 2010	19:53	-	
	pm10_228b		14:30	-	
	pm10_230a	18 Aug 2010	13:10	F	

In a total of 141 dives (41 from TDRs and 100 from Dtags) there were 36 complete dives and 5 partial dives from TDRs, and 96 complete dives and 4 partial dives from Dtags. From the 96 complete dives with depth data from Dtags, the two last dives from pm10_228a did not contain any acoustic data. Except for pm05_266a, that only performed “shallow dives” (with maximum depth of 358 m), the mean dive duration (descent + bottom + ascent durations) of all sperm whales tagged with TDRs and Dtags was 42±7 min. The average maximum depth during foraging dives was 924±116 m. Average

duration of descent, bottom, ascent and surface phases (only includes surface phases between foraging dives) was 10±2 min, 24±7 min, 8±2 min and 10±6 min, respectively. Sperm whales descended with a mean vertical velocity of 1.35±0.21 ms^{-1} and ascended with a mean vertical velocity of 1.60±0.19 ms^{-1}, with ascents being significantly faster than descents (paired t_{130}=-10.94, p<0.001) (Table II.II and Fig. II.1).

Sperm whales tagged with Dtags produced 14±6 buzzes per dive. The first usual click during the descent phase was produced at a mean depth of 199±120 m, the last usual click during the ascent phase was produced at a mean depth of 610±138 m and the mean search phase duration was about 34±5 min (81% of dive duration). The foraging phase lasted about 25±6 min (58% of dive duration) and the first and last buzzes occurred at a mean depth of 744±112 m and 727±115 m, respectively (Fig. II.1, Table II.III and Fig. II.2). Buzzes had a mean duration of 7.8±10.2 s and the mean estimated foraging efficiency was about 0.46. Codas were produced by five of the sperm whales between 0 and 650 m depth (Fig. II.1). Pauses usually occurred between periods of usual click production and after or between buzzes. The mean number of pauses within a dive was 31±6 and they lasted 6.7±10.6 s.

ANOVA was used to investigate if the depth where usual clicks and buzzes were first and last produced, was a distinctive feature of individual animals or was influenced by the characteristics of the dive itself. There were significant individual differences in the depth where usual clicks were first ($F_{6,90}$=5.8, p<0.001) and last ($F_{6,90}$=2.8, p<0.05) produced and where buzzes were last produced ($F_{6,86}$=4.9, p<0.001). We performed an ANCOVA to assess if, in addition to an individual effect, there was an effect of maximum dive depth on the depth at which whales produced usual clicks and buzzes. Depth where the first usual clicks were produced was influenced by individual as well as by the maximum depth of the dive (Wald Statistic, W_{indiv}=33, p<0.001 and $W_{maxdepth}$=15, p<0.001), whereas depth where the last usual clicks were produced was only affected by the maximum depth of the dive (W_{indiv}=9, p=0.186 and $W_{maxdepth}$=18, p<0.001). Depth where the first buzzes were produced was influenced by the maximum depth of the dive (W_{indiv}=8, p=0.223 and $W_{maxdepth}$=5, p<0.05), and the depth where the last buzzes were produced was influenced by the producing individual (W_{indiv}=24, p<0.001 and $W_{maxdepth}$=1, p=0.356).

The depth of the seafloor where sperm whales were foraging was always more than 500 m, and the great part (72%) of the tagged sperm whales was feeding close to or at depths beyond 1000 m (Fig. II.3, Table II.II). Except for pm05_181a, pm05_266a and pm05_271a that apparently were foraging away from the seafloor (about 600-850 m distance), maximum diving depths of the remaining whales were within 400 m from the ocean floor (Fig. II.1; Table II.II).

Duration of dives was similar during day and night periods (t_{77}=0.29, p=0.77, n_{day}=47, n_{night}=32).

Table II. II – Summary of dive data for sperm whales tagged with TDRs and Dtags: number of dives; percentage of time spent in foraging behaviour for tagging periods higher than 12 hours (FBehav; only calculated for Dtag data); mean ± 1 standard deviation values for (maximum value): dive duration (FD), maximum depth (MaxD), ocean bottom depths from surfacing positions (OBD), duration of descent phase (DP), duration of bottom phase (BP), duration of ascent phase (AP), duration of surface phase (SP), descent vertical velocity (DVV) and absolute ascent vertical velocity (AVV).

TDRs	**pm05_181a**	**pm05_266a**	**pm05_271a**	**pm08_204a**	**pm08_227a**	**pm09_146a**	**pm09_174a**	**pm09_175a**	**pm09_175b**	**pm09_198a**	**pm09_268a**
No. dives	5[a]	3[a]	5[a]	5[a]	2[a]	2	3	4	3	6	3
FD (min)	49±3	18±1	47±4	39±3	43±0	42±6	34±10	50±3	32±3	33±1	58±3
MaxD (m)	836±50 (879)	322±52 (358)	578±14 (731)	823±6 (827)	941±0 (941)	1149±101 (1220)	914±108 (981)	822±21 (850)	847±4 (852)	729±80 (808)	860±50 (914)
OBD (m)	[1360:1605]	[1209:1261]	[1767:1844]	[663:688]	1227	[1023:1191]	[796:1046]	[669:768]	[696:754]	[669:808]	[778:892]
DP (min)	9±1	3±1	9±2	8±1	9±1	12±1	10±2	8±0.5	9±1	8±1	8±1
BP (min)	31±4	10±0.5	29±4	24±3	26±0	20±6	15±8	34±4	17±3	19±2	43±5
AP (min)	8±2	5±2	8±1	6±0.5	8±0	10±1	9±0.5	7±1	6±1	6±1	8±2
SP (min)	11±1	04±0	10±4	10±2	9±0	9±0	13±3	9±1	8±0	8±1	8±1
DVV (ms^{-1})	1.34±0.11	1.30±0.10	1.25±0.07	1.64±0.11	1.65±0.21	1.40±0.14	1.57±0.38	1.43±0.10	1.30±0.20	1.32±0.08	1.47±0.15
AVV (ms^{-1})	1.50±0.12	1.00±0.42	1.24±0.24	1.90±0.12	1.80±0.00	1.40±0.28	1.67±0.23	1.58±0.15	1.70±0.30]	1.73±0.12	1.63±0.21

Dtags	**pm10_211b**	**pm10_222a**	**pm10_222b**	**pm10_226a**	**pm10_228a**	**pm10_228b**	**pm10_230a**	**Total mean TDRs+Dtags[b]**
No. dives	13	7	9	18[a]	23[a]	14[a]	16[a]	
FBehav	88%	-	69%	94%	87%	84%	100%	87%
FD (min)	50±3	43±4	46±4	40±3	38±4	44±3	42±5	42±7
MaxD (m)	978±84 (1172)	1050±92 (1214)	1053±52 (1141)	894±44 (960)	950±85 (1103)	937±125 (1075)	944±107 (1158)	924±116 (1220)
OBD (m)	[880:981]	[1172:1295]	[1102:1442]	[844:1289]	[1060:1304]	[1060:1111]	768	-
DP (min)	10±2	10±2	11±1	10±3	11±2	10±2	9±2	10±2
BP (min)	31±4	24±4	26±5	22±4	19±5	25±5	24±6	24±7
AP (min)	9±1	10±1	9±2	8±2	8±1	9±2	8±2	8±2
SP (min)	8±1	9±2	12±2	10±1	14±13	10±1	8±1	10±6
DVV (ms^{-1})	1.24±0.13	1.53±0.14	1.34±0.16	1.21±0.22	1.32±0.20	1.34±0.27	1.39±0.14	1.35±0.21
AVV (ms^{-1})	1.53±0.19	1.51±0.09	1.63±0.10	1.58±0.13	1.70±0.18	1.55± 0.20	1.54±0.23	1.60±0.19

[a] missing data due to detachment of the tag during bottom or ascent phases;
[b] total mean values without the values from "shallow dives" from pm05_266a.

Table II. III – Summary of acoustic and foraging data for sperm whales tagged with Dtags: mean ± 1 standard deviation values for (maximum value): number of buzzes, number of pauses, depth of first usual click (DFU), last usual click (DLU), first buzz (DFB), last buzz (DLB), buzz duration (BD), pauses duration (PD), duration of foraging phase (DFo), estimated foraging efficiency (FEff) and number of fluke strokes during descent (Dfluk) and ascent (Afluk) phases.

Dtags	pm10_211b	pm10_222a	pm10_222b	pm10_226a	pm10_228a	pm10_228b	pm10_230a	Total mean values
No. buzzes	16±4	19±4	23±4	9±3	13±4	17±5	10±3	14±6
No. pauses	36±3	37±7	36±5	26±3	28±5	29±4	30±8	31±6
DFU (m)	216±116	336±100	247±114	138±68	152±108	278±109	157±123	199±120
DLU (m)	699±72	724±112	706±49	554±100	566±195	615±99	534±108	610±138
DFB (m)	762±72	866±59	798±91	721±146	743±109	706±100	705±97	744±112
DLB (m)	767±76	809±110	744±61	722±128	734±118	684±125	680±122	727±115
BD (s)	6.9±4.6	8.1±4.5	6.8±4.2	6.6±7.3	8.2±6.2	8.1±5.9	9.8±26.4	7.8±10.2
PD (s)	7.3±10.8	5.6±4.6	6.2±12.7	7.7±10.8	7.4±15.7	6.6±6.3	5.1±3.8	6.7±10.6
DSe (min)	41±3	32±4	36±3	33±3	31±4	35±3	34±6	34±5
(% in a dive)	(81%)	(74%)	(78%)	(83%)	(82%)	(80%)	(82%)	(81%)
DFo (min)	31±4	25±4	28±4	20±6	21±4	28±4	25±6	25±6
(%in a dive)	(62%)	(58%)	(61%)	(51%)	(56%)	(64%)	(60%)	(58%)
FEff	0.53±0.04	0.50±0.07	0.50±0.06	0.39±0.12	0.40±0.10	0.50±0.12	0.50±0.10	0.46±0.11
No. Dfluk	98±14	109±20	110±10	116±23	110±22	98±15	95±17	105±20
No. Afluk	81±13	112±15	87±21	46±17	54±17	46±15	86±22	68±27

On the 30th July 2010, besides pm10_211b we tagged another sperm whale (pm10_211a), but we could not recover the tag. During the period when both pm10_211a and pm10_211b had the tag on, they were seen coming to the surface together and diving synchronously. We detected several coda exchanges (coda type 2+3) in the tag of pm10_211b starting at 240 m depth and ending at the surface. When the timing of acoustic events was crossed with information from visual observations, it became clear that coda exchanges occurred before the two whales were seen surfacing at the same time. After a period of recovery at the surface, they dived synchronously to forage once again. At 100 m depth, they started another period of coda exchanges (coda type 5Reg; Fig II.4a) and 27 s later pm10_211b emitted a few usual clicks. Three minutes later, an untagged whale (very likely pm10_211a) started producing usual clicks and 14 s later pm10_211b continued emitting usual clicks, while descending to a foraging dive (Fig. II.4b). At about 500-550 m depth it is no longer possible to distinguish aurally the usual clicks from pm10_211a. During the foraging phase (>800 m depth) of pm10_211b there are no recorded untagged usual clicks or buzzes as loud as the ones recorded in the beginning of descent. In the remaining foraging dives of pm10_211b, as well as in the foraging dives of other tagged sperm whales, there were no loud recordings of usual clicks or buzzes assigned to untagged whales, that would suggest the animals were foraging at very close range from each other.

The mean number of fluke strokes produced during descents was higher than the number produced during ascents (105±20 vs. 68±27; Table II.III; Figs. II.5 and II.6) and the majority of gliding periods produced during descents was of shorter duration than the ones produced during ascents (mainly during the final part of the ascents; Figs. II.5 and II.6).

Foraging sperm whales spent between 11 and 17% of their tagging time resting. Pm10_222b rested and/or slept for a longer period, 31% of the time the tag was on. The majority of these periods occurred during nighttime (Fig. II.1, Table II.IV) and in a greater part, whales were heads up or horizontally near the surface, except pm10_227a that preferred resting either horizontally or head down (Fig. II.7). However, all whales occasionally changed orientation during resting (Fig. II.7).

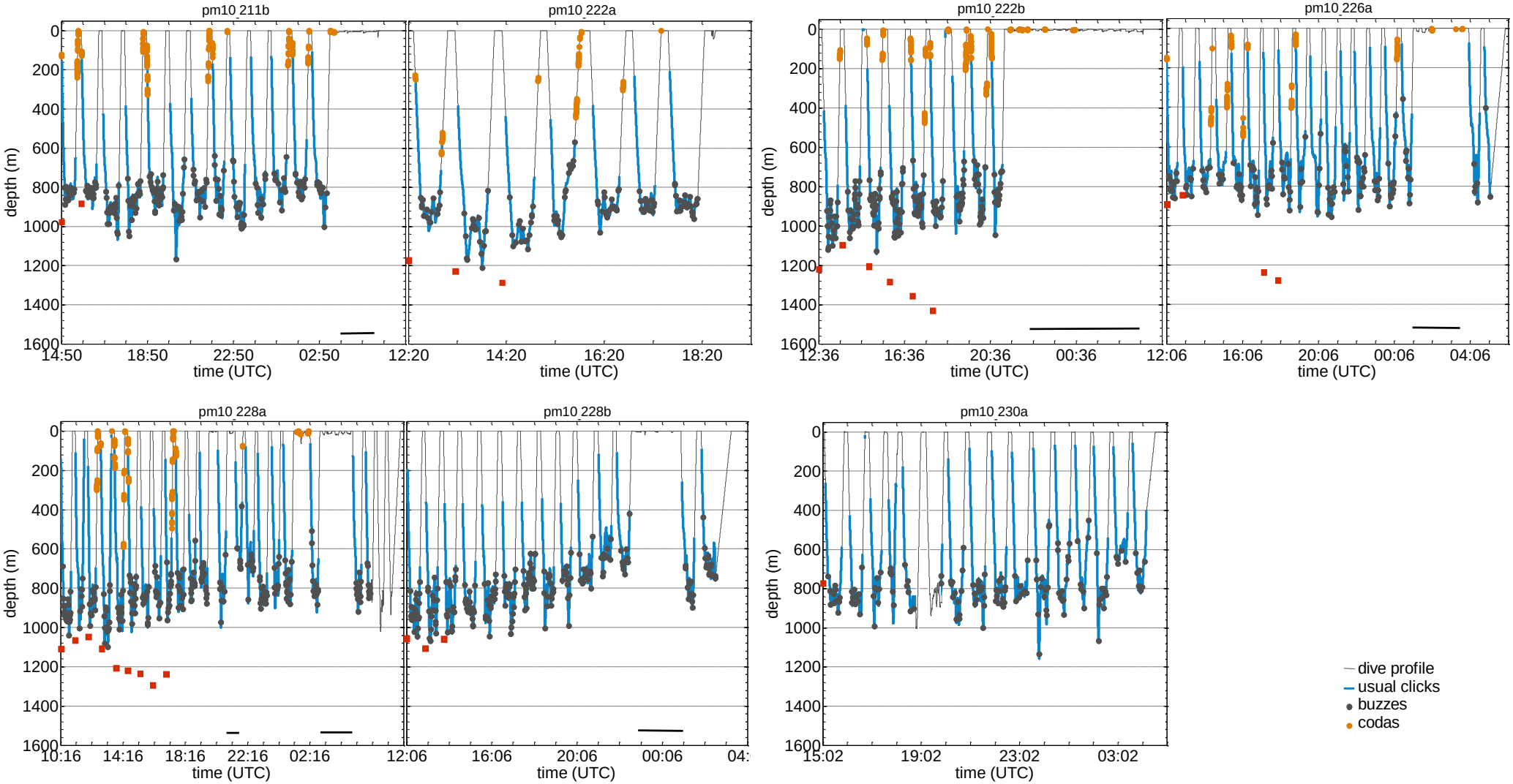

Figure II. 1 – Dive profiles of the sperm whales tagged with Dtags off the Azores showing the depth where usual clicks, buzzes and codas clicks were produced. Periods of resting behaviour are marked with a black line. Red squares indicate approximate seafloor depth from surfacing positions.

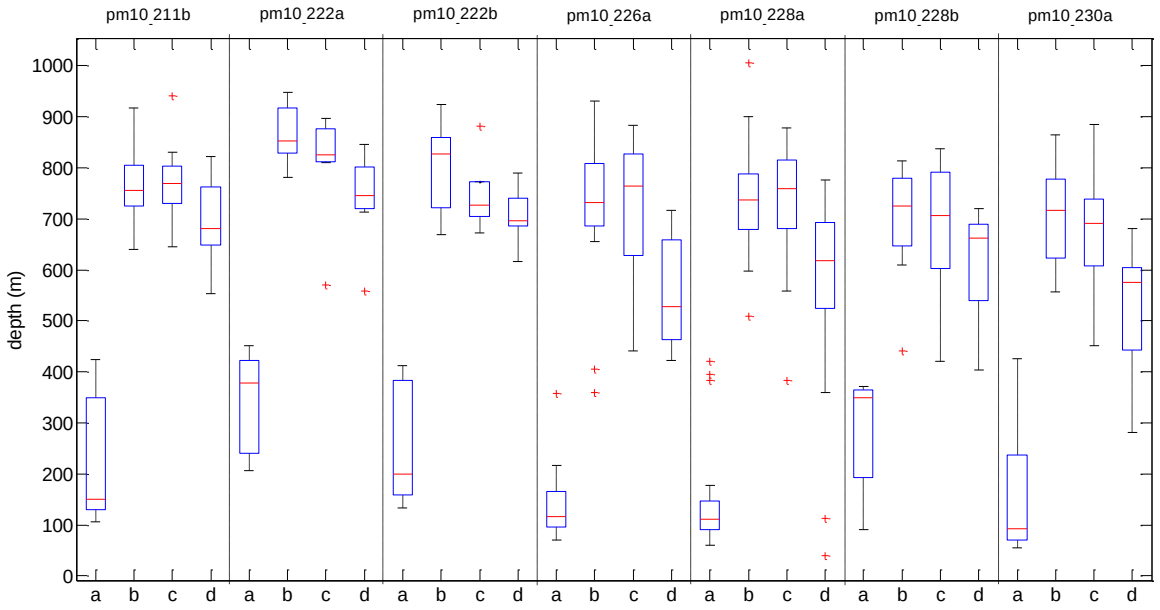

Figure II. 2 – Distribution of 95% of the values (blue box), median (red line), extreme observations (black whiskers) and outliers (red crosses) of the depths where each individual sperm whale produced first usual clicks (a), first buzzes (b), last buzzes (c) and last usual clicks (d) in a foraging dive.

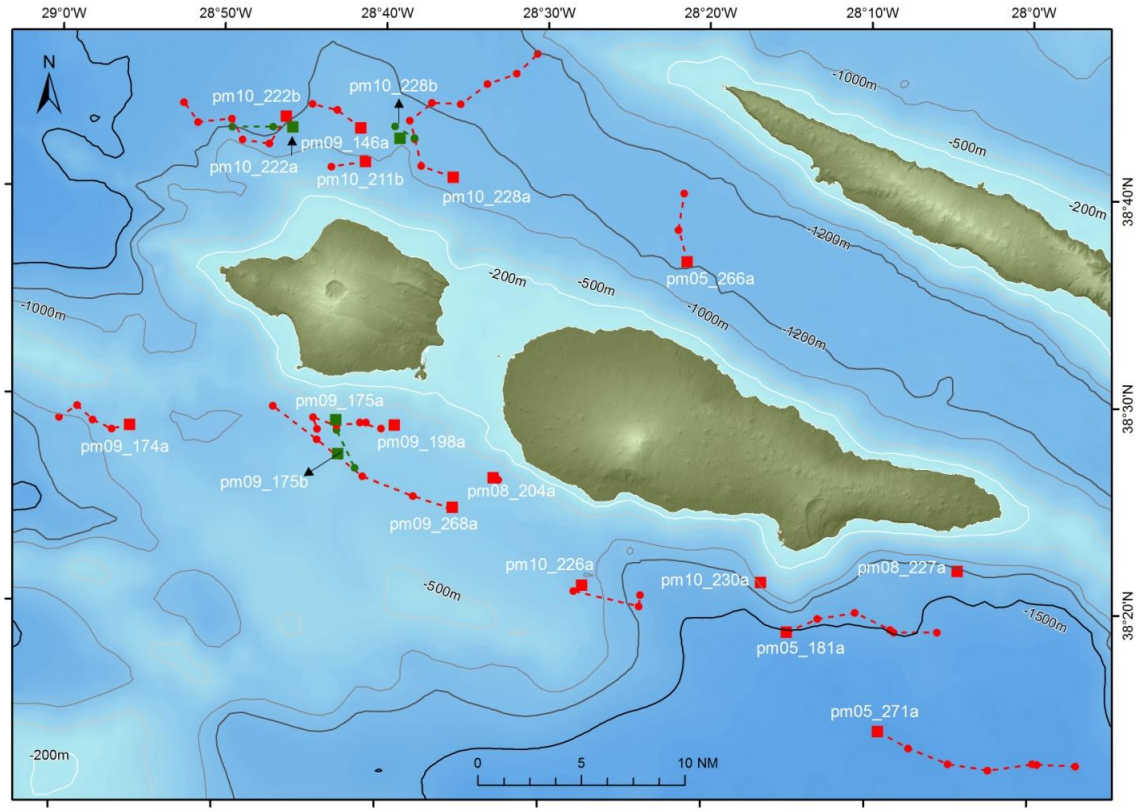

Figure II. 3 – Positions of the tagged sperm whales in 2005, 2008, 2009 and 2010. Squares represent the locations where the animals were tagged and the dashed lines represent the presumed track inferred from subsequent surfacing locations (dots). The different colors of squares, dots and lines were chosen to improve the visualization and distinction of different sperm whales. R.Medeiros©ImagDOP.

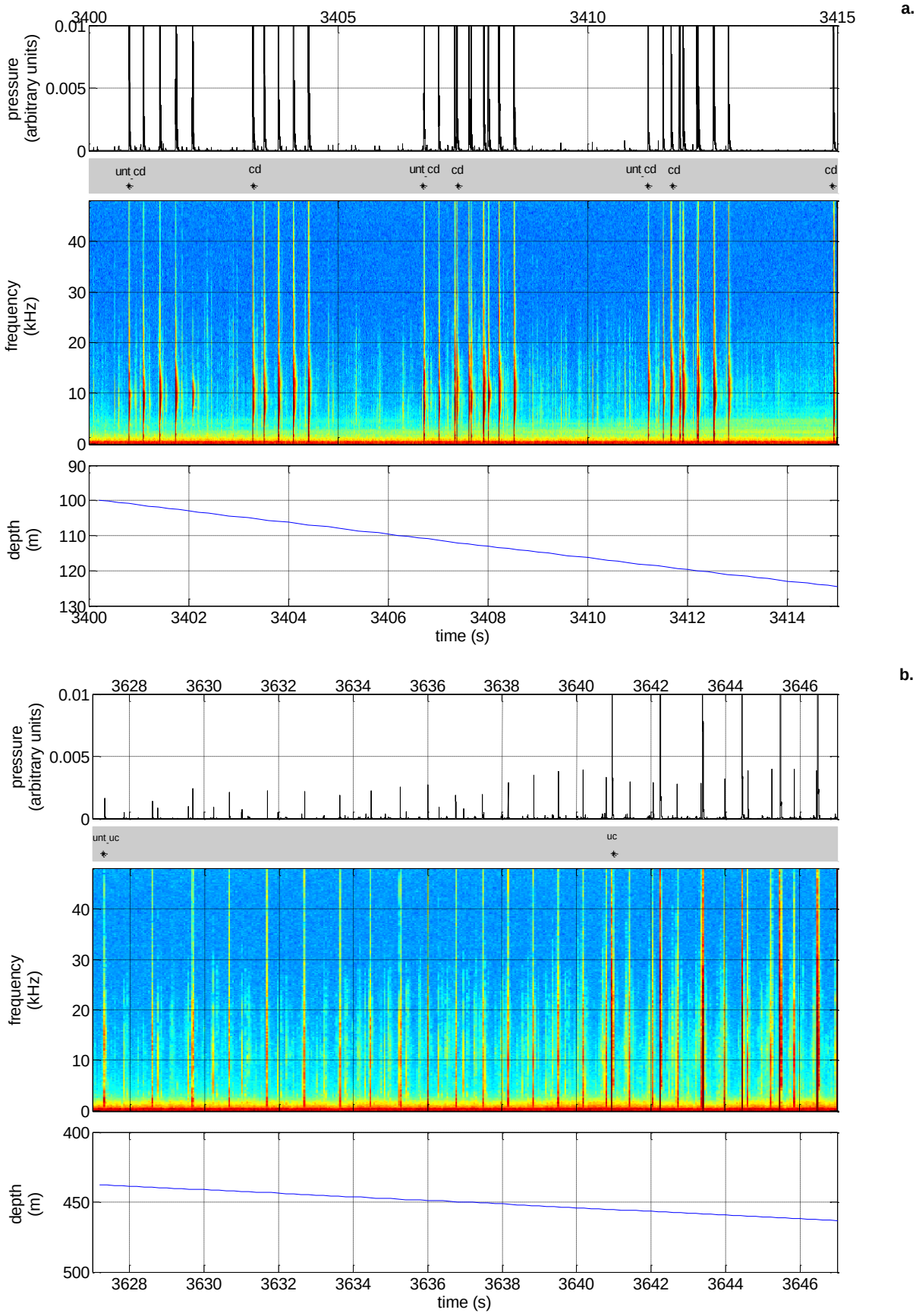

Figure II. 4 – Waveform, spectrogram and dive profile of **a.** coda exchanges of a tagged whale (cd; pm10_211b) and another untagged whale (unt_cd; very likely pm10_211a); and b. usual click production of a tagged whale (uc; pm10_211b) and an untagged whale (unt_uc; very likely pm10_211a).

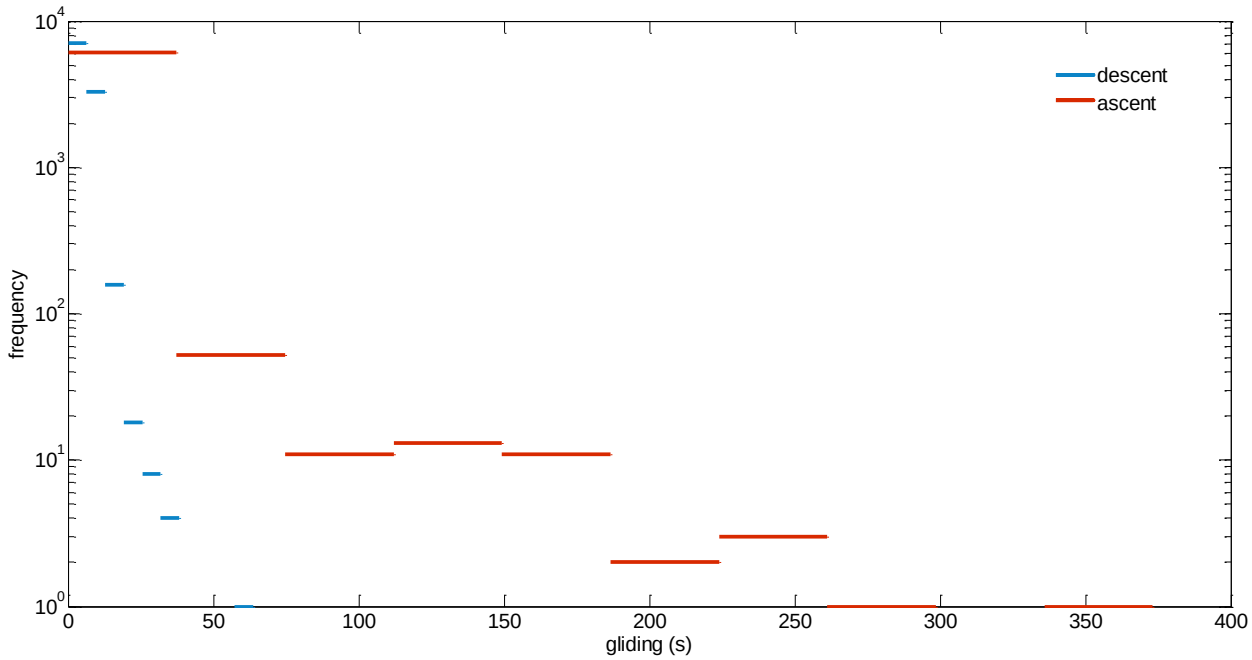

Figure II. 5 – Frequency of gliding periods (between fluke strokes) of sperm whales tagged with Dtags off the Azores.

Table II. IV – Percentage of time spent resting and resting periods of sperm whales tagged with Dtags off the Azores.

	pm10_211b	**pm10_222b**	**pm10_226a**	**pm10_227a**	**pm10_227b**	**pm10_228a**	**pm10_228b**
Resting (%)	12	31	6	90	84	13	16
Resting periods (time UTC)	03:41-05:29	22:24-23:03 23:11-00:20 00:41-03:39	01:06-01:53 03:25-03:40	11:17-13:25	11:26-14:24	20:57-21:27 02:56-04:58	22:40-00:58

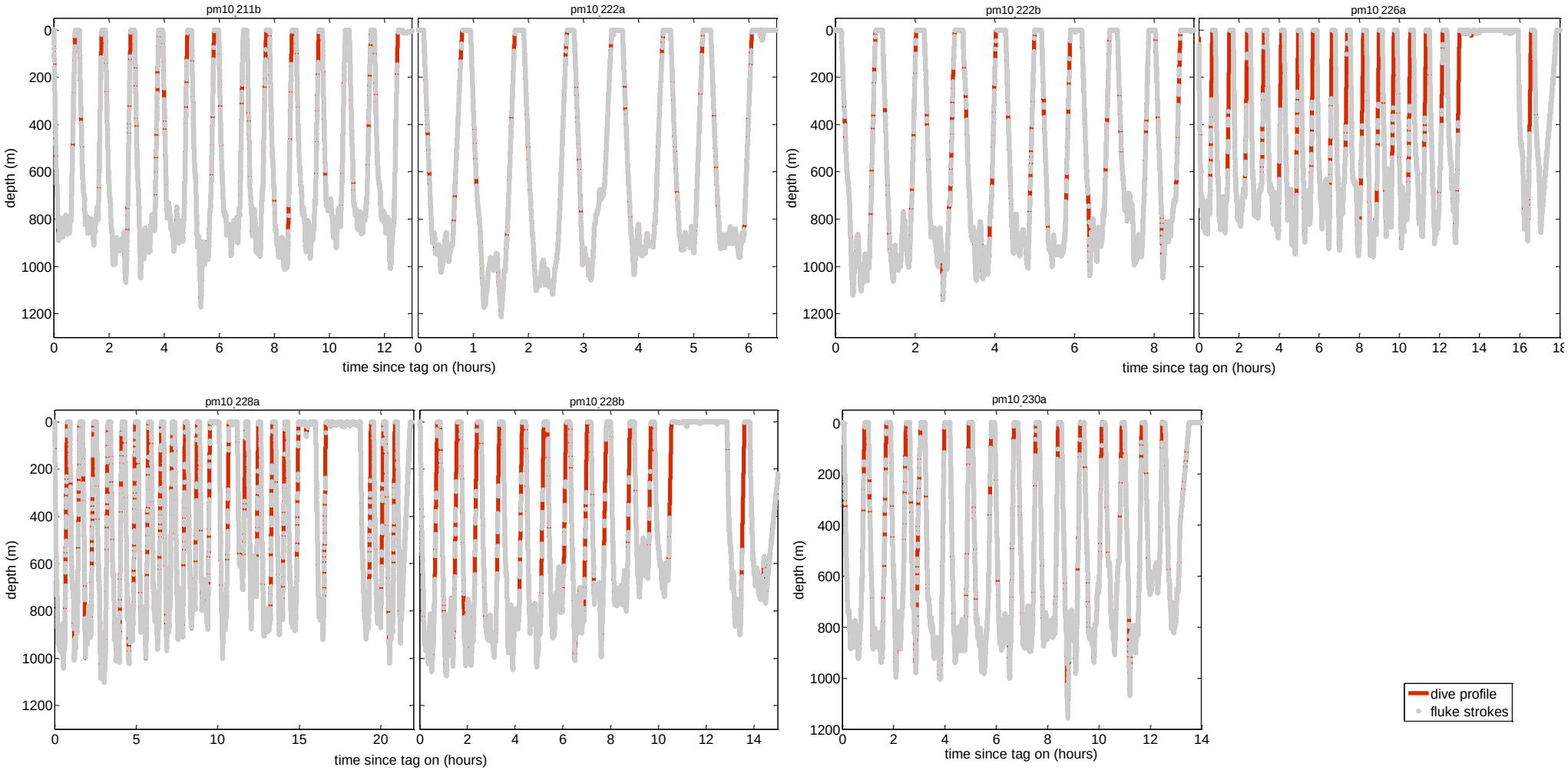

Figure II. 6 – Dive profiles of the sperm whales tagged with Dtags off the Azores, showing the fluke strokes (in grey) and gliding periods between fluke strokes (in red).

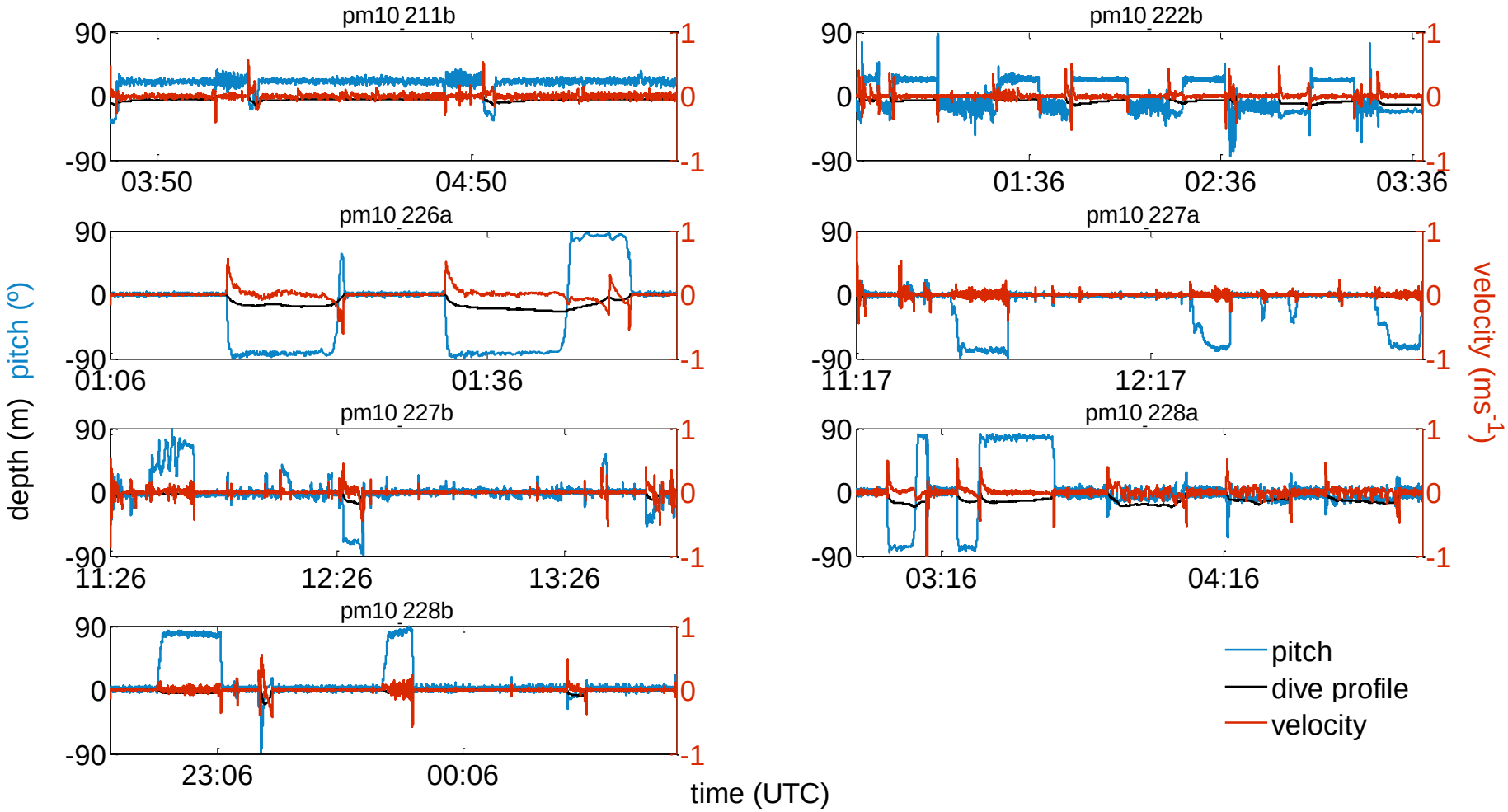

Figure II. 7 – Pitch, dive profile and vertical velocity values for periods of resting behaviour of sperm whales tagged with Dtags off the Azores.

Discussion

Mean dive duration (42±7 min), mean descent, bottom, ascent and surface durations (10±2, 24±7, 8±2 and 10±6 min respectively), and an average maximum depth (909±148 m) of sperm whales studied in the Azores were similar to values reported from other locations, such as in different parts of the Atlantic Ocean (Watwood et al. 2006). Sperm whale diving behaviour was previously studied in the Azores from surface observations (Gordon and Steiner 1992) that suggested that most dives were 40-55 min long and the maximum time spent at the surface for foraging sperm whales (i.e. between foraging dives) was 25%. In our study, a mean of 10±6 min at the surface after a foraging dive of about 42±7 min (representing 24% of surface time between foraging dives) is comparable to the previous research in the area.

Miller et al. (2004b) reported higher mean ascent vertical velocities in relation to mean descent vertical velocities for sperm whales tagged in the Ligurian Sea and the Gulf of Mexico. Velocities of descents and ascents of whales in the Azores showed a similar relation, although we found longer gliding periods during ascents, especially in their final stage (Figs. II.5 and II.6). Further, as also described by Miller et al. (2004b) sperm whales tagged in the Azores seemed to fluke more frequently during descents and the gliding periods were of shorter duration, meaning they perform much more “stroke and glide” behaviour during descent. This type of behaviour may be related with their buoyancy and likely implies a greater energy expenditure when compared with ascents that have much more “gliding” behaviour.

Bottom topography, distribution and abundance of prey, and individual features that determine their foraging efficiency may contribute to the depth at which sperm whales begin and stop producing usual clicks and buzzes. In our study, the depths where sperm whales started and ended the search phase were within the range observed in other locations (Watwood et al. 2006). However, the mean number of buzzes (14±6), the mean search phase (34±5 min) and foraging phase (25±6 min) durations were slightly lower than the values found elsewhere (Watwood et al. 2006). As a consequence, sperm whales feeding in the Azores seem to be less efficient in foraging than in other areas. The locations studied by Watwood et al. (2006) are frequented by sperm whales (Waring et al. 1993; Collum and Fritts 1985; Gordon et al. 2000) possibly due to a combination of factors, such as deep water and high productivity levels (Kenney and Winn 1987; Davis et al. 1998; Barale and Zin 2000).

The lower number of buzzes produced by sperm whales in the Azores may indicate that whales encounter less prey per dive. Combined with a shorter search and foraging phases found for these whales, this finding suggests a lower feeding rate for sperm whales in the Azores, possibly as a result

of lower prey availability in the area. Alternatively, the distinctive acoustic behaviour while foraging of sperm whales in this area may be related with the type of prey (Clarke et al. 1993), which may be of larger size (Clarke 1956). Thus, sperm whales in the Azores may consume fewer but more nutritious prey than in other sites, without the need to prolong their foraging dives.

Pauses between click trains and buzzes have been used as indications of air recycling (Wahlberg 2002). In our study, we detected an average of 31±6 pauses and of 14±6 buzzes per dive. Assuming that after a buzz there is a pause, about half of the pauses were produced after capturing or attempting to capture prey items, and the other half between blocks of usual clicks. The mean duration of pauses was 6.7 ±10.6 s and the mean duration of a foraging dive was 42±7 min. Therefore, air recycling to continue producing clicks represents about 0.3% of the whole foraging dive period, which may be considered a low amount of time for such a deep dive.

Sixty-two hours of time-depth recordings from a sperm whale tagged off the Japan revealed a foraging period of about 80% of the tagging time (Amano and Yoshioka 2003). In the present study sperm whales tagged for more than 12 hours spent 87% of their time foraging which is comparable to the results from the study off Japan. Blainville's beaked whales (*Mesoplodon densirostris*) spent about 4 hours per day hunting for food, meaning that about 50% of their time is dedicated to foraging (Arranz et al. 2011). Compared to these other deep divers, sperm whales seem to spend much more time foraging. This may be related to their increased body size and therefore possibly higher need for food supply. However, Arranz et al. (2011) suggested that Blainville's beaked whales may have a greater foraging efficiency than sperm whales, which could explain the shorter foraging periods and longer ascent periods of the former (Tyack et al. 2006).

In lower latitudes, social units in three different locations (eastern coast of USA, between Georges Bank and Cape Hatteras, called "Atlantic Ocean"; Gulf of Mexico; and Ligurian Sea) occasionally performed foraging dives to the seafloor (Watwood et al. 2006) and male sperm whales off northern Norway also foraged at a mean distance of 146 m from the seafloor (Teloni et al. 2008). Based on maximum depth of tagged whales and on ocean bottom values for each recorded surfacing, the majority of sperm whales tagged off the Azores exhibited a tendency to feed near the ocean floor (within a maximum of 400 m above the seafloor) (Fig. II.1; Table II.II and Fig. II.3). Additionally, the bottom and foraging phases of the majority of tagged sperm whales varied between 700-1200 m depth, meaning that these whales are targeting prey layers at this depth range. Therefore, the depth where these sperm whales were feeding is very likely determined by the vertical distribution of their prey, which may also be influenced by the ocean bottom topography.

The start and ending of the search phase, and the start of the foraging phase were significantly related to the maximum dive depth, which we assume reflects the prey vertical distribution. In a study performed with male sperm whales off northern Norway, the depths of the first and last usual clicks were also correlated with the maximum dive depth (Teloni et al. 2008). However, usual click and buzz production in relation to depth suggest some individual differences in the depths sperm whales started their search phase and ended their foraging phase. These results may be interpreted as a combination of external factors (e.g. prey distribution and possibly related ocean bottom topography) and, also to a unique set of individual features related with individual auditory and phonating capabilities, and possibly foraging efficiency. Further work will be necessary to investigate the influence of each of these factors. In particular, a higher number of whales tagged simultaneously in the same location could be used to distinguish individual-specific effects from environmental determinants of the foraging behaviour of this species.

Watkins and Schevill (1977a) mentioned the underwater dispersion behaviour of sperm whales, with data collected from 4 hydrophone arrays. Our results of the tagged whales on the 30th July 2010 are consistent to Watkins and Schevill (1977a) study and suggest that synchronous diving whales may be close to each other at the surface and at shallow depths, but they start to disperse at higher depths (>550 m) to forage singly. Additionally, there were no loud usual clicks or buzzes recorded on the tags, asides from the ones produced by the tagged individuals, implying that tagged whales were not near conspecifics while foraging at depth. Sperm whales may benefit from clustering and synchronizing dives by reducing the predation risk and maintaining social bonds (Whitehead 2003). Our data reinforce the latter hypothesis and extend the notion of increased foraging success by not interfering with each other while at depth, even when exhibiting synchrony with other individuals close or at the surface and at shallow depths.

There are some cetacean species that adapt their foraging behaviour to circadian rhythms which may be related with the vertical distribution of their prey (e.g. Baird et al. 2008; Aguilar Soto et al. 2008). Whitehead and Weilgart (1991) reported that groups of female sperm whales are more likely to make long foraging dives during the night and morning. On the other hand, Watkins et al (1993) reported shorter daytime average dive times. We found no evidence of diel differences in dive duration, which may be explained by short or no vertical movements of their prey between day and night periods.

Sperm whale units or groups frequently socialize near the surface for several hours, particularly during the afternoon, or remain quiet at the surface apparently resting (Whitehead and Weilgart 1991; Watkins et al. 1999). Sometimes it is possible to observe them in a vertical position with their heads or flukes breaking the surface (Gordon 1991b). Amano and Yoshioka (2003) described dives with little activity that were considered as probable resting dives. We found no deep dives with little activity. The majority of resting lasted 11-17% of the tagging period and occurred during nighttime shallow dives, as reported in Miller et al. 2008. As also described by these authors, sperm whales tagged in the Azores apparently rest in vertical position heads up or down, but also horizontally. The heads down position was associated with greater stability arising from an increased depth while resting (Miller et al. 2008). Positive buoyancy of sperm whales at the surface is very likely related with the way they rest in vertical position. Buoyancy may differ between individual sperm whales (Miller et al. 2004b), the same way body mass of individual fur seals seems to influence buoyancy and the duration of drift dives (Page et al. 2005). Even though our dataset is limited, results show slight differences in the time individual whales rest heads up or down, which may be related to differences in body weight (Fig. II.7).

To summarize, sperm whale diving, foraging and resting behaviour in the Azores seems to be highly patterned, as described in other locations (Watwood et al. 2006; Miller et al. 2008) and foraging seems to be equally dependent on the vertical distribution of their prey. However, the small differences in their foraging behaviour between the Azores and other locations in the world may be related to the type of prey sperm whales are consuming in this area. Analysis of stable isotopes or identification of prey collected in whale's faeces may help elucidating this hypothesis. We also found individual differences in the start of search phase and ending of foraging phase that could be related with their individual characteristics, either associated with the emission, reception and interpretation of acoustic signals, the swimming and manoeuvrability to capture prey, and the physical features of each individual.

Foraging and resting are usually interspersed by periods of socializing (i.e. communicating acoustically or by touch), and as described in the current study, sperm whales often synchronize their dives and remain together at the surface between foraging dives. Individual recognition is of major importance between sperm whale social units or groups in the maintenance of social bonds, either at the surface between foraging dives or in socializing and mating contexts. One may wonder how do they recognize each other to meet at the surface between foraging dives? In Chapter III, individual features in communication coda clicks will be studied in detail. Additionally to coda clicks,

sperm whales may communicate acoustically by performing aerial displays. When and how do sperm whales perform such spectacular events? In the following chapters of this thesis, different aspects of the acoustic and non-acoustic communications of sperm whales are investigated.

Chapter III

Are sperm whale codas only encoding clan identity or also individuality?

Sperm whales (*Physeter macrocephalus*) produce stereotyped click series called codas for communication that can be grouped into different types according to their temporal patterns. These distinctive vocalizations may help them identify groups or social units, but it is presently unclear if they also convey individual identification information suitable for communication within social groups. Individual recognition may be based on different temporal or spectral cues, or a combination of those. Here we report potential individual specific features in sperm whale codas from measurements of the inter-click intervals, inter-pulse intervals, centroid frequency, root-mean-square bandwidth and inter-pulse decay rate within codas. The codas were recorded with acoustic tags (Dtags) attached to the animal, making it possible for the first time to unequivocally identify each coda-producing individual. A total of 802 codas from five sperm whales were separated into different coda types using principle component analysis. A discriminant function analysis was used to distinguish 204 5Reg (meaning 5 regularly spaced clicks) codas from three sperm whales and 107 3Reg codas from two sperm whales. The results indicate that the inter-click intervals, inter-pulse intervals, centroid frequency, root-mean-square bandwidth and inter-pulse decay rate of coda clicks may contribute to individual identification within a social group. Additionally, two whales produced different coda types in different phases of the foraging dive cycle. Codas may therefore be used by sperm whales to convey individual information within a social group to a larger extent than has been previously assumed.

In preparation for submission with the following authors:
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Introduction

Many mammals have individual features in their communication calls which allow them to identify conspecifics. Whistles of dolphins (Caldwell and Caldwell 1965; Sayigh et al. 1990), social signals of bats (Melendez and Feng 2010) and rumbles made by African elephants (*Loxodonta africana*; McComb et al. 2003) have all been shown to hold individually recognizable components. These species belong to different orders of mammals but they rely strongly on acoustic signals for communication, and many of them, such as elephants and some delphinid species, live in long-term and complex social groups where it may be important to be able to discern the individual members (Tibbetts and Dale 2007).

Females, juveniles and calves of sperm whales (*Physeter macrocephalus*), the largest of the toothed whales, also live in stable family units (Weilgart et al. 1996; Gero et al. 2008; Whitehead et al. 2012; Gero et al. 2013). They produce clicks composed of a rapid series of pulses both for echolocation and communication. The pulses within individual clicks decrease in intensity and appear at intervals of 2-7 ms (Norris and Harvey 1972, Gordon 1991a, Møhl et al. 2003). These inter-pulse intervals (IPIs) are related to the length of the spermaceti organ (Møhl 2001) and, therefore, to the body length of the animal (Gordon 1991a). Sperm whale clicks can be grouped into at least four types: usual clicks, buzzes (also called 'creaks'), codas and slow clicks (or clangs; Norris and Harvey 1972; Weilgart and Whitehead 1993; Møhl et al. 2003; Madsen et al. 2003, Zimmer et al. 2005a). Usual clicks and buzzes are used for long- and short-range echolocation, respectively (Jaquet et al. 2001; Madsen et al. 2002a; Møhl et al. 2003; Miller et al. 2004a). Slow clicks are only produced by male sperm whales at low and high latitudes, but they appear to have a communication function in colder foraging areas (Mullins et al. 1988; Weilgart and Whitehead 1988; Madsen et al. 2002a; Oliveira et al. 2013). Codas are stereotyped patterns of 3-40 clicks and are mostly exchanged between individuals within long-term, stable social units (females and their immature offspring) for communication purposes, presumably to maintain social cohesion while the animals are close to the surface (Watkins and Schevill 1977b; Whitehead and Weilgart 1991; Weilgart and Whitehead 1993; Teloni 2005).

Codas were initially thought to be used for individual identification (Watkins and Schevill 1977b), but this was later questioned (Moore et al. 1993; Weilgart and Whitehead 1993). The main function of codas is currently believed to be to reinforce group cohesion via a shared vocal repertoire (Weilgart and Whitehead 1993; Whitehead 2003). Different coda types are geographically discernable (Moore et al. 1993; Weilgart and Whitehead 1997; Rendell and Whitehead 2005; Antunes 2009) and there are prominent unit-specific coda dialects among groups that share different coda types (Weilgart and Whitehead 1997). Large population subsets sharing coda types are called 'vocal clans' and the

clan signatures have been proposed to convey a cultural identity and thereby to be important for survival and reproduction (Rendell and Whitehead 2003a). Besides geographical and unit-specific variations, codas apparently also appear in a patterned order of coda types within a coda sequence (Weilgart and Whitehead 1993) and some coda families (e.g. root, regular and progressive coda groupings) seem to be related to different behavioural contexts such as foraging and socializing (Frantzis and Alexiadou 2008). Codas also seem to contain some individual characteristics in their temporal pattern of clicks (Antunes et al. 2011) and in the coda types between mothers and their calves (Schulz et al. 2011). In these studies the assignment of codas to individuals was made through measurements of IPIs. However, this method cannot be used for groups where several individuals have similar lengths and, thus, similar IPIs leaving open the question of whether codas generally contain consistent individual characteristics.

Here we investigate if codas carry information on individuality using onboard stereo-hydrophone tags (Dtags) attached to sperm whales. This is the first study to unequivocally assign codas to individually distinct animals. We examine several signal parameters to determine whether these can be used to assign coda clicks to individual whales. We then explore whether sperm whales would be able to detect these individual differences. Finally, we investigate the behavioral context in which codas are produced by correlating the occurrence of distinct coda types with the depth and foraging phase of the vocalizing animal. The results suggest that codas serve a greater array of functions within a group or social unit than just confirming unit or clan identity.

Methods

Study area

Sperm whales were studied during the summer of 2010 around the islands of Faial and Pico, in the Azores archipelago (38°N, 28°W), where they can be found almost daily year-round (Silva et al. 2014) and relatively close to the coast (Silva et al. 2003). Groups of females, juveniles and calves are commonly observed in these waters and mature males are occasionally encountered (Matthews et al. 2001; Silva et al. 2014).

Tagging

Field work was carried out using two boats: a 6 m long rigid-hulled inflatable boat (RHIB) and a 15 m long sailing boat. The RHIB located whales by visual observations and using a directional hydrophone (HTI-96-MIN, High Tech, Inc., with a custom-built baffle to add directionality), and served as a tagging platform. The sailing boat was used to detect sperm whales using a towed-hydrophone array and Rainbow Click software (Gillespie 1997), and also to recover the tags. Visual observations of whales were further supported by local whale watching lookouts ("vigias") that monitor some areas around Faial and Pico almost continuously during summer daytime hours.

During the study period sperm whales were tagged with digital acoustic recording tags (Dtag, Johnson and Tyack 2003) that record 2-channel acoustic data (96 kHz sampling frequency, 16 bit resolution) while also sampling pressure, temperature, and 3-D acceleration and magnetic heading with a sampling frequency of 50 Hz (16 bit). Tags were attached with 4 suction cups and automatically released from the animal after a programmed maximum deployment period of 24 hours.

Whales were tagged by carefully approaching them from behind at low speed (maximum 4 knots) and deploying the Dtag with an 11 m cantilevered pole. All Dtags were attached between the head and the dorsal fin, and the Dtag attachment details from the coda producing sperm whales are in Table III.I. Tag deployments were photographed with a Nikon D90 and a Nikkor AF 70-300 mm lens to collect information on the tag placement and photo-id of the tagged individual. Sperm whales responded mildly to the Dtag attachment typically performing a dorsal flex of the body, in some cases followed by defecation and a dive with or without fluking. Tagged animals were tracked using the VHF beacon built-in in the Dtag. The VHF transmissions were detected during the whale's surfacings using a 4-element Yagi antenna, attached to a VHF receiver (Communication Specialists Inc. R1000). The time and position of each surfacing were registered when possible, by moving the boat to the fluke print of the animal. After release, Dtags floating at the surface were recovered by radio tracking.

Sperm whale tagging procedures were approved by the Regional Directorate for Sea Affairs, Autonomous Region of the Azores under research permit number 49/2010/DRA issued to Peter Teglberg Madsen. All procedures in whales followed the guidelines of the American Society of Mammalogists (Gannon and Sikes 2007).

Table III. I – Deployment of Dtags on sperm whales producing codas.

Animal	Date (2010)	Duration (hours:minutes)[1]	Position of the Dtag
pm10_211b	30 Jul	14:44	about 2/3 distance between HT and DF, slightly to the right side
pm10_222a	10 Aug	06:14	about half distance between HD and DF, to the left side
pm10_222b	10 Aug	15:08	about 3/5 distance between HT and DF, to the right side
pm10_226a	14 Aug	17:03	about half distance between HD and DF, to the right side
pm10_228a	16 Aug	19:53	about half distance between HD and DF, to the right side

[1] – Duration of simultaneous recordings of audio and sensor data;
HD – head tip; DF – dorsal fin.

Data analysis

Data from the depth and movement sensors were decimated to a sampling rate of 5 Hz. To determine the orientation of the whale, the accelerometer and magnetometer data were corrected from a coordinate system with the tag as a reference ('tag frame') to one with the whale as a reference ('whale frame', as described by Johnson and Tyack 2003). Acoustic data were analysed using Matlab 7.0 (Mathworks, Inc.) with a custom spectrogram (512 FFT block size with 15 s segments with 2 s overlap) and dive depth display, to identify usual clicks, buzzes, codas, slow clicks and other sound emissions.

Codas were distinguished from other click types, both because of their distinctive temporal patterns and because of the castanet-like sound of individual clicks in codas (see Weilgart and Whitehead 1993). Codas produced by the tagged whales were distinguished from those of nearby whales by comparing the arrival angle of clicks at the tag, calculated from the time-of-arrival-difference between the two hydrophones of the tag (Johnson et al. 2006). If the angle-of-arrival of a coda was consistent with the angles-of-arrival from usual clicks emitted right before and after the coda by the tagged whale, the coda was assigned to the tagged whale (Fig. III.1). Usual clicks were associated with the tagged whale mainly based on their louder received level, their consecutive concordant angle-of-arrival and the depth where they were first and last produced in a foraging dive. On this basis, coda clicks were ascribed either to the tagged whale, to another whale, or were flagged as being of uncertain origin. Only the signals that were unequivocally attributed to the tagged whale were used in the analyses presented here.

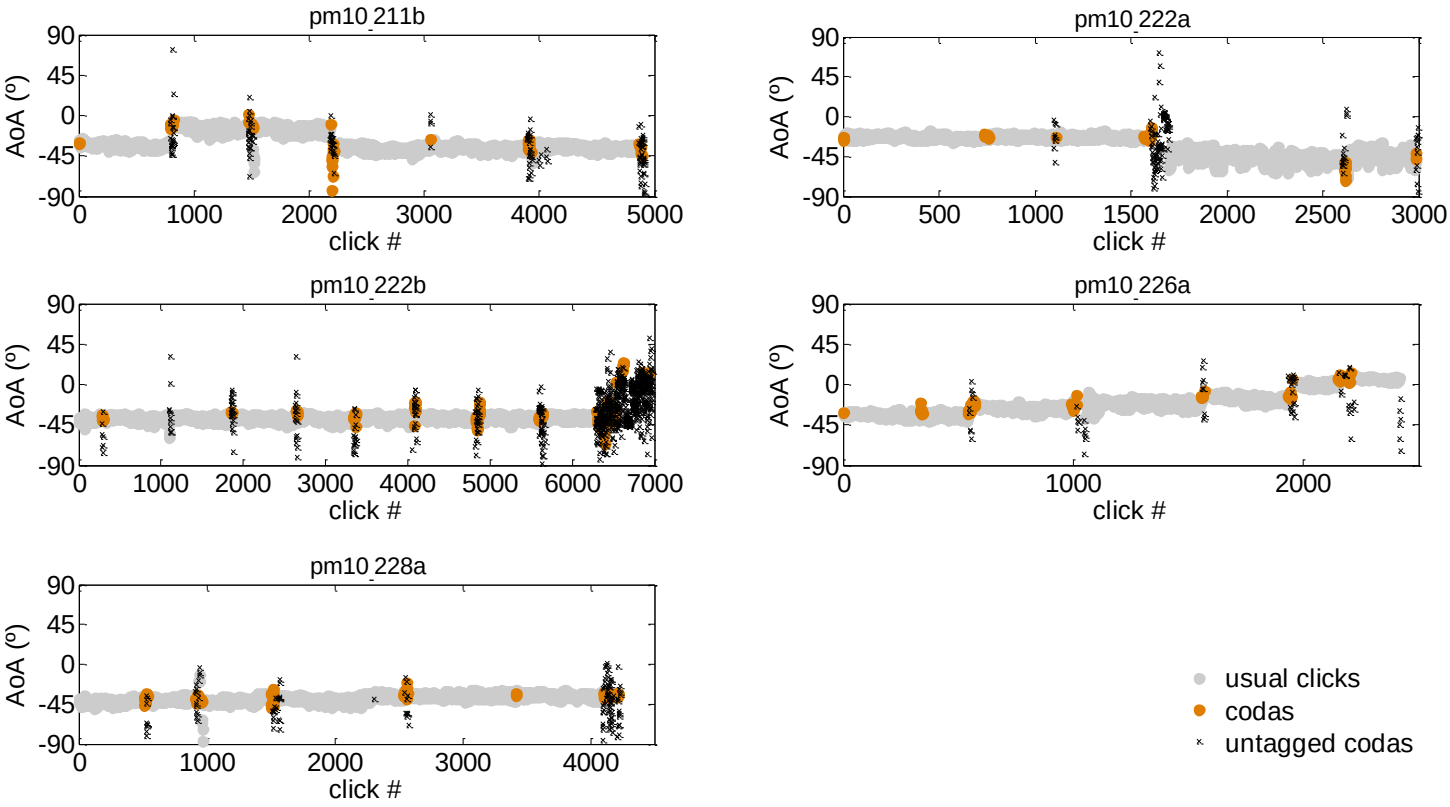


Figure III. 1 – Angle-of-arrival (AoA) of usual clicks and codas (tagged and untagged) recorded on the two hydrophones of the Dtag. 'Usual clicks' and 'codas' are recorded from the tagged whale while 'untagged codas' are assumed to come from neighboring whales. Note the step changes in the tag orientation in pm10_211b and pm10_222a due to movement of the tag on the whale.

The peak of each click in each coda was measured from waveforms to determine the start time and inter-click-intervals (ICIs) of the coda. Several parameters were also measured: decay rate between the first and second pulses of the first click (decay in dB), centroid frequency of the primary pulse of the first click (fc), centralized root-mean square bandwidth of the first click (rms_{bw}), ICIs (where ICI1 is the time interval between the first and the second click, ICI2 is the time interval between the second and third click, and so on) and IPIs for the first click. The measurement accuracy of these parameters depends on the signal-to-noise ratio (SNR) of the recorded clicks which is high given the short distance between the sound source and the tag. The IPI was calculated from the time difference between the peaks of the two first pulses as these have the highest SNR and as the IPIs of the remaining pulses are known to be identical to the first one (Madsen et al. 2002b). Thirty-eight percent of all selected clicks were clipped (i.e., transiently exceeded the maximum pressure level of the tag sound sensor), hence for the subsequent individual discrimination analysis we only used non-clipped clicks. Body lengths were calculated from IPIs (Gordon 1991a).

Codas containing the same number of clicks were compared using principal component analysis (PCA) of ICIs and were then classified into different coda types using a combination of observer classification and the PCA scores. Except for rare codas, the PCA classification was identical to the observer classification. Therefore, the combination of both methods seemed more robust for classifying the more frequent codas. Coda types were named according to Weilgart and Whitehead (1997) based on their timing patterns and click number. For example, the 5Reg and 4+1 codas both have five clicks but while the first one has regularly spaced clicks, the second one has a longer gap between the last two clicks.

Individual specific coda differences were investigated in non-clipped 3Reg and 5Reg codas (the most shared coda types among tagged individuals) using discriminant function analysis (DFA) with all the measured parameters. Three scenarios involving different subsets of the parameters were investigated with DFA: 1. all parameters; 2. all parameters except the ICIs; and 3. only the ICIs. The three scenarios were investigated to determine how ICIs contribute to discriminate codas produced by different individuals, as ICIs have previously been identified as being individually distinct in Antunes et al. (2011). Classification error rates were calculated using a jackknife procedure: each coda at a time was removed from the dataset and the remaining codas were used to calculate linear discriminant functions that then were used to classify the removed coda. The individual discrimination error rate is the proportion of the removed codas that were wrongly classified (Antunes et al. 2011). The DFA and classification error rates were performed using custom-written Matlab code, using a Discriminant Analysis Toolbox (Kiefte 1999) and STATISTICA software. Mahalanobis distances and posterior probabilities were calculated to obtain the confidence level at which the discriminated codas belonged to the coda-producing sperm whale. Statistical tests were performed in STATISTICA.

Differences in IPIs between different codas have previously been used to assign the codas to different individuals (Antunes et al. 2011; Schulz et al. 2011). Even though IPI is closely-related to the size of the spermaceti organ (Gordon 1991a), there can be a large spread in IPI measurements from the same individual when recorded with a hydrophone in the water (Teloni et al. 2007), and several individuals in the same group may be of similar size leading to ambiguity in this parameter. Body length estimates derived from the IPI were compared to investigate if IPIs alone are sufficient to correctly assign the recorded signals to individuals.

Results

Eleven sperm whales were tagged from 30th July to 18th August, 2010. Sequences of foraging dives were performed by 7 of the tagged sperm whales, and 5 of these produced codas. Of the remaining whales, three spent most of the time resting at or near the surface and did not produce codas while for one animal the tag detached 22 min after deployment.

A total of 802 codas were assigned to the five tagged whales. Codas were produced at depths from 0 to 650 m (Fig. III.2), most of them containing 5 (47%) or 3 clicks (23%). The complete coda repertoire (found with PCA and observer classification) comprised 21 types of codas (Table III.II). Of the 377 codas with 5 clicks, the large majority was ascribed to two coda types: 5Reg (n=290) and 2+3 (n=83). The first two PCA components explained around 91% of the variance in the 5-click codas, mainly separating these two major types (Fig. III.3). Codas of type 5Reg were produced by all five sperm whales, although one whale (pm10_226a) only produced this type twice. Type 3Reg was also produced by all five whales, but three whales only produced this coda once (Table III.II). Examination of the PCA results by individual (Fig. III.3) suggests that there are some differences in 5Reg coda type production between the whales.

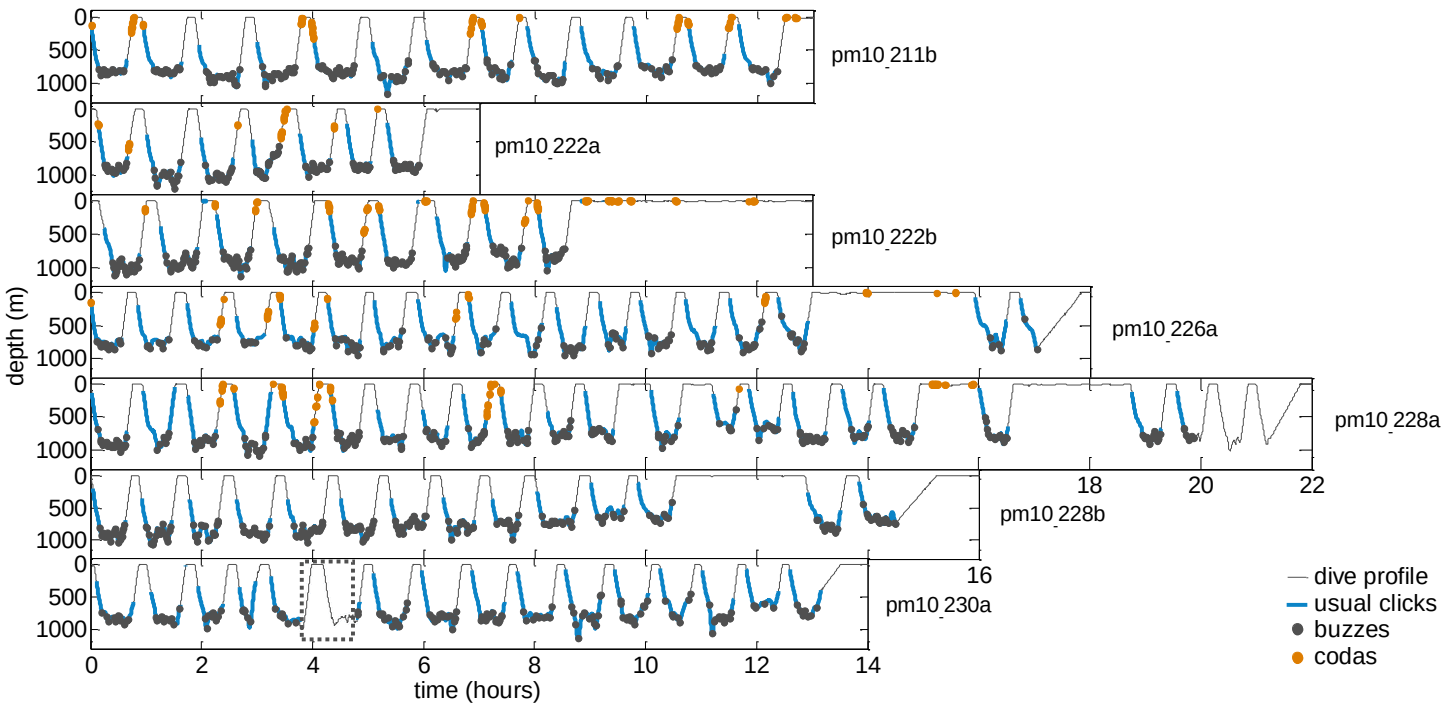


Figure III. 2 – Depth profiles and acoustic signals (usual clicks, buzzes and codas) produced by tagged sperm whales. Usual click blue lines represent the interval between the first and last produced usual clicks within a foraging dive. Note: pm10_228a acoustic data ends at about 20 hours of recordings and depth was logged for two more hours, and for pm10_230a there is a period (from 3:46 to 4:47, indicated with a dotted rectangle) without acoustic data due to an error in the audio file.

Table III. II – Estimated body length from IPIs and types of codas produced by sperm whales tagged in the Azores.

	pm10_211b	**pm10_222a**	**pm10_222b**	**pm10_226a**	**pm10_228a**	
Mean body length (m)	9.6	9.1	9.3	9.1	9.4	
Coda type						**Total**
3Reg	1	1	1	81	103	187
4Reg	2	-	2	20	36	59
3+1	-	-	1	1	-	3
5Reg	37	57	164	2	30	290
2+3	80	-	3	-	-	83
3+2	-	-	2	-	-	2
4+1	1	-	1	-	-	2
6Reg	-	-	42	-	2	44
5+1	37	1	5	-	-	43
7Reg	-	1	23	-	-	24
4+3	12	-	-	-	-	12
6+1	-	-	4	-	-	4
8Reg	1	1	14	-	-	16
7+1	-	-	6	-	-	6
9Reg	-	-	10	-	-	10
8+1	-	-	4	-	-	4
10Reg	-	-	5	-	-	5
9+1	-	-	3	-	-	3
11Reg	-	-	3	-	-	3
10+1	-	-	1	-	-	1
13Reg	-	1	-	-	-	1
Total	171	62	294	104	171	802

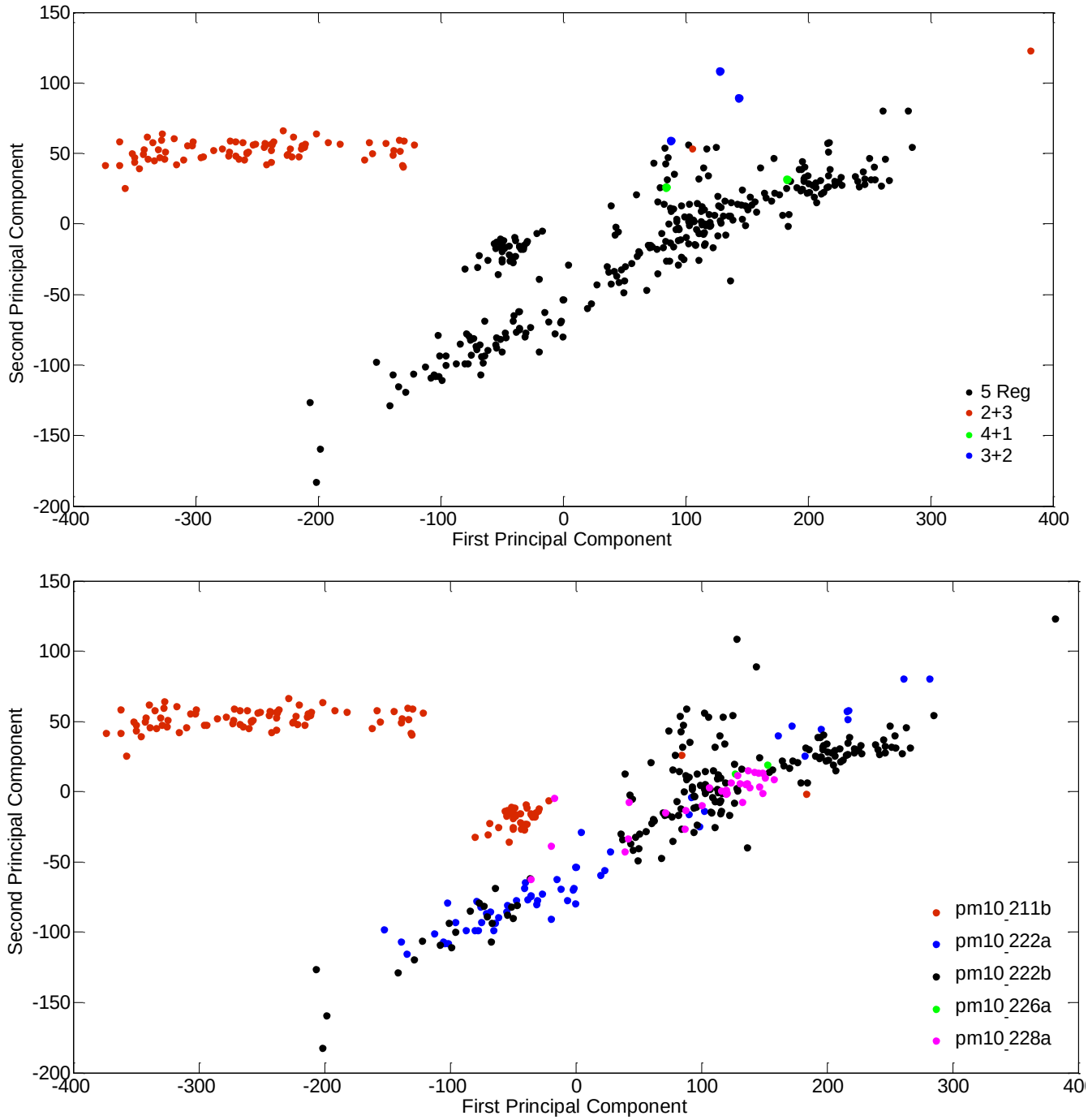


Figure III. 3 – Two principal components of the Principal Component Analysis (PCA) used to classify 5 click codas. Coda types 5Reg and 2+3 are separated with a 91% explained variance. In the upper panel the different colors represent the distinct coda types obtained from the PCA, and in the lower panel the different colors represent the distinct individuals.

To test if the measured signal parameters contributed to individuality in coda production, three different DFA scenarios were investigated with a total of 204 non-clipped 5Reg codas produced by 3 different tagged sperm whales (the three non-clipped codas from pm10_228a were not used in this analysis). The number of possible discriminant functions in DFA is either the number of groups minus

one or the number of predictors, whichever is smallest. In this case the DFA resulted in two canonical discriminant functions (the number of individuals minus one) for each scenario. Both functions in the three scenarios were statistically significant (Table III.III). The canonical function values for each coda were plotted to evaluate the ability to visually differentiate among individuals (Fig. III.4). Generally, in all DFA scenarios, the differentiation was mostly between pm10_211b and the other individuals, but the clusters of points of the sperm whales that were tagged in the same day (pm10_222a and pm10_222b) could also be distinguished. The confidence levels of individual correct discrimination from Mahalanobis distances and posterior probabilities for these two animals in the three DFA scenarios were 74%, 58%, 37%, and 97%, 93%, 82%, respectively. The explained variance of the first canonical discriminant functions was higher than 75% in the three scenarios (Table III.IV). The standardized canonical discriminant coefficients indicate the contribution of each of the individual predictor variables to the discriminant functions (Table III.IV). For the first DFA scenario, the discriminant functions were mostly determined by ICI1, ICI2 (with individual differences of ICI1 and ICI2 of 21-62 ms) and rms_{bw}. In the second DFA scenario, the discriminant functions were mainly determined by IPI, fc and rms_{bw}. For the last DFA scenario, the discriminant functions were determined by ICI1, ICI2, ICI3 and ICI4 (Table III.IV). The general DFA performed correct classifications for 70-88% of the iterative test runs (Table III.III).

Table III. III – Significance values for the Discriminant Function Analysis (DFA) scenarios (1, 2 and 3) and the DFA correct classification of non-clipped 5Reg and 3Reg coda types produced by tagged sperm whales in the Azores.

5Reg	Canonical R	χ^2	p	DFA correct classification
scenario 1: all the parameters	86%	380	<0.001	88%
scenario 2: without the ICIs	79%	272	<0.001	83%
scenario 3: only ICIs	75%	194	<0.001	70%
3Reg				
scenario 1: all the parameters	74%	82	<0.001	83%
scenario 2: without the ICIs	55%	38	<0.001	77%
scenario 3: only ICIs	59%	44	<0.001	74%

For the DFA of the 3Reg coda type the dataset is smaller (107 non-clipped 3Reg codas) but the DFA also found one function statistically significant in all the three scenarios (Table III.III). The discriminant function of the first scenario was mostly determined by fc and rms_{bw}, the function of the second DFA scenario was mostly determined by IPI and decay, and in the last scenario, the discriminant function was mostly determined by ICI1 and ICI2 (Table III.IV). The general DFA resulted in 74-83% correct classifications in the test runs (Table III.III).

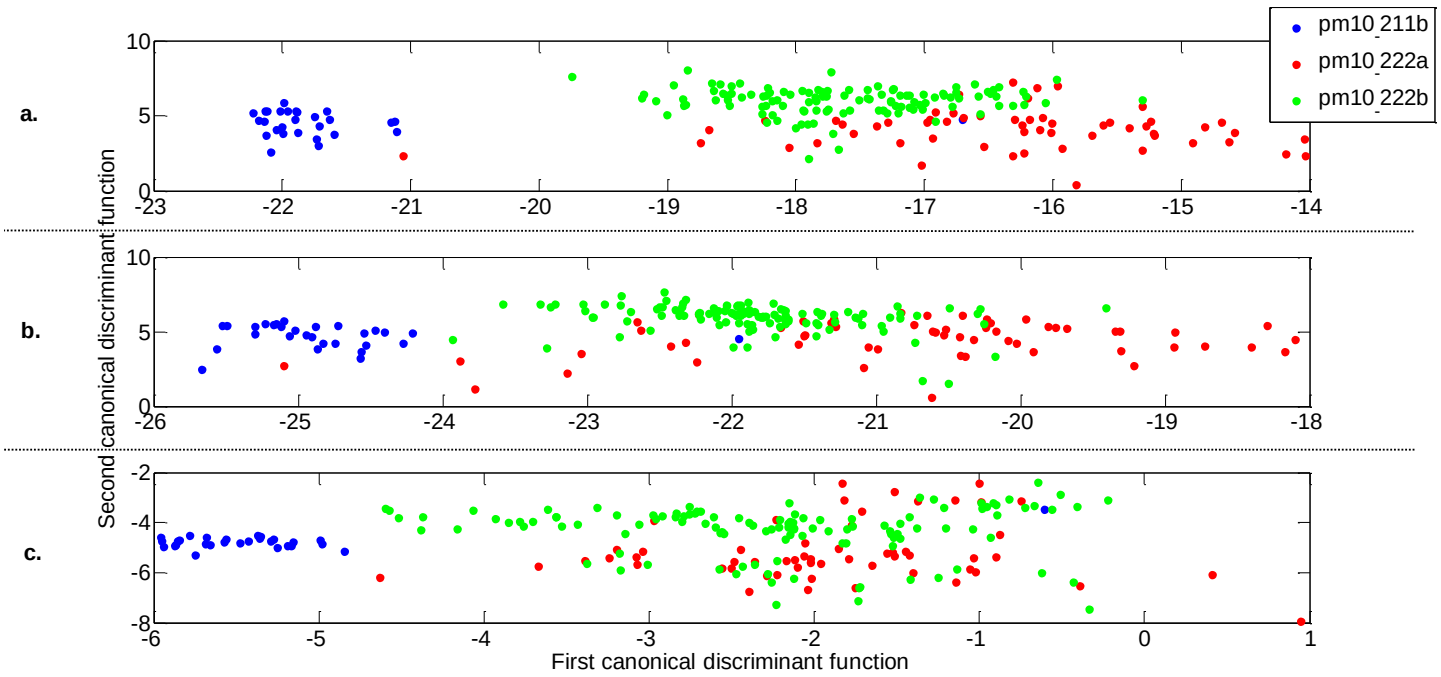


Figure III. 4 – Canonical discriminant functions from Discriminant Function Analysis (DFA) of 5Reg non-clipped codas. Three DFA scenarios were performed for non-clipped 5Reg codas produced by three sperm whales: a. DFA using all parameters (ICIs, IPI, decay, fc and rms_{bw}), b. DFA without the ICIs and c. DFA only with the ICIs.

To investigate if these relationships between the measured variables in the DFA could be explained by the depth of coda production, we plotted the different variables as a function of depth (ICIs and IPI for all clipped and non-clipped codas, and fc, rms_{bw}, decay only for non-clipped codas; Fig. III.5). The depth range of 5Reg coda production was 0-250 m, 30-635 m, 0-480 m and 0-20 m for pm10_211b, pm10_222a, pm10_222b and pm10_228a respectively. The depth range of 3Reg coda production was 30-550 m and 0-590 m for pm10_226a and pm10_228a respectively. The coefficients of determination between the variables and depth for both coda types were always below 0.5 (Table III.V).

To eliminate any depth effects in the individual coda classifications we performed additional DFAs for codas produced within a smaller depth range (100-200 m depth for non-clipped 5Reg codas and 0-100 m depth for non-clipped 3Reg codas). These classes were chosen as having the highest number of codas per individual within a 100 m interval. The DFAs found two statistically significant functions for the non-clipped 5Reg codas (Canonical R=92%, 84% and 86% for the first, second and third scenarios respectively, with $p<0.001$ for all the tests). For the non-clipped 3Reg codas the DFA results were: Canonical R=96%, 95% and 57% for the first, second and third scenarios respectively, with $p<0.001$ for all the tests.

Two whales appeared to produce distinct codas linked to dive phases. For pm10_211b, 2+3 codas were mainly produced in ascents, 5+1 codas were mainly produced when reaching the surface, and 5Reg codas were mainly produced in descents. For pm10_228a, 3Reg codas were produced during the ascent phase while 5Reg codas were produced upon reaching the surface (Fig. III.6).

Table III. IV – Explained variance and standardized coefficients for the canonical variables in three Discriminant Function Analysis scenarios of non-clipped 5Reg codas produced by tagged sperm whales in the Azores.

	Canonical Discriminant Functions	
scenario 1: all the parameters	1	2
Explained cumulative variance (%)	78	100
Standardized coefficients for the variables		
IPI	-0.60	-0.29
rms_{bw}	0.10	**0.90**
ICI3	-1.04	0.47
ICI1	**2.11**	-0.00
fc	-0.42	-0.22
decay	-0.30	0.14
ICI2	-**1.61**	**0.72**
ICI4	0.64	-0.59
scenario 2: without the ICIs	1	2
Explained cumulative variance (%)	77	100
Standardized coefficients for the variables		
IPI	-**0.77**	**0.26**
rms_{bw}	0.06	-**0.88**
fc	-**0.56**	-0.03
decay	-0.42	-0.23
scenario 3: only ICIs		
Explained cumulative variance (%)	90	100
Standardized coefficients for the variables		
ICI3	**-**1.99	**0.79**
ICI1	**2.94**	**-**0.55
ICI2	-**2.05**	**-**0.62
ICI4	0.98	-**0.62**

Notes: boldface values are the two higher absolute standardized coefficients, which correspond to the most important variables in the respective canonical discriminant function. The parameters were ordered according to the DFA Wilk's lambda value.

To test the accuracy of coda assignment to individual using IPI measurements only, the length distribution of the coda clicks produced by the five sperm whales was plotted (Fig. III.7). There is a common range of individual body length distributions of about 54 cm derived from IPI measurements. Pm10_222b had the highest percentage of error of individual coda assignments through IPI measurements (97% of its codas had IPIs within the common range). Altogether, 573 of 802 codas are within the common range of sperm whale length indicating a potential classification error rate of 71% in allocating codas based on IPI measurements to these individuals.

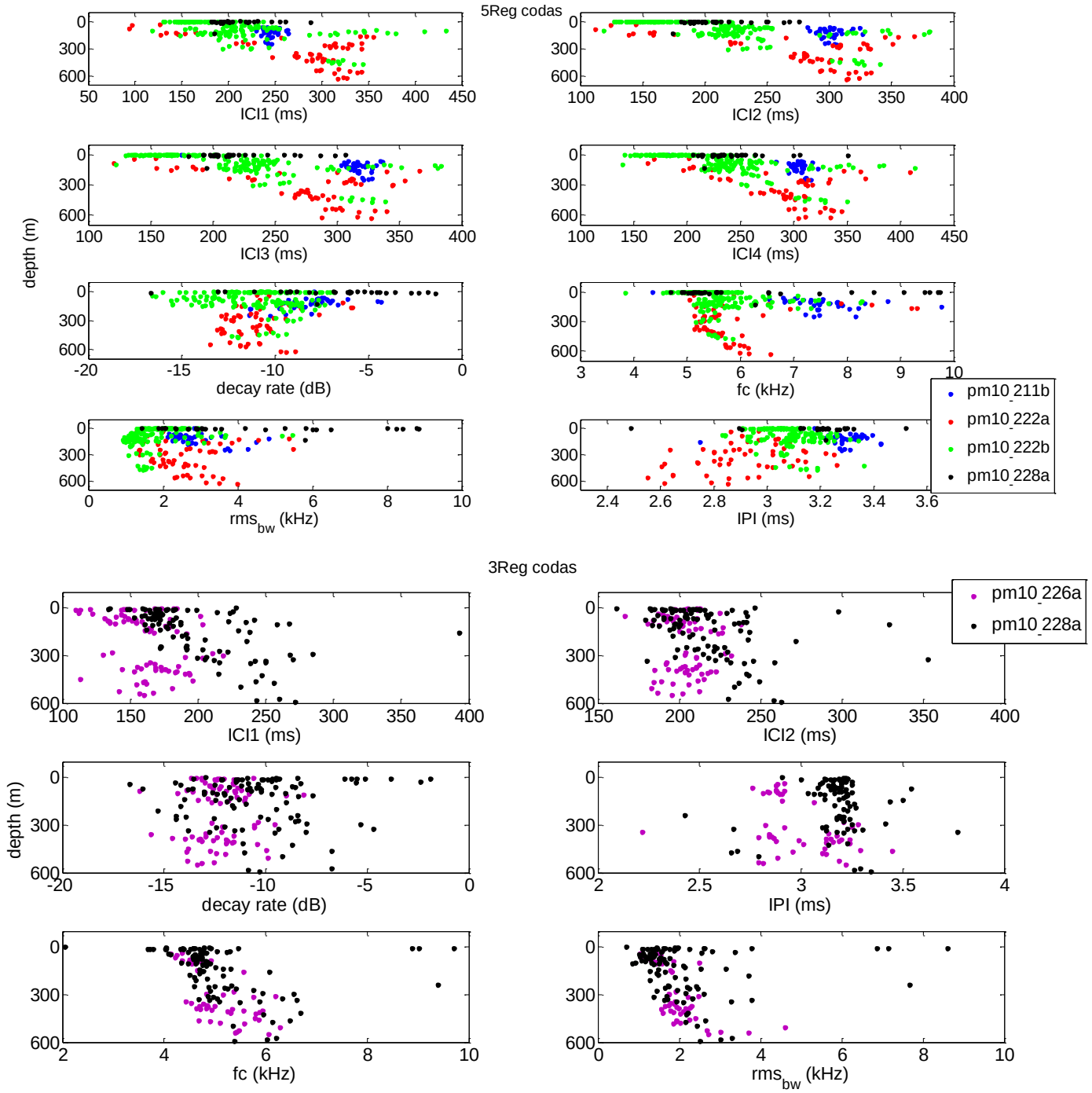


Figure III. 5 – Discriminatory parameters in relation to depth where codas were produced. The upper panel represents the 5Reg coda type and the lower panel the 3Reg coda type.

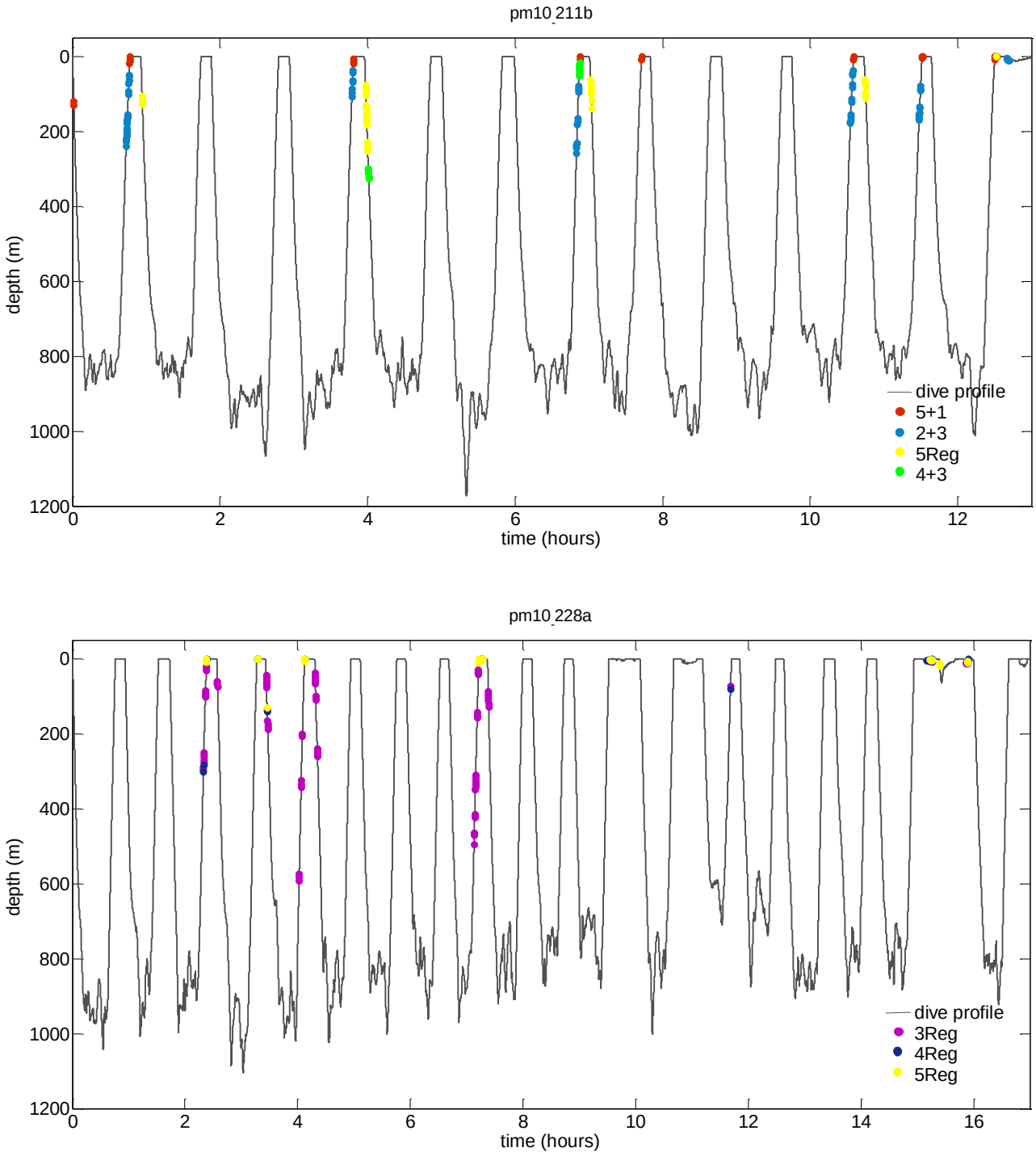


Figure III. 6 – Distinct coda types in relation to depth for two tagged sperm whales (pm10_211b and pm10_228a). Coda types emitted less than four times were omitted for clarity.

Table III. V – Linear regression values (r^2 and p) for the parameters as a function of depth.

5Reg codas	pm10_211b	pm10_222a	pm10_222b	pm10_226a	pm10_228a
all codas					
ICI1	r^2=0.04, p>0.05	r^2=0.38, p<0.001	r^2=0.34, p<0.001		r^2=0.04, p>0.05
ICI2	r^2=0.11, p<0.05	r^2=0.33, p<0.001	r^2=0.43, p<0.001		r^2=0.08, p>0.05
ICI3	r^2=0.18, p<0.05	r^2=0.32, p<0.001	r^2=0.44, p<0.001		r^2=0.03, p>0.05
ICI4	r^2=0.20, p<0.001	r^2=0.27, p<0.001	r^2=0.40, p<0.001		r^2=0.03, p>0.05
IPI	r^2=0.00, p>0.05	r^2=0.09, p<0.05	r^2=0.08, p<0.001		r^2=0.01, p>0.05
non-clipped codas					
fc	r^2=0.30, p<0.001	r^2=0.02, p>0.05	r^2=0.00, p>0.05		
rms_{bw}	r^2=0.19, p<0.05	r^2=0.00, p>0.05	r^2=0.02, p>0.05		
decay	r^2=0.35, p<0.001	r^2=0.09, p<0.05	r^2=0.01, p>0.05		
3Reg codas					
all codas					
ICI1				r^2=0.09, p<0.001	r^2=0.35, p<0.001
ICI2				r^2=0.00, p>0.05	r^2=0.17, p<0.001
IPI				r^2=0.18, p<0.001	r^2=0.01, p>0.05
non-clipped codas					
fc				r^2=0.28, p<0.001	r^2=0.38, p<0.001
rms_{bw}				r^2=0.38, p<0.001	r^2=0.20, p<0.001
decay				r^2=0.01, p>0.05	r^2=0.11, p<0.05

Note: ICIs and IPIs values are for all codas (clipped and non-clipped) and the remaining parameters values only for non-clipped codas.

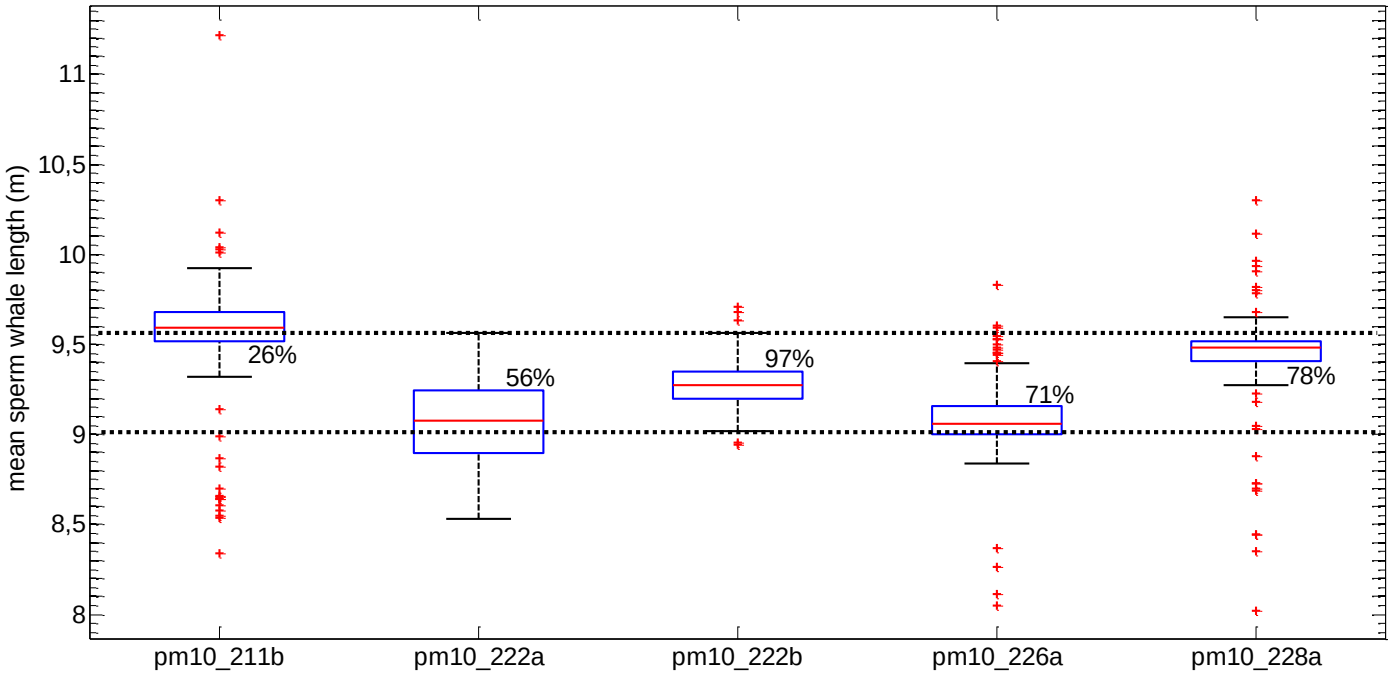


Figure III. 7 – IPI-based length measurements of the five sperm whales that produced codas. The inter-pulse intervals (IPIs) measured from each coda were transformed into length distributions (Gordon 1991a) and their individual distribution was plotted. Blue boxes represent lower to upper quartiles distribution, red lines are the medians, black whiskers are 1.5 times the interquartile range and red crosses are outliers. The black dotted lines represent the common range of lengths that all whales share (about 9.01-9.55 m). The values represent the percentage of codas of each animal that is within the 54 cm common range.

Discussion

In previous studies codas have been assigned to individual sperm whales through measurements of IPIs of clicks in codas recorded with hydrophones several meters away from the clicking whales (Antunes et al. 2011; Schulz et al. 2011). This is the first study to investigate individual coda production and its variation during a dive cycle using on-animal recordings that allow unequivocal individual coda assignments. The identification of codas produced by the tagged animal was performed using the angle-of-arrival of the coda clicks obtained from the two Dtag hydrophones. From the IPI measurements made here (Fig. III.7) it is clear that the individual coda assignment from IPIs is not an appropriate methodology for the current study as there would be a 71% probability of erroneous assignment of individual whales due to their large overlap in size and the variation in IPIs for the same animals.

Previously, classification of coda types has used measurements of ICIs on codas normalized to a constant total duration (standardized ICIs), and k-means clustering (Weilgart and Whitehead 1997; Rendell and Whitehead 2003a, b, 2004). While k-means clustering using standardized ICIs appeared to work well to classify codas from the Pacific, where vocal clans exhibit strong differences, but it did not perform as well in other cases, when using non-standardized ICIs and on large datasets where differentiation is not as strong (Antunes 2009). K-means requires that the number of clusters is specified in advance, and while some methods exist to determine this (e.g. Rendell and Whitehead 2003b), they do not always provide a clear solution. Also k-means partitions clusters into Voronoi cells, forming similarly sized clusters and there is no a priori reason to think that coda ICI data occur naturally like this. Another study used observer-based classification with absolute ICIs for sperm whale codas recorded in the Mediterranean Sea (Frantzis and Alexiadou 2008) and Antunes et al. (2011) also concluded that the use of absolute ICIs is important to avoid discarding important coda information. In the current study, the classification of coda types used absolute ICIs and was based on PCA and observer classification. We are confident that our final classification was sufficiently robust and unbiased, as the first two principal components of the PCA explained 91% of the variance, and the only codas that were classified differently from the observer classification in the PCA were the very rare ones. Therefore, our choice to combine the PCA and manual classification methods seems appropriate.

In our study, the coda types found in the sperm whales tagged around the Azores mainly comprised 5Reg, 3Reg, 2+3 and 4Reg, and the 5Reg was the coda type most frequently shared among all individuals. Previous studies reported that the 5Reg coda type also was the most frequently found in

the Azores archipelago and the majority of codas tended to belong to the *regular* type (Antunes 2000, 2009).

One coda type, 5Reg, has been suggested to initiate coda exchanges (Weilgart and Whitehead 1993), while the behavioural context of different coda groupings was found to vary among male sperm whales (Frantzis and Alexiadou 2008). Additionally, coda production seems to vary according to the reproductive status of the group members (Schulz et al. 2011), and differences found in individual-specific information between coda types point towards different functions of distinct coda types (Antunes et al. 2011). We found a patterned behaviour in the production of different types of codas and the depth or dive phase of the animal (Fig. III.6). Although these observations came from only two individuals, they suggest a specific depth context or function of coda types which may also be related with an individual signature function of coda clicks. These observations also indicate that studies of variation in coda repertoire should take into consideration the context in which codas are produced. Comparing sperm whale coda repertoires recorded in different contexts may highlight variation due to context instead of other factors of interest. Good characterization of coda repertoire variability (e.g. geographic) should ideally include recordings in as many different contexts as possible, and comparison among repertoires should also include a range of contexts or at least be made in the same context.

Our results indicate that individual sperm whales may be distinguished based on their coda production (Fig. III.4). The individuality is not only found in the coda types produced (Table III.II), but apparently also in several features of each coda signal. For 5Reg codas, the first two inter-click-intervals contributed most to the discriminatory power of the first and third DFAs (with individual differences of ICI1 and ICI2 of 21-62 ms). If sperm whales are able to acutely alter the ICI of usual clicks and buzzes and resolve the small delays between clicks and echoes when echolocating for prey (Teloni et al. 2008), there is reason to believe that they are able to control and decode individual ICI differences of this magnitude within the same coda type from vocalizing conspecifics. Individual differences in ICIs of 5Reg codas were indeed found in a previous study from another area (Antunes et al. 2011). Our results also suggest that individual discrimination is possible without using the information in the ICIs, by using IPIs, rms_{bw}, fc and decay. The Canonical R from the DFA without the ICIs was similar to the one from the DFA using only the ICIs implying that the combination of IPIs, rms_{bw}, fc and decay provide equivalent discriminatory power to the ICIs. Therefore, individual traits in coda clicks seem to occur also in other coda parameters besides ICIs. However, it is not clear if sperm whales are capable of perceiving these differences in IPI, rms_{bw}, fc and decay. Perception of small changes in inter-pulse timing (i.e. in IPI and decay) is more likely to be affected by propagation effects (i.e. multi-path arrivals, especially near the surface where codas are often produced) and the

relative aspect of the whale (Zimmer et al. 2005b) and might be less useful in discrimination of individuals at long ranges where ICI based discrimination might be more robust. Whether or not other cues than ICIs are used, we argue that there is plenty of information available within shared coda types for conveying individuality, social status and behaviour. Such a level of complexity has largely been overlooked in previous considerations of the function of codas, but it would not be surprising given the complex social behaviour in sperm whales.

For the 3Reg coda type the individual discrimination abilities were also high (Canonical R 55-74%) and was mainly related to the parameters fc, IPI and ICI1 (the most important parameters from the three scenarios). IPIs are related to the animal's size (Gordon 1991a) and therefore age class, both of which are relevant to identify conspecifics, as in humans, where age is coded into vocal output (Endres et al. 1971). In our dataset the IPIs revealed a wide range of overlap between individuals. Nevertheless the IPI seems also to contribute to the discriminatory power found in the DFAs, possibly also conveying information about the age of the individuals. It is conceivable that in a sample having individuals with more variable body lengths than in our recordings, this parameter may be even more useful for individual discrimination.

In African elephants, frequency-related components contribute to the acoustic discrimination of individuals (McComb et al. 2003; Soltis et al. 2005). In the present study, the centroid frequency of the primary pulse also contributes to the individual discrimination in the second DFA scenario of the 5Reg codas and the DFA for 3Reg coda type. An obvious drawback of the technique used here (tagging) is that the signals will be recorded at an off-axis angle from the presumably directional sound source, and this angle varies from individual to individual, depending on where on the whale the tag was attached. This will not modify IPI measurements but may influence the spectral components included in the analysis, like the fc and rms_{bw}. Although the fc and rms_{bw} parameters are closely related to the position of the tag on the animal, in 3Reg DFA the individual discrimination in the first scenario was obtained mainly due to fc and rms_{bw}. The positions of the tag on both pm10_226a and pm10_288a are very close to each other, which may counterweigh the influence of tag placements in signal parameters derived from these two individuals. Therefore, we cannot conclusively say if spectral parameters may serve as information carrying vehicles in coda communication, but the variation within and between animals is large enough to preclude falsification of that hypothesis (Antunes et al. 2011). From all the DFAs performed in different coda types it is thus possible to identify several candidates (absolute ICIs, fc, rms_{bw}, IPI and also decay) for encoding information in otherwise shared coda types. There is thus much more to sperm whale coda communication then to radiate just clan identity.

It is possible that the differences found between individuals in the DFA may be influenced by the depth at which codas were produced. As codas signal parameters showed only small correlations with depth there is not sufficient power to test the mechanisms underlying this relationship. However, if the relationship with depth was due to purely physical effects, we would expect to see high correlation values and the parameters consistently changing in one direction. That was not the case, so any depth effects are likely a mixture of physical and behavioral effects. Nevertheless, the DFAs performed with codas produced in limited depth ranges revealed similar individual discrimination results. This reinforces results obtained from the DFA with codas produced in all the depth ranges and, thus, the individual function of coda production.

The individual sperm whales studied here do not necessarily belong to the same social group. The individuality in codas found in these animals may be explained by the tagged whales belonging to different groups/social units. It is however possible to distinguish the clusters of points of the two whales tagged in the same day (pm10_222a and pm10_222b; Fig. III.4) that were observed together in the area in 2010, 2011 and 2013 (Steiner, unpublished photo-id data). If a pair of sperm whales is associated during at least two years they are considered belonging to the same social unit (Christal et al. 1998; Gero et al. 2013). Moreover, genetic studies carried out in the Azores suggest that sperm whales sighted together on the same day, as were these two whales, are genetically related and should be part of the same social unit (Pinela et al. 2009). Even though it is not possible to assure that pm10_222a and pm10_222b were permanently associated during these years, their consecutive sightings indicate they probably belong to the same social unit. So, the individual discrimination from coda production between these two animals is in line with the coda signature function we are presenting in our study. Additionally, even though the clusters of points of these two animals are distinct, they are closer to each other than to the other sperm whales (with DFA correct individual discrimination confidence levels of 47-68% for pm10_222a and 82-97% for pm10_222b), indicating there may also be a unit/group effect described in previous studies of vocal clans and dialects (Weilgart and Whitehead 1997; Rendell and Whitehead 2003a, 2005).

Until recently (Antunes et al. 2011), most studies on sperm whale codas emphasized their function in allowing different units and clans to separate each other on an acoustic basis (Weilgart and Whitehead 1997; Rendell and Whitehead 2003a). From our data it is clear that individual encoding of codas is possible from ICIs as well as other coda parameters such as IPIs, centroid frequencies, rms bandwidths and inter-pulse decay rates. Furthermore, we document differences in individual coda types depending on depth or dive cycle phase. The individuality features in coda production demonstrated here reveal that these signals very likely encode individual information to a much larger extent than previously thought. This may have important consequences for our understanding

of the social system of sperm whales where acoustic communication is about much more than the clan.

Chapter IV

Underwater 3-D behaviour of breaching sperm whales

Breaching is an intentional leap out of water, which function is not well understood. In whales, breaching is believed to be mainly associated with parasite removal, play and/or communication. Until now, breaching behaviour has only been described from surface observations. Here we describe the underwater movements associated with breaching behaviour of sperm whales instrumented with Dtags. These non-invasive devices allowed us to describe the swimming velocity, acceleration, frequency of flukings, time-depth profile, and 3-D underwater movements of the whale prior to breaching. Before breaching, sperm whales perform shallow V-shaped dives of 13.4-31.2 s to 11-41 m depth. Vertical velocity and acceleration were significantly different between descent and ascent phases of these dives. During descent sperm whales rolled frequently to both sides and performed an average of 3 fluke strokes, meaning their movement was mostly characterized by stroke and glide. Ascents were steeper than descents. Ascents had on average 1 fluke stroke and they were mainly performed by gliding, which may be a result of both buoyancy forces and speed attained during descents. The swimming velocity and acceleration during ascents increased gradually until the animals broke the water surface. Rotational body movements during the dives that precede breaches in sperm whales may be comparable to the movements performed by baleen whales during lunge feeding events, and apparently allow them to gain speed to perform such spectacular events.

In preparation for submission with the following authors:
Cláudia Oliveira, Peter T. Madsen, Jeremy Goldbogen, Mark Johnson, Malene Simon, Susan Parks and possibly more authors

Introduction

Whale breaches have been described as an intentional leap from the water, in which the animal emerges more than 40% of its body (Whitehead 2002). It is observed in many species of both baleen and toothed whales. In baleen whales it is often associated with socializing or mating (Whitehead 1985a). For the sperm whale (*Physeter macrocephalus*) the largest of the toothed whales, breaches are common, but their function is not well understood (Whitehead 2003).

Prior to a sperm whale breach the animal usually performs a steep dive, probably to 70-110 m depth, which is followed by a change to ascent, with the whale emerging out of the water 25-40 s later, with an angle of 30°-50° to the horizon (Beale 1839; Waters and Whitehead 1990; Whitehead 2003). While in the air sperm whales often twist their body and appear to splash on their side. Typically, these events occur in bouts, their intensity decreases through the sequence of breaches and the splash onto the water is usually done with the same side of the body, being visible many kilometres away (Gordon 1987b; Waters and Whitehead 1990; Whitehead 2003). Breaching seems to be more common among sperm whales found in groups and among females (Waters and Whitehead 1990).

Within sperm whale social units or groups, breaching appeared to occur more frequently during socializing, but not as clearly as for other surface activities, such as fluke-ups, spyhops and sideflukes (Whitehead 2003). In the Galapagos Islands, breaching and lobtailing (i.e. hitting the water surface with the tail) seemed to occur mostly during the afternoon, which is also the time of the day with higher rates of socialization activities (Waters and Whitehead 1990). Also, breaches were more frequent when males were present and when more than one group was identified, and bouts of breaches seemed to be related with splitting rather than joining of groups (Waters and Whitehead 1990). Humpback whale (*Megaptera novaeangliae*) breaches were found to be moderately correlated with wind speed, although the reason for this relationship remains unknown (Whitehead 1985a).

Breaches must involve some energy expenditure, which points towards an important function of this behaviour. Using breach speed calculations from photographic records, values of the body angle in relation to the horizon, and previous relations of daily food consumption (Lockyer 1981), Whitehead (1985a, 2003) performed theoretical calculations of the energy that is necessary for a 13.5 ton sperm whale to breach, which is about 617 kcal (only 0.075% of its daily active metabolic rate).

The function of breaching in cetaceans is not clear. Multiple purposes have been proposed (Clapham and Mead 1999): parasite removal (Beale 1839), exhibition of annoyance, aggression (Würsig et al.

1989) or excitement, play behaviour (Caldwell et al. 1966; Pryor 1986; Whitehead 2002; Kot et al. 2013), stretching, breathing free of any water spray, a display of power (Whitehead 1985b, 2003) or it may have a communicative function (Whitehead 1985a, b; Tyack and Miller 2002), where the loud signal may convey information on the animal's size and position (Dunlop et al. 2008). Even though none of these possible explanations can be ruled out, parasite removal, play behaviour and communication seem to be the more likely functions for breaching in large whales (Herman and Tavolga 1980; Whitehead 2002).

Until now, the breaching behaviour has only been described from surface observations. The underwater movements needed to perform a breach have not yet been described, limiting our ability to understand the hydromechanics and energetic requirements of this impressive behaviour. In the present study we describe the swimming velocity, acceleration, fluking, depth profile and 3-D movements of breaching sperm whales using Dtags, in order to understand the way these odontocetes perform the breaching behaviour.

Methods

Study area

The breaching behaviour of sperm whales was studied in the Azores archipelago (38°N, 28°W), around the islands of Faial and Pico. In this area, it is common to observe sperm whale social units and occasionally mature males (Silva et al. 2014). Tagging locations can be found on Chapter II (Fig. II.3).

Tagging

Field work was carried out in July and August 2010, using a 6 m long rigid-hulled inflatable boat (RHIB) and a 15 m long sailing boat. Localization of sperm whales from the RHIB was performed visually and acoustically with a directional hydrophone (HTI-96-MIN, High Tech, Inc., with a custom-built baffle). The sailing boat was used to detect sperm whales visually and acoustically, using a towed-hydrophone array and Rainbow Click software (Gillespie 1997), and also to recover the tags. Visual observations were supported by whale watching lookouts ("vigias") that monitor some areas around Faial and Pico islands on a daily basis during spring and summer.

Sperm whales were tagged with non-invasive digital acoustic recording tags (Dtag, Johnson and Tyack 2003). These devices have two stereo hydrophones (96 kHz sampling frequency, 16 bit resolution) and also record pressure, temperature and 3-D orientation data with a 50 Hz sampling frequency (16 bit). Dtags were attached with 4 suction cups and they released automatically from the animal after a programmed maximum deployment period of 24 hours.

The approach to the whales was made carefully from behind at a very low speed (maximum 4 knots) and tag deployment was made with an 11 m cantilevered pole. All tag placements were made between the head of the animal and its dorsal fin (see Chapter III). Tagging events, individual photo-id and tag placements were photographed with a Nikon D90 and a Nikkor AF 70-300 mm lens. The response to the Dtag attachments was mild. The animals frequently performed a dorsal flex of the body, and sometimes they also defecated and dived with or without fluking. There were no breaching events in response to the Dtag attachments. Sperm whale surface tracking was made with the emission of a VHF beacon built-in the Dtags and the reception with a 4-element Yagi antenna, attached to a VHF receiver (Communication Specialists Inc. R1000). Whenever possible, time and position of each surfacing were registered by approaching the boat to the fluke print of the animal. Once the tag released from the animal, it was recovered while floating at the surface by VHF signal tracking.

Field work was approved by the Regional Directorate for Sea Affairs, Autonomous Region of the Azores under research permit number 49/2010/DRA. All procedures in whales followed the guidelines of the American Society of Mammalogists (Gannon and Sikes 2007).

Data analysis

Data from the depth and movement sensors were decimated to a sampling rate of 5 Hz. The accelerometer and magnetometer data were corrected from a coordinate system with the tag as a reference (‘tag frame’) to one with the whale as a reference (‘whale frame’, as described by Johnson and Tyack 2003) so that the orientation of the whale could be described. Acoustic data were analysed visually and aurally using Matlab 7.0 (Mathworks, Inc.) with a custom spectrogram (512 FFT block size with 15 s segments with 2 s overlap) and dive depth display, to identify usual clicks, buzzes, codas, slow clicks and other sound emissions.

Descents and ascents were classified according to the pitch of the animal (descent when pitch<0 and ascent when pitch >0; Miller et al. 2004a; Watwood et al. 2006).

Breaching events were detected both from the very shallow depth dive profile and also by listening to the recordings of the high flow noise during descents and ascents, just before the breaches, and the intense splashing sound when the animal slams the water (Fig. IV.1).

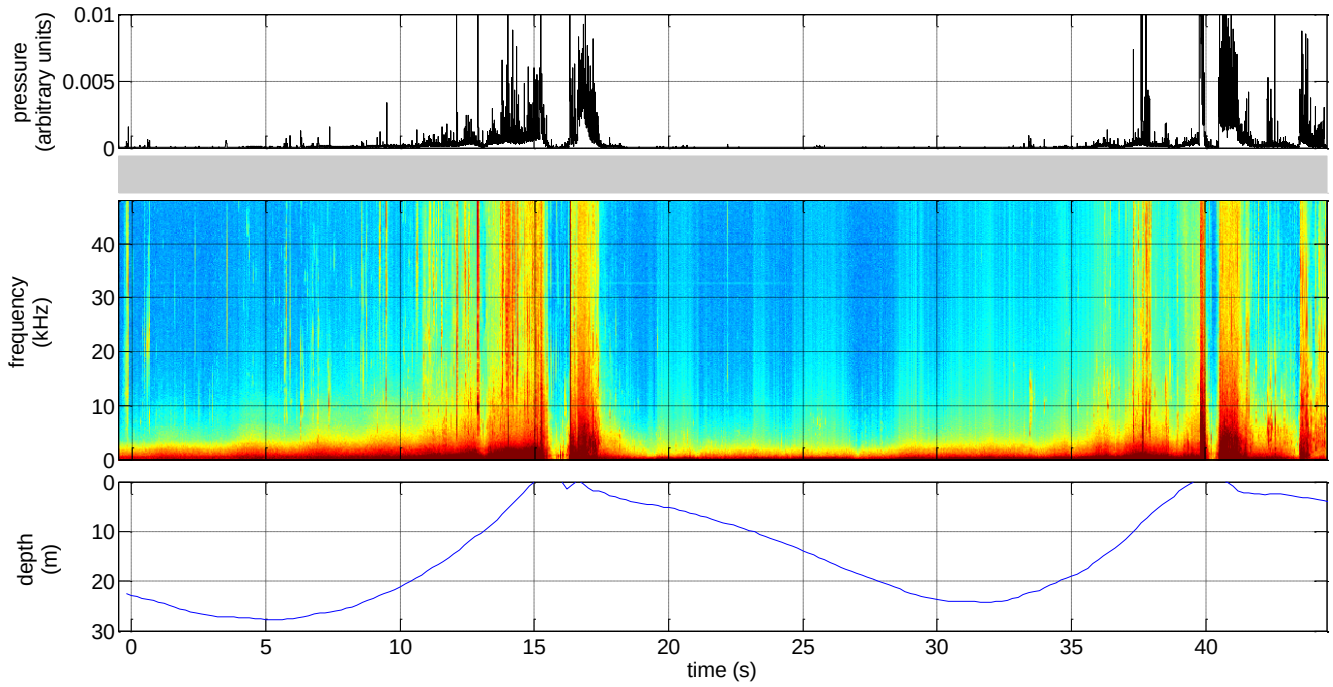


Figure IV. 1 – Example of the dive profile, high flow noise and intense splashing sound in breaching events (512 FFT block size with 25 s segments, 5 Hz sampling rate).

Vertical velocity and acceleration were calculated after applying a low-pass filter with a cutoff frequency of 0.2 Hz. Johnson et al. (2004) detected an increase in the minimum specific acceleration (MSA) in the end of buzzes of foraging beaked whales, which is related with an increase in movement (fast acceleration) to capture prey. During lunge feeding events of humpback whales, Simon et al. (2012) also found peaks in the MSA that correspond to periods of fast fluke strokes. For the present study, the MSA was calculated by bandpass filtering the 3-axis accelerometer dataset to investigate the existence of rapid acceleration before and during breaching events.

Fluke strokes were detected by small oscillations in the pitch of the animals (see Johnson and Tyack 2003; Miller et al. 2004b) and the gliding periods occurred between fluke stroke events.

Body length of tagged sperm whales was calculated with inter-pulse intervals (IPIs) in Gordon's equation (1991a), using coda clicks (pm10_227a was not "vocal" during the whole time the Dtag was on). The peaks of all the individual clicks within each coda were marked and for IPIs only the first two

pulses in the first click of each coda were used, as the IPIs of the remaining pulses are known to be identical to the first one (Madsen et al. 2002b).

Body weight and estimated daily food consumption (DFC), which is about 3% of the body weight for sperm whales up to 15 tons, were calculated according to Lockyer (1981), except for pm10_227a as its body length was undetermined.

Statistical tests were made in STATISTICA 6.0.

Results

We detected nine complete breaches (with complete descents and ascents before the actual breaches) in four of the 11 sperm whales tagged in 2010. The majority of breaching events took place after the whales had spent some time resting near the surface, occurred during distinct hours of the day and appeared in bouts. These bouts were not fully recorded due to tag detachment from the animals; Fig. IV.2). None of the breachings occurred between foraging dives.

Vertical velocity plots of whale's ascensions show negative values due to their decreasing depths while moving. Therefore, for magnitude order we will refer to absolute vertical velocity and acceleration values (Fig. IV.3).

The average inflection depth, where these sperm whales changed from descent to ascent, to be able to perform a breach was 24 m (range 11-41 m) and the average duration of the dive was 22.2 s (range 13.4-31.2 s) (Table IV.I). Descents were always longer and slower than ascents and the majority of vertical velocities and vertical accelerations were significantly different between descents and ascents, during the dive right before the breach (Table IV.I; Table IV.II; Fig. IV.3).

Pm10_222a exhibited a tendency for a decreasing duration of breaching events with time. Although pm10_222b had a first breach that was the result of a non-clear descent preparation phase and possibly compromised the breach duration, the duration of the third breach was smaller than the duration of the second breach (Table IV.I).

Among sperm whales that exhibited bouts of breaches, the increase of acceleration while ascending happened with some regularity. Pm10_222a abruptly increased accelerating at 14-18 m depth,

nearly 3.2-4.0 s before leaping out of water. Pm10_222b suddenly increased its acceleration 3.6–5.8 s before the actual breach, when it was at 10-15 m depth (Table IV.III).

The number of fluke strokes performed during descents and ascents varied from 1-6 and 0-2, respectively. During descents, the interval between fluke strokes ranged from 1.1 to 10.4 s. In the only ascent that had 2 fluke strokes they were separated by 6.9 s. Therefore, descents were mostly characterized by stroke and glide behaviour and ascents mainly by gliding.

The MSA remained approximately constant during descents and increased in the end of ascents and during the breach itself (Fig. IV.3).

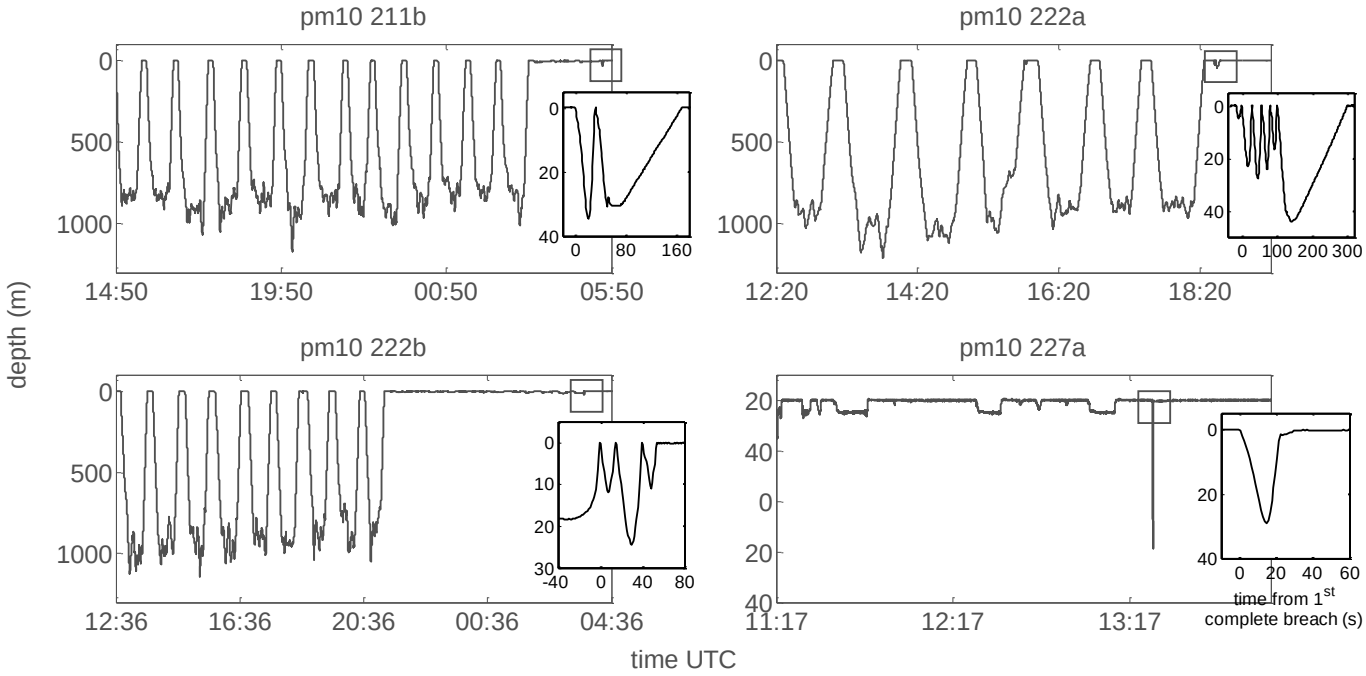


Figure IV. 2 – Dive profiles of four sperm whales showing the timing of breaching events (delineated by a square). Details of breaches are shown on the inset on the right side of each dive profile.

Table IV. I – Number of breaches, inflection depths (ID) (the depth where the animals changed from descent to ascents), duration of descent (D), ascent (A), of the whole dive before breaching (WD), and of the breach (B), for the four breaching sperm whales.

Animal ID	No. breach	ID (m)	Duration (s) D	A	WD	B	Observations
pm10_211b	1	35	20.0	11.2	31.2	1.0	
	2	31	18.0	-	-	-	Dtag released during ascent
pm10_222a	1	23	18.0	9.4	27.4	2.4	
	2	28	16.0	9.4	25.4	2.0	
	3	24	15.0	7.6	22.6	1.4	
	4	17	11.6	6.8	18.4	1.4	
	5	41	24.6	-	-	-	Dtag released during ascent
pm10_222b	1	17	-	15.2	-	0.4	no clear descent
	2	12	7.6	6.6	14.2	1.2	
	3	25	14.0	10.0	24.0	0.4	
	4	11	8.8	4.6	13.4	-	Dtag released at the surface
pm10_227a	1	29	14.4	8.6	23.0	-	Dtag released at the surface
mean		24	15.3	8.9	22.2	1.3	

Table IV. II – Mean and (maximum) absolute vertical velocity (VV) and vertical acceleration (VA) during descent and ascent phases within a dive to breach, for the four breaching sperm whales. The table shows the results of Mann-Whitney tests comparing VV and VA during descent and ascent. Statistically significant values are indicated: *** at $p<0.001$, ** at $p<0.01$ and * at $p<0.05$.

Animal ID	No. breach	Vertical velocity (ms^{-1}) descent	ascent	Vertical acceleration (ms^{-2}) descent	ascent	Mann-Whitney test VV	VA
pm10_211b	1	1.7 (2.5)	3.0 (5.3)	0.02 (0.75)	0.09 (1.97)	U=0, Z=10.36***	U=1767, Z=3.89***
	2	1.6 (2.4)	-	0.02 (1.02)	-		
pm10_222a	1	1.2 (1.6)	2.2 (4.6)	0.05 (0.68)	0.26 (1.86)	U=0, Z=9.61***	U=1110, Z=4.62***
	2	1.7 (2.4)	2.7 (4.7)	0.09 (1.04)	0.25 (1.92)	U=0, Z=9.41***	U=815, Z=5.38***
	3	1.6 (2.3)	3.0 (4.7)	0.08 (1.23)	0.19 (1.99)	U=0, Z=8.68***	U=919, Z=3.16**
	4	1.4 (2.0)	2.2 (3.9)	0.01 (1.17)	0.35 (1.72)	U=1, Z=7.99***	U=537, Z=3.72***
	5	1.6 (2.0)	-	0.02 (1.39)	-		
pm10_222b	1	-	1.0 (3.1)	-	0.04 (1.71)		
	2	1.4 (2.3)	1.6 (2.6)	0.07 (1.76)	0.14 (1.46)	U=6, Z=7.20***	U=460, Z=2.07*
	3	1.7 (2.5)	2.2 (4.0)	0.04 (1.44)	0.19 (1.78)	U=0, Z=9.34***	U=813, Z=5.06***
	4	1.0 (1.6)	2.0 (2.7)	0.10 (1.80)	0.19 (1.03)	U=7, Z=6.62***	U=425, Z=1.20
pm10_227a	1	2.0 (2.8)	3.2 (4.8)	0.05 (1.32)	0.09 (1.63)	U=0, Z=8.97***	U=1377, Z=1.10

Table IV. III – Time to breach and depth of the increase in vertical acceleration, the number of fluke strokes performed in descents and ascents, and the interval between fluke strokes.

Animal ID	No. breach	Increase in acceleration time to breach (s)	depth (m)	No. of fluke strokes descent	ascent	Interval between fluke strokes (s) descent	ascent
pm10_211b	1	9.6	34	5	0	4.5; 3.5; 3.7; 2.3	-
	2	-	-	3	-	3.2; 10.4	
pm10_222a	1	3.2	15	6	0	2.1; 1.1; 3.2; 4.2; 2.9	-
	2	3.4	17	1	1	-	-
	3	4	18	3	1	6.4; 5.6	-
	4	3.4	14	3	0	3.3; 2.0	-
	5	-	-	3	-	4.1; 4.2	-
pm10_222b	1	3.6	11	-	2	-	6.9
	2	5.8	12	1	1	-	-
	3	3.6	15	3	1	4.9; 3.5	-
	4	4.2	10	1	1	-	-
pm10_227a	1	7.8	29	2	0	9.9	-
mean		4.9	18	3	1	4.2	-

Two examples of the 3-D underwater movements of sperm whales preparing to breach is shown in Fig. IV.4 (the remaining breaches are in Annex I). The ascents were steeper compared to the descents. During the whole dive just before breaching, the whales seemed to roll frequently from right to left side and vice-versa during descents but not so much during ascents, apparently gradually choosing either right or left side (Figs. IV.3 and IV.4).

In relation to body side twisting while breaching, pm10_211b enters the water slightly twisted to its right side. Pm10_222a enters the water twisted to its left side after three breaches and once to its right side. The sperm whale tagged in the very same day, pm10_222b splashes into the water with its right side once and twice with the left side of its body (Figs. IV.3 and IV.4).

The calculated length, weight and daily food consumption (DFC) of the breaching sperm whales (except for pm10_227a) are in Table IV.IV.

Table IV. IV – Length (from inter-pulse intervals), inferred weight and estimated daily food consumption (DFC; both from Lockyer 1981) of the four breaching sperm whales.

Animal ID	Length (m)	Weight (ton)	DFC (kg)
pm10_211b	9.55	8.70	261
pm10_222a	9.07	7.36	221
pm10_222b	9.27	7.92	238
pm10_227a	-	-	-

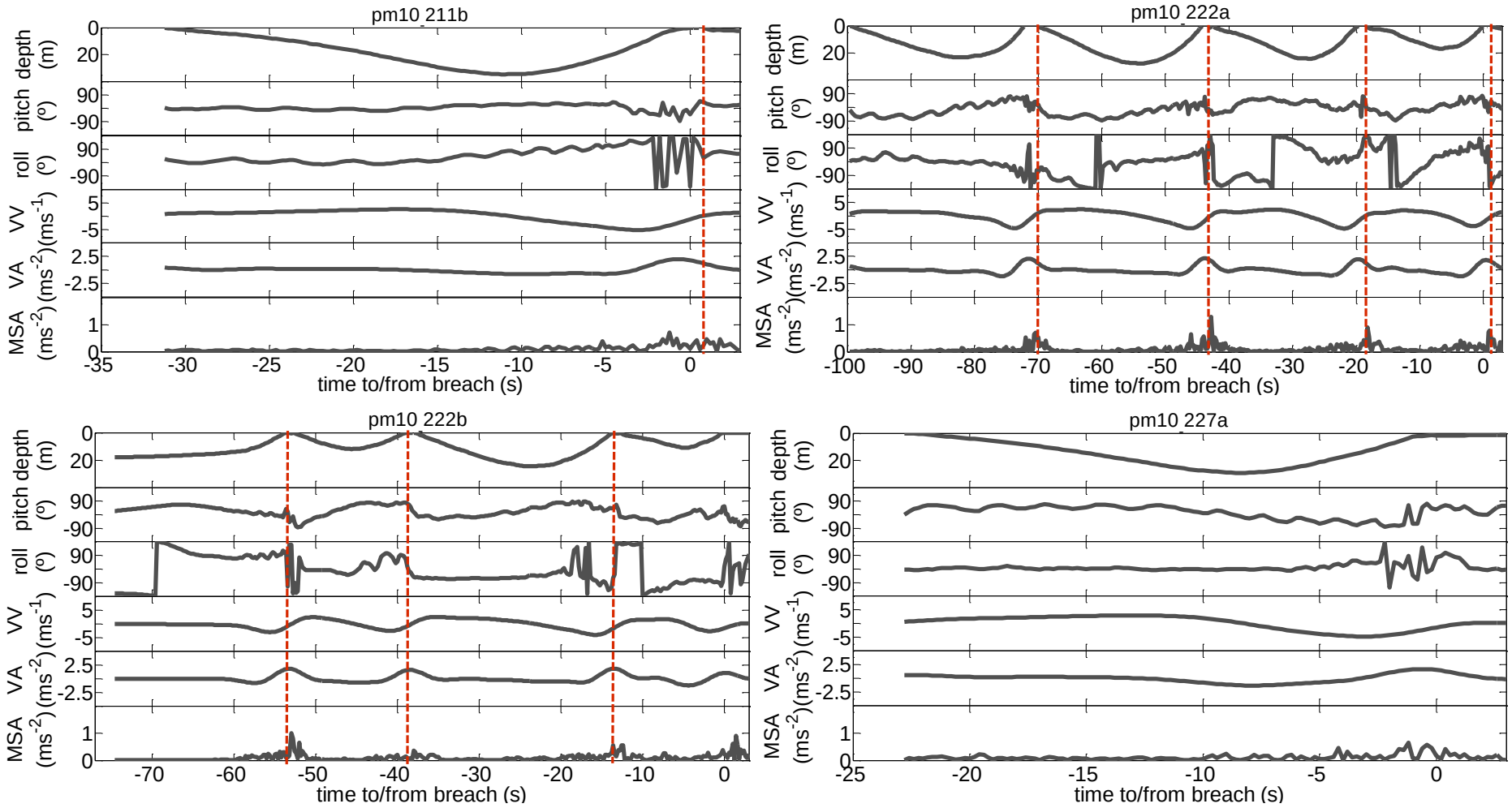


Figure IV. 3 – Dive profile, pitch, roll, vertical velocity (VV), vertical acceleration (VA) and minimum specific acceleration (MSA) of the breaches of four breaching sperm whales. Dashed red lines represent the moments when the animal splashed onto the water, after each breach.

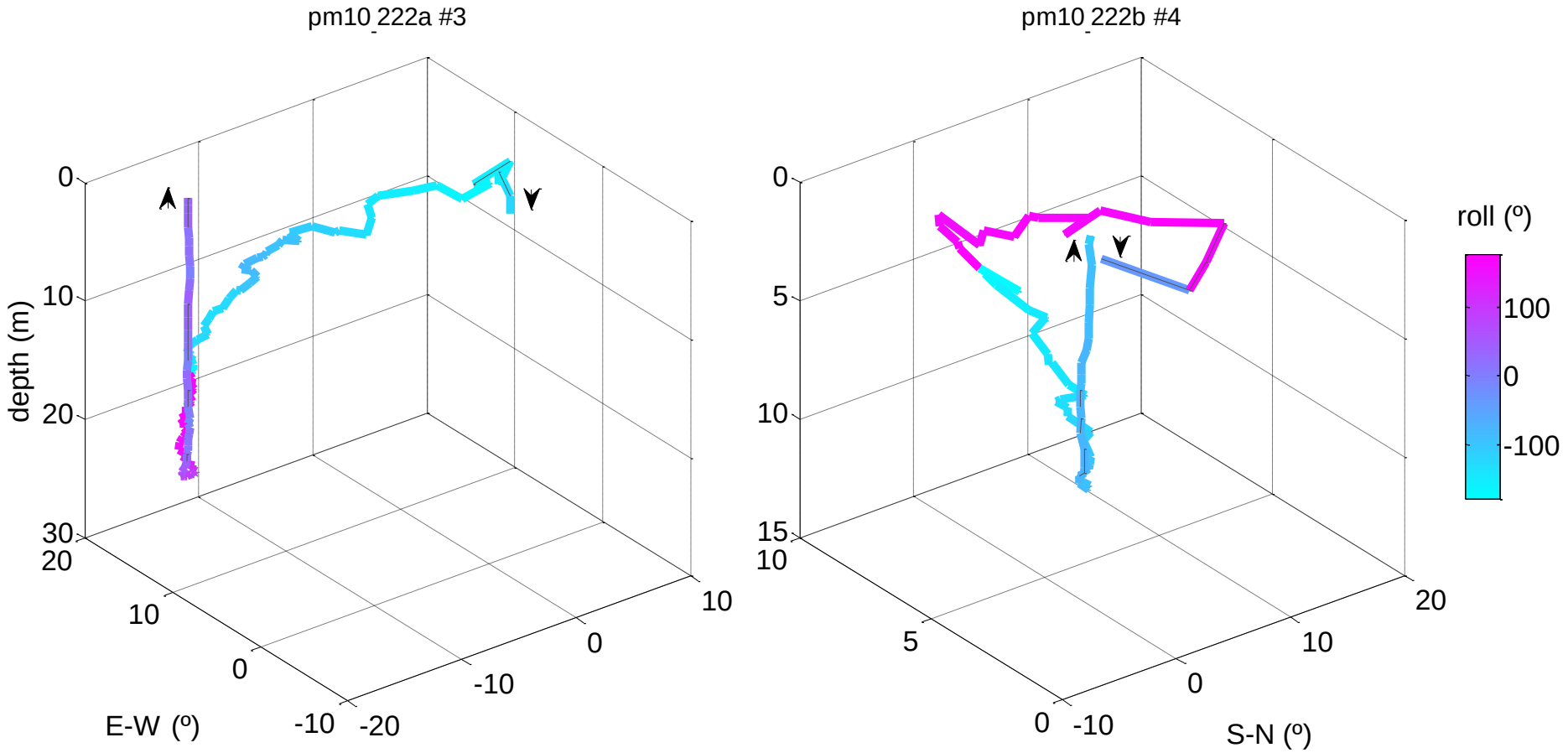


Figure IV. 4 – Pseudotracks of the descent and ascent before breaching, of the third breach of pm10_222a and the fourth breach of pm10_222b. Body rolling is shown as a color gradient, with positive values meaning the animal is turned to its right side and negative values to its left side.

Discussion

Dtags deployed on 11 sperm whales contained data from nine complete breaches, with full descent and ascent phases. Even though it is a small sample, it enabled the first detailed description of the underwater 3-D movements of these odontocetes when preparing to breach.

Humpback whales swim horizontally until they reach enough speed to leap out of the water (Whitehead 1985a). In contrast, sperm whales perform a shallow, V-shaped dive prior to the breach. During these dives the sperm whale dives to depths varying from 11 to 41 m, which is much less than half the 70-110 m depth range previously hypothesized (Whitehead, 2003).

The duration of the dives that preceded breaching events varied between 13 and 31 s, which was similar to the values obtained from surface observations (20 s intervals between consecutive breaches in Gordon 1987b; and 25-40 s in Waters and Whitehead 1990). We detected a tendency for subsequent breaches to be of decreasing duration (pm10_222a and pm10_222b), which is concordant with a decreased intensity in breaching (Gordon 1987b; Waters and Whitehead 1990) and with the predictable hypothesis that the animals get fatigued during a sequence of breaching events (Whitehead 1985b).

Within a dive before breaching, descents were always longer than ascents, which is explained by the higher velocities and accelerations and also by the steeper angle of ascents relative to descents (Fig. IV.4). Several studies have suggested that sperm whales may ascend vertically before breaching (Beale 1839; Gaskin 1964; Waters and Whitehead 1990). From our data we can add more detail into their underwater movements: they frequently roll from one side to the other, move more slowly and consequently take more time descending, and ascend faster and more vertically to finally breach when crossing the surface.

According to Waters and Whitehead (1990), the splash onto the water is usually done with the same side of the body. Pm10_222a entered the water with its left side in 3 out of 4 breaches. Pm10_222b entered the water with its left side in 2 out of 3 breaches. Although we cannot exclude the possibility that individual whales show a preference for falling on the water surface on any given side, our small dataset suggests that during the same breaching bout sperm whales switch sides.

Similarly to lunge feeding events (Simon et al. 2012; Goldbogen et al. 2013), breaches seem to need powerful underwater movements. Our study supports this hypothesis indicating that whales increased vertical acceleration while ascending to breach. Although these observations came from only two individuals, we found a pattern for increased ascent acceleration between 3 and 6 s before breaching (Table IV.III). Additionally, the MSA also increased in the final part of ascents which may

be explained by fast acceleration (as in Johnson et al. 2004). Humpback whales reach a maximum speed of 3-4 ms^{-1} during lunges by performing three strong fluke strokes. They finish the lunges with 1-1.5 ms^{-1} and continue gliding, keeping the speed previously obtained and not requiring additional thrust to keep forward motion (Simon et al. 2012). The decrease in speed of these lunges is due to the transfer of momentum to the engulfed water mass. The number of fluke strokes performed by breaching sperm whales during ascents is null or only a few. The mechanics of breaching sperm whales can be explained by drawing a parallel to humpback whale lunge behaviour: sperm whale ascents prior breaching are performed mainly by gliding; their ascent velocity and acceleration appear to be a product of the velocity and acceleration attained during descent (by stroke and glide) and of their natural buoyancy, by carrying air from the surface (Miller et al. 2004b).

Blue whales (*Balaenoptera musculus*) perform 360° manoeuvres to reorient their body in lunge feeding events, while in transit between lunges and during the ascent and descent phases of a dive (Goldbogen et al. 2013). In our study, we detected underwater rotations of 360° (pm10_222a) and sometimes 180° (pm10_222b) during descents and, less frequently, during the last part of ascents (pm10_211b, pm10_222a). Rotational movements of baleen whales seem to be related with optimization of their field of view and also repositioning of their jaws to engulf prey. Another rotational movement example is that of spinner dolphins which start generating their spins still underwater with a corkscrewing motion (Fish et al. 2006). For sperm whales, rotational movements before breaching may be related with an increase of velocity and acceleration necessary for subsequent leap out of the water.

Whitehead (1985a, 2003) estimated that, when crossing the water surface, a sperm whale would reach a maximum velocity of 22 kmh^{-1} (i.e. 6.1 ms^{-1}). In this study, maximum absolute vertical velocities during ascent varied from 2.6 to 5.3 ms^{-1}, slightly lower than previously reported. This may be explained by a combination of factors. First, in this study we considered only the vertical component of velocity, whereas in the former study the velocity was calculated with consecutive photos of their breach. Second, animals likely attain higher speed when most of their body is in the air which has lower density than water and, consequently, exerts lower drag forces. Examples of the change water-air are the spins of spinner dolphins (*Stenella longirostris*) that increase their speed by as much as a factor of three (Fish et al. 2006).

According to the energy expenditure method developed for humpback whale breaches (Whitehead 1985a), the apparent energy that a sperm whale with 13.5 tons spends to breach is about 617 kcal (Whitehead 2003). In the present study we were not able to record the angle at which sperm whales crossed the surface, thus we could not use Whitehead's formula. Based on a rough linear relation

assumption between weight and energy spent in breaching, pm10_211b would need 398 kcal, pm10_222a 336 kcal and pm10_222b 362 kcal for each breach. Sperm whales studied in the Azores mainly feed on squids of families Octopoteuthidae and Histioteuthidae (estimated mass consumption of 39.8% and 32.7%; Clarke et al. 1993). Thus, the breaching sperm whales would need to consume per day 88-104 kg of squids of the family Octopoteuthidae and 72-85 kg of Histioteuthidae squids per day. Additionally, *Histioteuthis bonnellii* was the most frequently found species (about 80%) and the only species of family Histioteuthidae found in their stomachs (Clarke et al. 1993). The energy content of *Histioteuthis* sp. is about 2.65 kJ/g (Clarke et al 1985) which is approximately 0.63 kcal/g. Consequently, sperm whales spend about 0.74% of their daily consumption of *Histioteuthis* sp. performing each breach.

Whitehead (2003) mentioned that breaching is not well correlated with, but apparently occurs more frequently during socializing. Here we never recorded breaches between foraging dives and the majority of breaches happened after the whale spent some time resting at or near the surface. In agreement with previous studies (Waters and Whitehead 1990), breaching events were recorded during different times of the day. However, if breaches occur more frequently within social context and after resting periods, a bigger sample size may reveal a clearer relationship between breaches and the time of the day.

In the present study, we add information to the sperm whale breaching behaviour by exploring their underwater movements just before leaping out of the water. In summary, sperm whales are able to breach with shallow preparation dives where they descend by fluking once to six times and frequently roll to both sides. During ascents their movement is performed mostly by gliding, taking advantage from buoyancy and speed gained during descents, in a steeper trajectory that has increasing acceleration and ends with a spectacular leap out of the water surface.

Even though the function of breaches is not yet fully understood, one of the most accepted functions is communication. The tagged animals were members of social units and, therefore, are known to communicate “vocally” (e.g. with codas), by touch or with other sound emissions (Bradbury and Vehrencamp 1998; Perrin et al. 2009). What about mature male sperm whales, which are known to have a weak social organization and almost never breach, how do they communicate? In the following chapter we will focus on slow clicks that are produced by male sperm whales and may be related with communication purposes.

Chapter V

The function of male sperm whale slow clicks in a high latitude habitat: Communication, echolocation or prey debilitation?

Sperm whales produce different click types for echolocation and communication. Usual clicks and buzzes appear to be used primarily in foraging while codas are thought to function in social communication. The function of slow clicks is less clear, but they appear to be produced by males at higher latitudes, where they primarily forage solitarily, and on the breeding grounds, where they roam between groups of females. Here the behavioural context in which these vocalizations are produced and the function they may serve was investigated. Ninety-nine hours of acoustic and diving data were analysed from sound recording tags on 6 male sperm whales in northern Norway. The 755 slow clicks detected were produced by tagged animals at the surface (52%), ascending from a dive (37%) and during the bottom phase (11%), but never during the descent. Slow clicks were not associated with the production of buzzes, other echolocation clicks or fast manoeuvring that would indicate foraging. Some slow clicks were emitted in seemingly repetitive temporal patterns supporting the hypothesis that the function for slow clicks on the feeding grounds is long range communication between males, possibly relaying information about individual identity or behavioural states.

Published as:
The function of male sperm whale slow clicks in a high latitude habitat: Communication, echolocation or prey debilitation?
Cláudia Oliveira, Magnus Wahlberg, Mark Johnson, Patrick J. O. Miller and Peter T. Madsen
J. Acoust. Soc. Am. 133, 3135 (2013), http://dx.doi.org/10.1121/1.4795798

Introduction

The sperm whale (*Physeter macrocephalus*), the largest of the toothed whales, lives in matrifocal social systems where females, juveniles and calves are found in social units limited to temperate and tropical waters. The males leave these social units at 10-20 years of age and migrate to higher latitudes to target food resources in colder waters, returning to warmer waters in search of females when they are physically and sexually mature (Best et al. 1984; Rice 1989). As the males get older they seem to be less social than the family units, whereas the bachelor groups, with younger males, apparently move with some degree of cohesion also at higher latitudes (Lettevall et al. 2002). The cohesive distribution of male sperm whales at high latitudes may arise from patchy food resources or from a combination of reduced predation risk, benefits of practicing jousting with other males and cooperative behaviour against other males (Connor 2000).

The sperm whale has a hypertrophied nasal complex (up to 1/3 of the body length) which is used to produce clicks for echolocation and communication (Norris and Harvey 1972; Møhl et al. 2003; Madsen et al. 2003; Zimmer et al. 2005a). Sperm whales are recognized to produce at least four types of clicks termed usual clicks, buzzes (also called 'creaks'), codas, and so-called slow clicks (or clangs). All of these signals are sharp-onset broadband impulses with their main energy centred between 2 and 25 kHz (Madsen et al. 2002a, b). Although clicks comprise the large majority of their phonations, sperm whales also produce occasional tonal sounds described as trumpets, squeals, and pips (Goold 1999; Whitehead 2003; Teloni 2005).

The high directionality and source levels of usual clicks (Møhl et al. 2000) and their change in ICIs with depth (Madsen et al. 2002b; Thode et al. 2002) strongly support the contention advanced by Norris and Harvey (1972) that these signals are used for long range echolocation (Madsen et al. 2002b). Buzzes are rapid series of clicks with very short ICIs (15–100 ms) that occur in a foraging context and are associated with rapid manoeuvring in prey capture attempts (Jaquet et al. 2001; Miller et al. 2004a). Codas on the other hand are stereotyped patterns of 3 to 20 clicks that may last 0.2–5 s (Watkins and Schevill 1977b). They are communicated between individuals within social units, probably to maintain social cohesion (Whitehead and Weilgart 1991; Weilgart and Whitehead 1993) with regional variation in coda types (Weilgart and Whitehead 1997; Rendell and Whitehead 2005).

While the function of usual clicks, buzzes, and codas is somewhat understood, the use of slow clicks is still largely unresolved. Slow clicks, which are readily distinguished by their long ICI and distinctive metallic sound, are seemingly only produced by males (Mullins et al. 1988; Weilgart and Whitehead 1988; Jaquet et al. 2001; Madsen et al. 2002b). The signals have a low frequency emphasis around 2-

4 kHz, a longer duration, and they are probably more omnidirectional than usual clicks (Madsen et al. 2002b). In previous studies, slow clicks have been detected in the breeding areas at lower latitudes (Gordon 1987b), as well as at higher latitudes (Weilgart and Whitehead 1988; Douglas et al. 2005) where only adult males are present (Best 1979). Jaquet et al. (2001) reported that slow clicks (called surface clicks) from male sperm whales were produced mainly in the final part of the ascent phase of foraging dives, apparently at depths between 180 and 360 m.

The biological function of slow clicks has been attributed to either echolocation (Gordon 1987b; Mullins et al. 1988; Goold 1999; Tyack and Clark 2000; Jaquet et al. 2001) or communication (Gordon 1987b; Weilgart and Whitehead 1988; Mullins et al. 1988; Whitehead 1993; Tyack and Clark 2000; Madsen et al. 2002b; Barlow and Taylor 2005). Proposed communication functions include practicing of courtship displays at higher latitudes before migrating to the breeding grounds (Mullins et al. 1988), where they may be used in vocal displays used in competition for females (Tyack and Clark 2000; Weilgart and Whitehead 1988). A related or possibly the same type of sperm whale signal referred to as a 'gunshot' has been proposed to be used for prey debilitation (Gordon 1987b). In addition, Norris and Møhl (1983) and Cranford (1999) hypothesized that intense low frequency clicks from sperm whales might be used to debilitate prey to facilitate capture suggesting a possible foraging function for slow clicks. All of these hypothetical functions for slow clicks have been inferred from far-field acoustic recordings without any additional behavioural information. From the existing data it is therefore difficult to test which, if any, of these hypotheses reflects the true function of slow clicks.

To establish the behavioural context of slow click production, we here employed archival, multisensor tags (Dtags; Johnson and Tyack 2003) to record the sound production and movements of male sperm whales foraging in a high latitude habitat. We use these data to test the following predictions: if slow clicks are used for communication, they are expected to be audible at ranges commensurate with the separation distance of individuals. Alternatively, if the main function of slow clicks is to echolocate the sea floor or other bathymetric features, we expect them to be emitted mainly during the descent and bottom phases of the dives, so the whale can orient itself in relation to the bathymetry while searching for food. If slow clicks are used for prey debilitation, we predict them to be extremely powerful and to be associated with foraging phases of dives and with foraging indicators such as buzzes. We find that the combination of diving and acoustic data collected in this study indicates that slow clicks are likely used for long range acoustic communication and not for orientation or foraging.

Methods

Study area

Fieldwork was conducted in July 2005 and May 2010 in or adjacent to the Andøya underwater canyon off Andenes, Northern Norway (69°25'N, 15°45'E). Adult and sub-adult male sperm whales that forage in this area are usually found several kilometres from each other with little or no apparent social interactions between them, except for rare occasions where two whales may rest for a period close together at the surface (Lettevall et al. 2002).

Tagging

Digital acoustic recording tags (Dtags) were attached to the dorsal surface of six whales with suction cups. Dtags have two hydrophones spaced 20 mm apart along with sensors for depth, temperature and orientation (3-axis accelerometers and magnetometers; Johnson and Tyack 2003). The two hydrophones were sampled at 96 kHz each using 16-bit sigma-delta analog-to-digital converters and stored as a stereo wav-format file. The inertial sensors were sampled using sigma-delta conversion at 50 Hz with 16-bit resolution, and subsequently decimated to 5 Hz for analysis. Acoustic data were recorded until 99% of the memory capacity was consumed, after which time only non-acoustic sensor data were recorded.

Sperm whales were approached at less than 3 knots from behind with a 7 m rigid-hulled inflatable boat. The tags were placed on the animal using a 15 m cantilevered carbon fibre pole mounted on the boat. The apparent responses of the sperm whales were minor (e.g. rolling and moving slowly away from the tag-boat). Once the suction cups detached from the whale, the tag floated to the surface and was recovered via tracking of its VHF radio beacon from a sailing boat (2005) or a 29 m research vessel (2010).

Data analysis

Both acoustic and non-acoustic sensor data were used in the analyses. Sound files were examined using custom spectrogram display functions in Matlab 7.0 (Mathworks, Inc.). The orientation of the tag on the animal was corrected using the method described in Miller et al. (2004b). This resulted in a time series representing the orientation of the whale in terms of the Euler angles pitch, roll and heading (Johnson and Tyack 2003).

Sperm whales were named with a sequence that includes the year, Julian day and order of tagging (e.g. sw05_199a means that the sperm whale was tagged in 2005 on the 199th Julian day, and 'a' means that it was the first tagged individual that day).

Audio files from all the tagged whales were examined by listening and by visual inspection of spectrograms to identify slow clicks, usual clicks and buzzes. Slow clicks were distinguished from usual clicks by their ICI (minimum value was 2.2 s) and their metallic and reverberant timbre (see Fig. V.1) as described by Gordon (1987b) and Jaquet et al. (2001). Slow clicks produced by the tagged whale were distinguished from those of other whales in the vicinity by comparing their angle-of-arrival on the two tag hydrophones with that of usual clicks ascribed to the tagged whale. Based on this, clicks were ascribed to the tagged whale, from another whale, or to be of uncertain provenance. Only the clicks unequivocally attributed to the tagged whale were used in further analyses. In this study, it was not possible to compare acoustic individual differences (e.g. received levels, decay rate, root-mean-square bandwidth, etc.) because the slow clicks from the tagged whale were consistently clipped in the recordings.

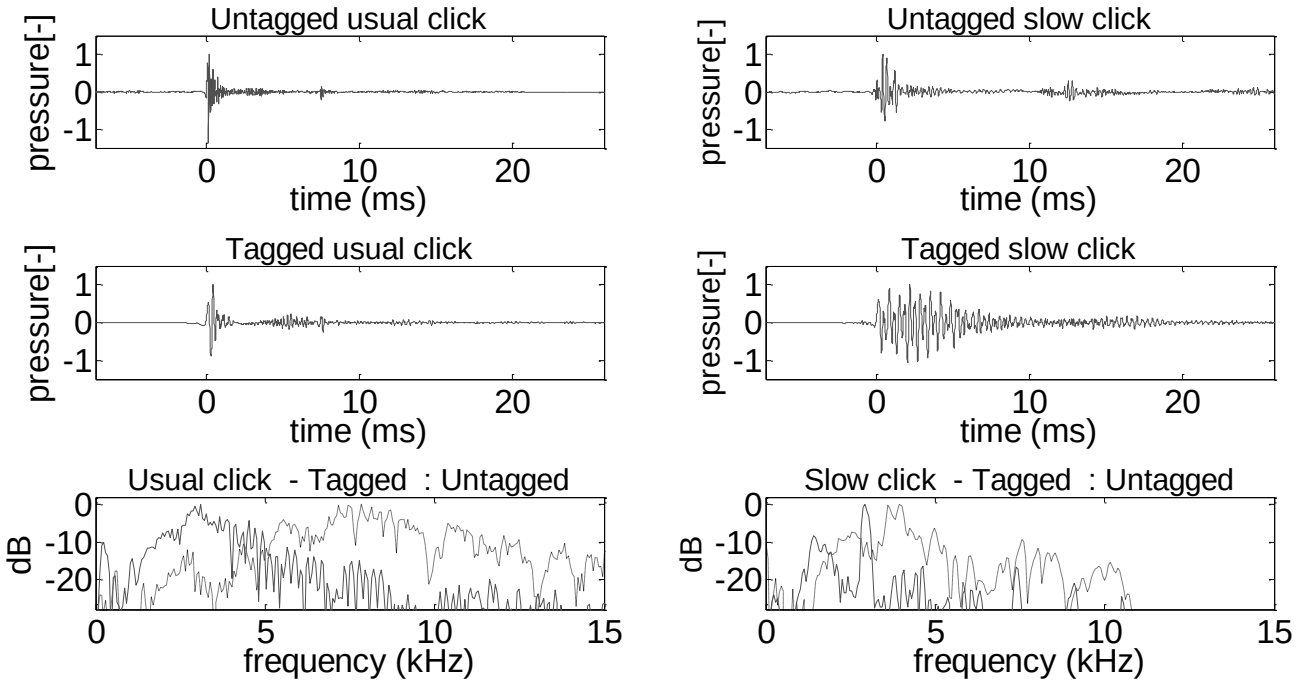


Figure V. 1 - Waveforms and spectra of untagged and tagged usual and slow clicks recorded from Dtags on sperm whales off Northern Norway (FFT size 1700, sampling rate 96 kHz, Hanning window).

Slow clicks were divided into bouts using a log survival plot of slow click ICIs pooled from all animals (Slater and Lester 1982; Sibly et al. 1990). This analysis gave an upper limit for bout duration of 24.9 s (which is consistent with the sequences of 24 s found in Jaquet et al. 2001). The log survival

regression equation was: Log_e (frequency of ICIs) = $2.5e^{-0.063 \cdot ICI\ class}$ (r^2=0.84; p<0.0001). The proportion of the duration of slow click periods was calculated as the percentage of total time of the slow click bouts in relation to the length of the whole recorded file.

Tagged whales spent their time either foraging at depth or resting at or near the sea surface (Miller et al. 2008). Surface time was defined as the interval between dives in which the whale dove deeper than 20 m. Following Miller et al. (2004a), we defined descents as extending from when the whale left the surface until the pitch of the whale exceeded 0 degrees (a positive pitch means that the animal is oriented upwards). Likewise, ascents started when the pitch was continuously greater than 0 degrees. A few brief episodes (duration up to 11 s) of downward pitch angle during ascents were ignored. The ascent phase was considered to end when the whale reached the surface. The period between descent and ascent was called the bottom phase and the foraging phase was defined as the period between the first and last buzzes (Watwood et al. 2006).

In foraging beaked whales, according to Johnson et al. (2004), it is often possible to detect an increase in the minimum specific acceleration (MSA) in the end of buzzes, indicating fast acceleration associated with prey capture. Consistent with that, Miller et al. (2004a) found spike changes in the roll and pointing angle in the end of buzzes produced by sperm whales. In our study, the 3-axis accelerometer dataset was filtered to compare the MSA in the end of the buzzes with the MSA during slow clicks. The root-mean-square (rms) of the MSA within -5 to 5 s relative the end of buzz and beginning of slow click, respectively, was compared with two control periods of -40 to -30 s and 30 to 40 s relative to the end of the buzz/beginning of the slow click. As this analysis computed 12 ANOVA tables, we adjusted the significant p-value to 0.05/12 or 0.004 (a so-called Bonferroni correction; Legendre and Legendre 1998).

The sound velocity profile in the study areas were calculated from CTD (ValePort MiniCTD, Serial Number 32956, Calibration Number 24319) measurements to a maximum depth of 470 m. The CTD data were collected within 2 days of the tag deployments in 2010 and in the same general location in the Andenes canyon.

Results

Tags were attached to six sperm whales in 2005 and 2010, yielding a total of 98.8 hours of recordings. A single animal was tagged each day except on the 18th of July 2005, when three whales

were tagged and 11.6 hours of simultaneous recordings were collected (Table V.I). The three whales were tagged with the following distances from each other: 3.4 km (sw05_199a to sw05_199b), 2.5 km (sw05_199a to sw05_199c), and 4.9 km (sw05_199b to sw05_199c).

All six whales produced usual clicks, buzzes and slow clicks. The usual clicks and buzzes indicate that all the animals were involved in foraging during the major part of the tag recordings. Foraging behaviour of the whales in the 2005 dataset has been reported in detail by Teloni et al. (2008). Clicks from other sperm whales in the area were also frequently audible in the recordings. The diving and foraging behaviour of the whales was more diverse than that reported for female sperm whales (Watwood et al. 2006), ranging from short, shallow dives to more typical long deep dives (Table V.I and Figure V.2; see also Teloni et al. 2008).

Table V. I – Local time of tag deployment, total time of recording (hours:minutes), number of dives, maximum depth and dive duration (mean ± 1 standard deviation), of the six tagged sperm whales.

				Maximum depth (m)		
Whale	Deployment Time	Total time	No. of dives	Deepest dive	Shallowest dive	Dive duration (min)
sw05_196a	14:44	21:21	32	537	22	28 ± 9
sw05_199a	13:06	18:05	28	1602	48	31 ± 12
sw05_199b	14:43	13:50	17	1862	143	34 ± 14
sw05_199c	16:57	13:24	14	1838	20	30 ± 15
sw10_147a	13:03	15:53	26	684	34	25 ± 7
sw10_149a	06:35	16:12	27	1122	141	27 ± 8
Total		98:45	144			

The whales emitted slow clicks in the ascent (37%), bottom (11%) and surface (52%) phases of their dive cycles (Table V.I, Fig. V.2 and Figs. V.3a and V.3b). Although a total of 755 slow clicks were recorded, the whales spent only an average of 1% of their time producing bouts of slow clicks (Table V.II) compared to 61% producing usual clicks.

All slow clicks were emitted at depths <300 m (Fig. V.3a) with the majority (82%) occurring during ascent and surface phases. Only 11% of the slow clicks were emitted during the bottom phase and then predominantly in the second half of the bottom phase. No slow clicks were produced by tagged whales during the descent phase. Slow clicks were not produced during the bottom or foraging phase of deeper (>300 m) dives and only 26 slow clicks (produced by two whales) of 755 slow clicks were produced in the foraging phase, between the first and last buzz, of any dive (Fig. V.3b).

There was no apparent causal link between slow clicks and buzzes (Table V.III). The minimum interval between a slow click and the closest subsequent or previous buzz was 30 s, and the median

interval ranged between 194 s and 1496 s. Linear regressions were made to evaluate if there was any linear relationship between the number of buzzes and the number of slow clicks per dive for each of the tagged whales. Significant negative linear regressions were found for sw05_199a, sw05_199b and sw10_149a, indicating that slow clicks production was higher when buzz production was lower in these samples. For the remaining sperm whales, the buzz-slow click data had non-significant negative linear regressions (Table V.III). There is thus no positive correlation and therefore no apparent functional link between buzz production and slow clicks.

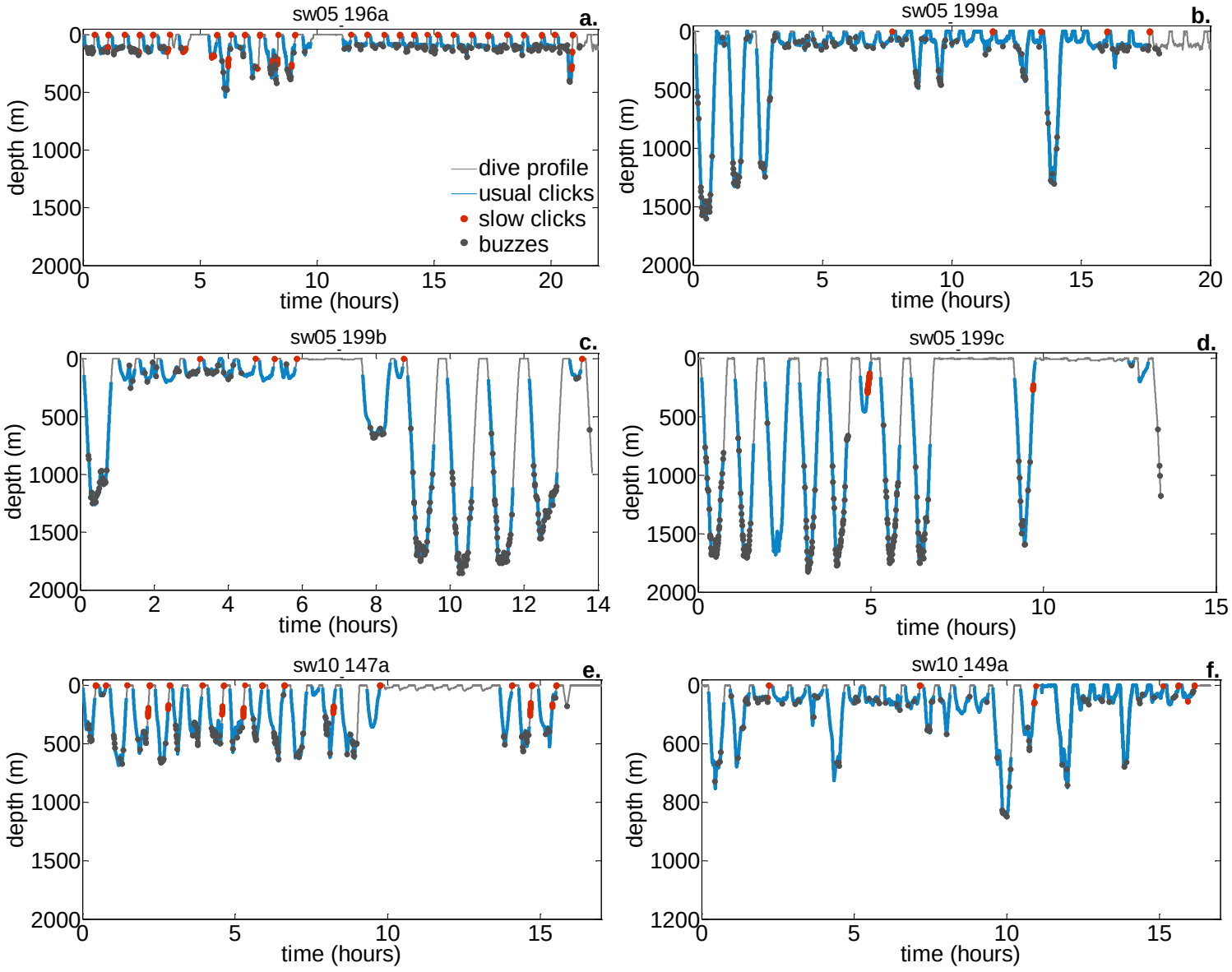


Figure V. 2 - Dive profiles, usual clicks, slow clicks and buzzes of the six tagged sperm whales off Northern Norway, **a.** sw05_196a, **b.** sw05_199a, **c.** sw05_199b, **d.** sw05_199c, **e.** sw10_147a, **f.** sw10_149a. In sw05_199c there is a gap in the sound file from time 2:00:46 to 2:29:36 due to an error in the original sound file.

Table V. II – Inter-click interval (ICI), total number of slow clicks from each whale (N), the number of slow click bouts, and the proportion of the duration of the slow click bouts and total recorded duration.

	ICI (s)					
Whale	Mean ±1 s.d.	Min	Max	N	No. slow click bouts	Proportion of slow click bouts (%)
sw05_196a	8.0 ± 4.5	2.5	24.1	394	43	3.17
sw05_199a	10.0 ± 5.2	6.1	20.6	33	5	0.31
sw05_199b	9.2 ± 4.4	6.6	20.0	36	6	0.41
sw05_199c	4.0 ± 2.2	2.2	9.0	61	3	0.47
sw10_147a	6.0 ± 2.6	3.3	16.8	191	21	1.77
sw10_149a	5.0 ± 2.5	2.2	12.4	40	6	0.27

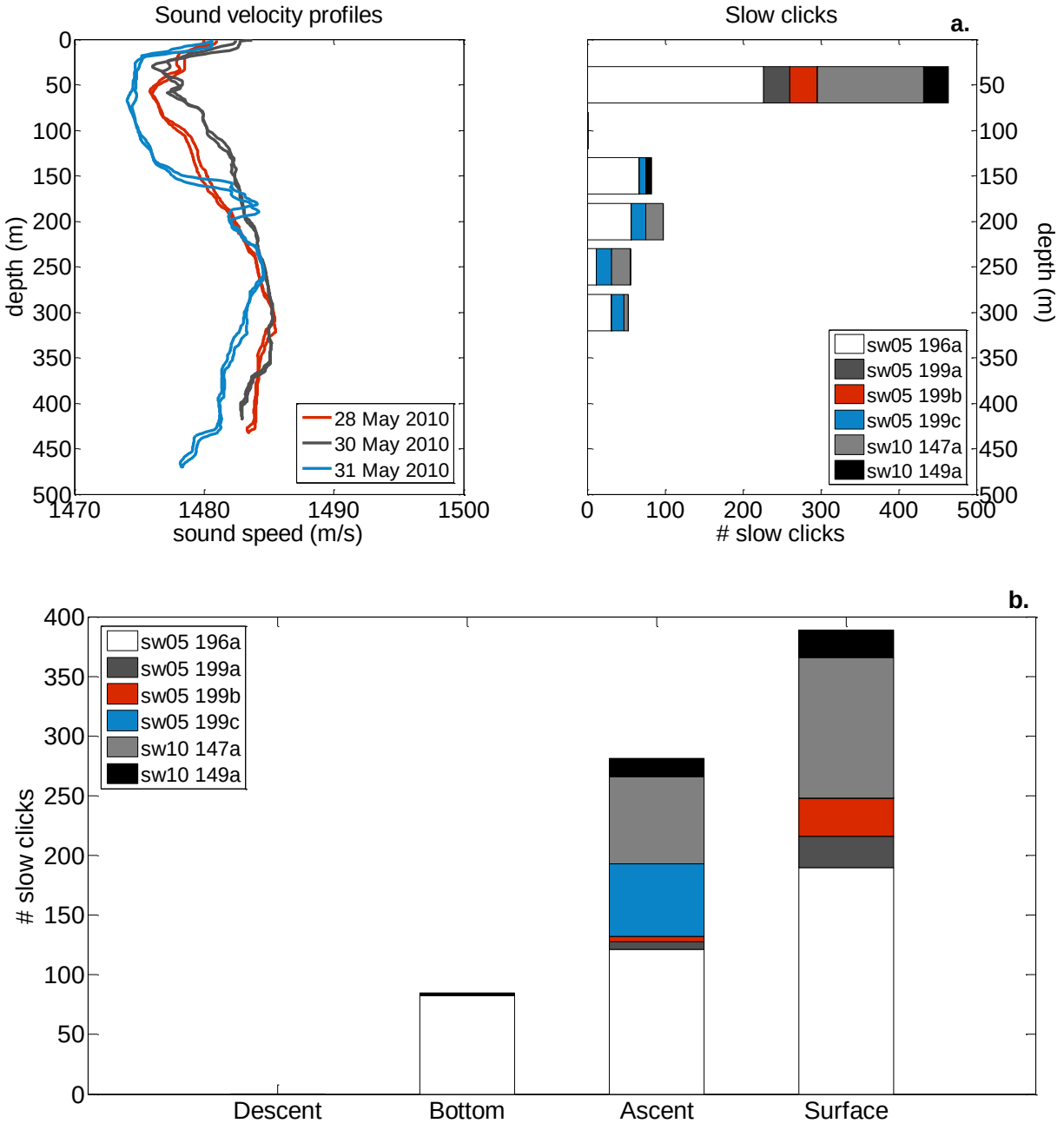


Figure V. 3 - **a.** Sound velocity profiles on the 28, 30 and 31 of May 2010 and depth distribution of slow clicks produced by six tagged sperm whales in 50 m depth bins, **b.** Slow click production in six tagged sperm whales as a function of the phase of the dive cycle.

Table V. III – Median, minimum and maximum interval from a slow click and a buzz recorded on the tagged sperm whales. The buzz may have preceded or followed the slow click, whichever appeared within the shortest time interval. N is the total number of slow clicks analysed from each whale. Nr periods: the number of distinct periods with buzzes and slow clicks counts. Slope L. reg.: slope of the linear regression equation for the number of slow clicks as a function of the number of buzzes, r^2: regression coefficient of determination, p: ANOVA probability that the regression slope is different than 0.

Whale	Median (s)	Min (s)	Max (s)	N	No. periods	Slope L. reg.	r^2	p
sw05_196a	359	29.9	1558	394	57	-0.55	0.05	0.10
sw05_199a	194	114	605	33	31	-0.14	0.17	0.02
sw05_199b	662	263	1416	36	23	-0.08	0.20	0.03
sw05_199c	1496	328	1652	61	11	-0.41	0.17	0.20
sw10_147a	445	98.6	2802	191	33	-0.20	0.04	0.29
sw10_149a	358	75.6	1067	40	30	-0.33	0.15	0.03
Total				755				

The average ICI in bouts of slow clicks produced by the 6 animals ranged from 4 s to 10 s (Table V.II). Although the ICI in bouts was often variable, some possible temporal patterns were visually observed in the ICI of slow clicks produced by sw05_199c (Fig. V.4a). However, there is insufficient data to establish definitively whether that slow clicks were produced in rhythmic patterns.

We detected one possible exchange of slow clicks between sw05_196a and an untagged sperm whale, with some overlap of the bouts produced by the two animals (Fig. V.4b). This occurred when sw05_196a was approaching the surface (2-20 m depth). Other slow clicks from the untagged whale may have been missed if they occurred when the tagged whale, and therefore the tag, was at the surface where splashing sounds may mask sounds from distant whales. Such sounds would likely be heard by the tagged whale, having its lower jaw well underwater when surfaced.

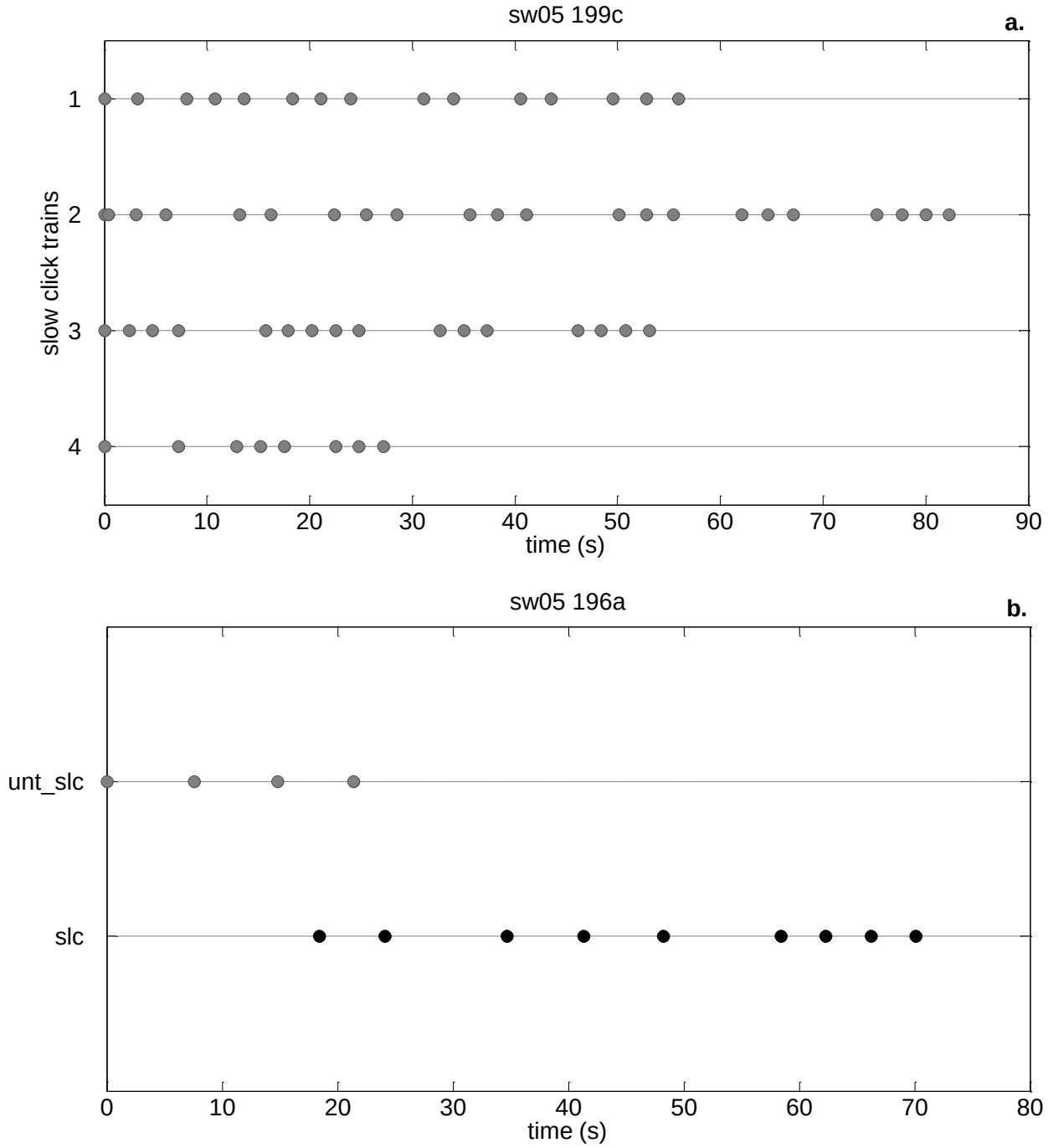


Figure V. 4 - **a.** Example of slow clicks produced in regular temporal patterns by sw05_199c. **b.** Example of a possible slow click exchange from the tagged sw05_196a. Slow clicks from the tagged whale (slc) and an untagged whale (unt_slc) are displayed as a function of time (seconds).

One of the key sources of evidence relating buzzes with prey capture attempts in beaked and sperm whales is an increase in movement of tagged animals during buzzes compared to other similar-length intervals (Johnson et al. 2004; Miller et al. 2004a). This increase in movement is consistent with the last-second manoeuvring needed to acquire agile prey. Similar results were obtained for the MSA of buzzes recorded in the present study (Fig. V.5). Repeating the analysis with slow clicks

instead of buzzes, we found no clear peak in acceleration associated with slow clicks (Fig. V.5). There was a significant ($p<0.004$; corresponding to $p=0.05$ after Bonferroni correction; Legendre and Legendre 1998) increase in acceleration in the interval -5 s to 5 s from the end of the buzz compared to a chosen control period from 30 s to 40 s after the end of the buzz, except for sw05_199c with $p>0.5$ (Table V.IV). For slow clicks, there was no significant difference between the MSA during the chosen control period 30 s to 40 s after the beginning of the slow click and the interval from -5 s to 5 s relative to the time of the slow click, for 5 of the 6 whales (Table V.IV). There were significant changes in MSA during slow clicks when comparing to another chosen control period lasting from -40 s to -30 s relative the onset of the slow click (Table V.IV). This may however often be attributed to the change in the whales' position when it approaches the surface, as more than 61% of the slow clicks were produced between 50 m depth and the surface.

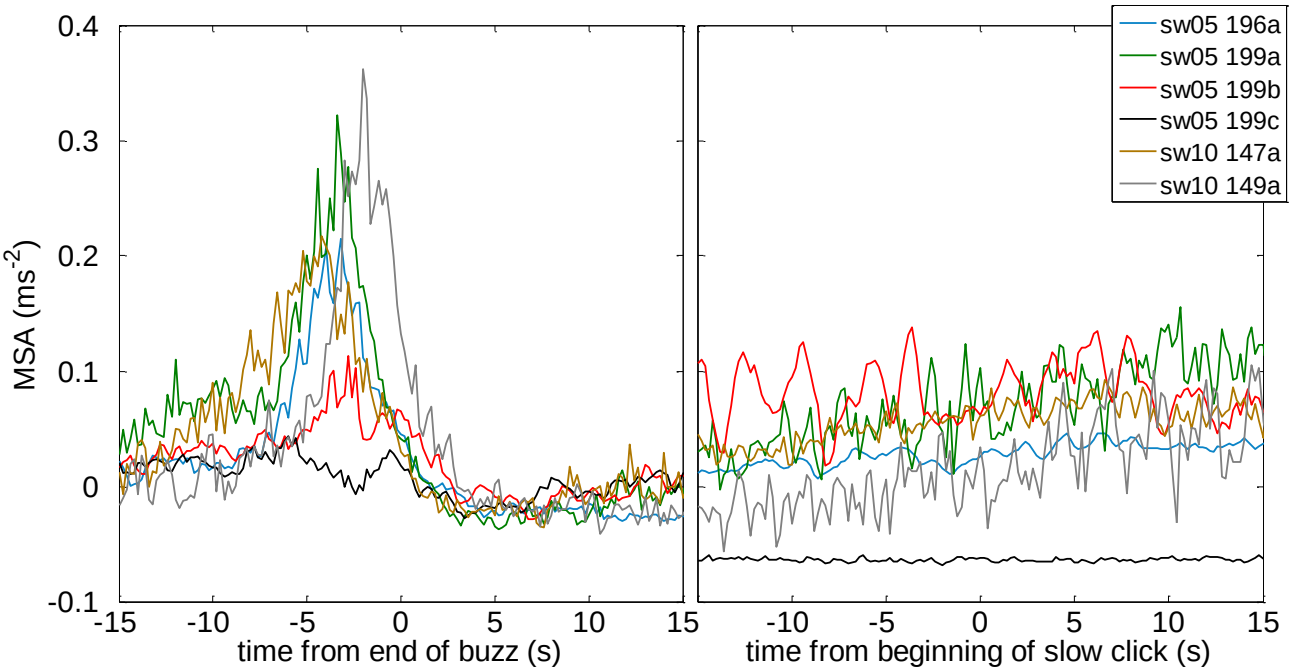


Figure V. 5 - Mean of the minimum specific acceleration (MSA) relative the end of buzzes (left panel) and the start of slow clicks (right panel) of the 6 tagged whales. Buzzes and slow clicks numbers are, respectively: 169 and 394 for sw05_196a, 151 and 33 for sw05_199a, 201 and 36 for sw05_199b, 210 and 61 for sw05_199c, 142 and 191 for sw10_147a and 92 and 40 for sw10_149a.

Table V. IV – Results from ANOVA and Tukey's range tests for rms values of the minimum specific acceleration for two control groups and one test group, defined relative to the end of the buzz or the beginning of the slow click. Control groups C_1: -40 to -30 s, and C_2: 30 to 40 s; Test group T: -5 to 5 s. * indicates statistically significant p values (Bonferroni-corrected p<0.05 to p<0.004 from 12 tests; see Legendre and Legendre 1998).

		ANOVA		Tukey's range test, p		
Whale		$F_{df,df}$	p	C_1 vs. T	C_2 vs. T	C_1 vs. C_2
sw05_196a	buzz	$F_{2,504} = 173$	<0.001*	<0.001*	<0.001*	<0.01
	slow click	$F_{2,1179} = 46$	<0.001*	<0.001*	0.613	<0.001*
sw05_199a	buzz	$F_{2,450} = 39$	<0.001*	<0.001*	<0.001*	0.100
	slow click	$F_{2,96} = 48$	<0.001*	<0.001*	0.061	<0.001*
sw05_199b	buzz	$F_{2,600} = 37$	<0.001*	<0.001*	<0.001*	0.400
	slow click	$F_{2,105} = 20$	<0.001*	<0.001*	0.535	<0.001*
sw05_199c	buzz	$F_{2,626} = 0.5$	0.604	0.593	0.764	0.960
	slow click	$F_{2,180} = 5.5$	<0.01	0.023	0.900	<0.01
sw10_147a	buzz	$F_{2,421} = 23$	<0.001*	<0.001*	<0.001*	0.985
	slow click	$F_{2,570} = 44$	<0.001*	<0.001*	0.964	<0.001*
sw10_149a	buzz	$F_{2,270} = 106$	<0.001*	<0.001*	<0.001*	0.918
	slow click	$F_{2,117} = 30$	<0.001*	<0.001*	0.262	<0.001*

Discussion

All 6 whales tagged in this study produced occasional bouts of slow clicks resulting in an average rate of 7.6 slow clicks per hour. Thus, slow clicks represent a very small portion of the total vocal output of sperm whales but their production by apparently solitary males in Arctic feeding grounds nevertheless raises questions as to the possible function of these sounds. Possible functions suggested in the literature include communication, echolocation, orientation or prey debilitation – or a combination of several of these.

The distinctive metallic sound of slow clicks, whether recorded by a tag on the vocalizing animal or in the far-field, make these clicks easy to distinguish from usual clicks, and therefore few mis-classified clicks are likely to occur. It can be more challenging to determine if a click is produced by the tagged whale or a nearby conspecific. The angle-of-arrival of clicks at the tag is usually a strong indicator but this method breaks down when a vocalizing conspecific is directly in front or behind the tagged whale. However, very few (27 out of 782) clicks could not be conclusively allocated to either the tagged whale or another animal. These ambiguous vocalizations were excluded from the analyses but, even if the excluded clicks were actually produced by the tagged whales, they represent around 3% of the slow clicks and so would have little impact on our results.

If slow clicks are used for prey debilitation, we expect the signals to occur during the parts of the dives where the whales are involved in foraging. However, slow clicks were most prevalent in

normally otherwise silent dive phases, i.e., during ascents from foraging dives and at the surface. Critically, no slow clicks were produced by whales at depths >370 m in foraging dives even though 5 of 6 whales performed deep dives (Table V.III and Fig. V.2). Although some of the sperm whales were also foraging during shallow dives (Teloni et al. 2008), only 26 of 755 slow clicks were produced by tagged whales during the foraging phase of any dive. Thus, if slow clicks indeed signify prey debilitation attempts, their low production rate is difficult to reconcile with the number of prey it takes to meet the energy demands of a 40 to 60 ton predator (Lockyer 1981). The weak overlap of slow clicks with echolocation sounds does not eliminate the possibility that slow clicks are used primarily to debilitate prey that is hunted visually. This would be consistent with the typically shallow production depth of slow clicks. However, there are no indications that whales manoeuvre rapidly while producing slow clicks as is the case during foraging buzzes (Fig. V.5, Table V.IV, Miller et al. 2004a).

Further, the acoustic debilitation of prey would demand sound pulses of extremely high levels. Debilitation of potential sperm whale prey species using high intensity transient signals has not been achieved in the laboratory despite considerable efforts (Benoit-Bird et al. 2006) and it has proven difficult to affect the behaviour of some fish and squid species at all even with received sound pressure levels beyond 210 dB re 1 µPa (pp) (Wilson et al. 2007, Schack et al. 2008). Measurements made by Madsen et al. (2002b) indicate that slow clicks have source levels of 200 dB re µPa (pp), more than 30 dB lower than the source level of on-axis usual clicks. The lower frequency emphasis of slow clicks (Madsen et al. 2002b) suggests that they are also less directional than usual clicks, although little is known about the sound emission beam pattern of these sounds. Taken together, these considerations make it very unlikely that slow clicks are used for prey debilitation.

Whether or not slow clicks are used for echolocation is more difficult to test. The acoustical properties of slow clicks (i.e., their low frequency emphasis, probable low directionality, and their low and mostly irregular ICIs) are atypical for signals specifically evolved for biosonar in any echolocating animal whether bat or toothed whale. If slow clicks are used to echolocate prey, these phonations should be associated with the descent or foraging phase of dives (Miller et al. 2004a). We find weak negative correlations between the number of slow clicks and the number of buzzes in a dive (Table V.III and Fig. V.2) counter to the hypothesis that slow clicks function with echolocation-based foraging of individual prey.

If slow clicks are used for any form of echolocation, their frequency content (around 2 kHz peak frequency, Madsen et al. 2002b) suggests echolocation of large targets such as scattering layers, conspecifics or hydrographical and bathymetry features (Gordon 1987b; Weilgart and Whitehead

1988; Mullins et al. 1988; Whitehead 1993; Goold 1999). It is difficult to discount such a function, as the reverberation pattern produced by any signal provides information about the large scale composition of the environment. However, the predominance of slow clicks during the ascent phase of dives as well as near or at the surface is inconsistent with the idea that these sounds could help in locating prey layers or bathymetric features while foraging. Such information would presumably be most useful in the early part of foraging dives, where few if any slow clicks are produced, rather than in the final parts of the dive or at the surface.

Given that there is no strong support in the data for slow clicks being used for either prey debilitation or echolocation, the most plausible function is communication. The parts of the dives where slow clicks are most prevalent (ascent and surface phases) are also the parts where there is little or no production of usual clicks or buzzes (Teloni et al. 2008).These otherwise silent phases could therefore be appropriate to produce signals to communicate with conspecifics, as is the case for at least part of female sperm whale coda production (Whitehead and Weilgart 1991; Weilgart and Whitehead 1993). The finding of a negative correlation between slow click and buzz production is consistent with a communication function that largely takes place in time not allocated to foraging, i.e., less time may be available for communication in more successful foraging dives.

If slow clicks do serve for communication, the question arises as to what messages would male sperm whales wish to communicate to other males? The actual function of these vocalizations may depend on whether they are used on the feeding grounds (as the ones studied here) or on the breeding grounds.

Despite little evident social interactions at high latitudes, slow clicks perhaps serve to maintain group cohesion (Whitehead et al. 1992). A possible exchange of slow clicks (Fig. V.4b) and potential temporal patterning in slow click bouts (Fig. V.4a) observed here provide intriguing hints of a complex social function of slow communication. However, the fact that only one such exchange was found from a total of 755 slow clicks in this study indicates that slow click production at high latitudes is not necessarily induced by hearing other slow-clicking animals. Thus, a chorusing function of the slow clicks is unlikely.

Killer whales (*Orcinus orca*) are known to sometimes attack groups of sperm whales, albeit usually groups of females and calves, and coordinated social responses to predation have been observed (Arnbom 1987; Pitman et al. 2001). Slow clicks were emitted frequently by a bachelor group of sperm whales trapped in the Scapa Flow (Goold 1999) which may indicate a function of cohesion calls during danger or stress. Social cohesion may also be important during bachelor group migrations in which individuals are known to travel together towards higher latitudes (Best et al.

1984; Rice 1989; Lettevall et al. 2002). Aggressive signalling is used by other species of toothed whales, as well as other marine animals. Clausen et al. (2010) report acoustic aggressive behaviour between captive female and male harbour porpoises (*Phocoena phocoena*) during competition for fish, involving up-sweeping high repetition rate click trains. Slow clicks may serve analogous functions in competitively foraging sperm whales. The idea that slow clicks are used to maintain a foraging space free from other males fits well with the fact that slow clicks are produced during ascent periods, after presumably successful foraging events.

Irrespective of their social function it has previously been speculated that slow clicks convey information on the presence, location, identity, size and age of the clicking whale (Gordon 1987b; Weilgart and Whitehead 1988; Tyack and Clark 2000; Madsen et al. 2002b; Whitehead 2003). While presence and location are inevitably revealed by any phonation, the other information could conceivably be encoded in the waveform or in the ICI of the clicks. In this study, clicks produced by tagged whales were consistently clipped in the recordings and therefore not available for spectral analysis, while clicks from untagged whales could not be allocated to individuals making encoding via spectral features untestable. The inter-pulse-intervals within sperm whale clicks are known to provide information about the size, and therefore age, of the vocalizer (Gordon 1991a; Rhinelander and Dawson 2004). On the breeding grounds, this could be important information when reproductive competitors are present, or when males try to get the attention of females (Gordon 1987b; Weilgart and Whitehead 1988; Tyack and Clark 2000; Madsen et al. 2002b; Whitehead 2003). However, the multi-pulse structure often seen in usual and coda clicks is rarely, if ever, seen in slow clicks (Madsen et al. 2002b). The possible temporal patterns of slow clicks within bouts (Fig. V.4a) detected in this study may be speculated to reflect some degree of individual identity or characteristics although Jaquet et al. (2001) argue that slow click ICIs vary widely within each individual, and are therefore unlikely to identify individuals. If information is indeed relayed via the ICI patterns over many clicks, it is an example of a very slow way of communicating, but one that offers a potentially large active space both because of the high source levels of sperm whale clicks and because ICIs are more resilient to distortion from propagation that are within click information.
Madsen et al. (2002b) estimated that other whales may be able to hear slow clicks at ranges up to 60 km. Such an estimate is critically dependent on the sound velocity profile, which will cause the sound paths to refract over long ranges. Depending on the depth of the caller and the receiver, the actual detection distance may therefore be much shorter or longer than when assuming spherical spreading conditions. In figure V.3a, we have plotted the sound velocity profiles taken within a maximum of two days from the tag deployments to evaluate if the whales produce slow clicks at depths with the lowest sound speeds to maximize their active space. Although the sound speed minimum is shallow as expected for cold high latitude waters, many slow clicks are produced even

shallower, at or near the surface (Figure V.3b), where a downwards refracting sound velocity profile will preclude long range communication to other surfaced animals. However, the active space of slow clicks will, even when produced by surfaced callers, still be probably many kilometres when addressing listeners at depths closer to the sound speed channel.

Among the previously hypothesized functions of slow clicks, prey debilitation can be ruled out due to a lack of any relationship between slow click production and buzzes, and also because there is no indication of rapid manoeuvres while producing slow clicks. Likewise, even though echoes from slow clicks may provide bathymetric information, the context in which they are produced (mainly at the surface and during ascents from foraging dives) is inconsistent with a primary echolocation function. The signal structure reported in earlier studies as well as the behavioural context of the signals as described here all point towards a communicative function for slow clicks. The click interval and conceivably the waveform of slow clicks could carry individual information, making these sounds a possible long-range communication signal provided that both sender and receiver are at depths at which such propagation is supported. The fact that slow clicks are produced both among foraging males in the Arctic as well as by males encountering females on the breeding grounds in warmer waters indicate that the communicative function of slow clicks may vary depending on the behavioural context in which they are produced.

Chapter VI

General discussion

The importance of sound to sperm whales

Cetaceans need to communicate while socializing, reproducing and bearing their offspring, either acoustically, visually or by touch (Perrin et al. 2009). Inhabiting an environment where visual range is limited, hearing is the major sense to cetaceans. Toothed whales produce sounds not only to communicate but also to search and capture prey (e.g. Johnson et al 2006; Aguilar Soto et al. 2008).

Sperm whales forage by echolocation, that is emitting clicks, receiving and interpreting the echoes from prey items and other structures. They make U-shaped dives to a depth of 400-1900 m and spend about 80% of their lives submerged (Amano and Yoshioka, 2003; Miller et al. 2004a). Their social units seem to benefit from living with conspecifics, either by reducing their predation risk, using babysitters in the care of young, or increasing their foraging success (Whitehead 2003). Sperm whales are known to stop "vocalizing" or be mostly silent when they sense the presence of predator killer whales (*Orcinus orca*; Brennan and Rodriguez 1994; Whitehead 2003). Calves need to recognize their mothers, allomothers or babysitters, while they are not yet able to dive at the same depths as juveniles and adults, to obtain protection and nursing (Best et al. 1984; Gordon 1987a; Whitehead 1996). Therefore, individual and group recognition is of great importance to sperm whales. In other species of whales, such as cooperatively feeding delphinids or humpback whales, there is an increase in foraging success (Hain et al. 1982; Pitman et al. 2001; Benoit-Bird and Au 2009). Sperm whales on the other hand do not seem to improve their foraging abilities by cooperatively feed. While foraging, they seem to avoid interfering with each other, or perhaps they eavesdrop for their conspecifics' acoustic emissions in search of clues for good foraging locations (Whitehead 1989). Male sperm whales in higher latitude foraging grounds apparently live more solitary lives (Whitehead et al. 1992; Whitehead 2003). Despite this, they occasionally seek the company of conspecifics (Letteval et al. 2002) probably by keeping acoustic contact with each other. Moreover, male sperm whales exhibit cohesive behaviour under stressful conditions, like in the Scapa Flow (Orkney Islands) where they were trapped and emitted a remarkable wide repertoire of "vocalizations" (Goold 1999). On the breeding grounds male sperm whales apparently compete for females through occasional fights (Clarke and Paliza 1988; Whitehead 2003) and presumably by emitting slow clicks that seem to encode individual information (Tyack and Clark 2000; Weilgart and Whitehead 1988; Whitehead 1993).

To communicate, sperm whales use both vision and touch, but by far the most important sense is hearing. The emission of clicks and other sounds, the sudden changes to silent or the production of "non-vocal" sounds such as breaches (Weilgart and Whitehead 1993; Madsen et al. 2002a;

Whitehead 2002, 2003; Oliveira et al. 2013) are examples of how important sound is for both social units and mature males, in foraging, reproducing, maternal care, survival and socializing contexts.

Behavioural ecology of the sperm whale in the North Atlantic Ocean: major findings

The main goal of this study was to contribute to the overall knowledge of the sperm whales' behaviour, focusing on gaps of information both at regional and global levels. The use of on-animal tags allowed us to describe with great detail several aspects of their foraging and resting behaviours, individual coda communication, underwater movements before breaching and the function and context of slow clicks production among mature males in high latitudes.

In the North Atlantic Ocean, sperm whales are born in lower latitudes (such as in the Azores archipelago), where they receive care from their mothers and other social unit members (Best et al. 1984; Whitehead 2003). As they grow and gradually get weaned, they start exploring other food supplies similarly to juveniles and adults (Best 1979). The Azores seem to constitute an important foraging ground for North Atlantic sperm whales but very little was known about their foraging strategies in the area. In Chapter II of this thesis, we showed that in the Azores sperm whales forage at 700-1200 m depth and return to the surface after 42±7 min to breathe and recover. They spend about 10 min at the surface before diving again. Their prey seems to be distributed in relation to the seafloor. While underwater, they produce usual clicks to search for prey and, when they are at a closer range, they start emitting buzzes to zoom on the prey and finally capture it (Miller et al. 2004a; Chapter II). At the Azores, they emit about 14±6 buzzes per dive and they spend about 34±5 min and 25±6 min in search and foraging phases, respectively (Chapter II). We also showed that foraging periods were often interspersed with socializing and resting activities, as described on other areas (Whitehead and Weilgart 1991; Watkins et al. 1999).

While socializing, sperm whales exchange coda clicks that apparently are related with the maintenance of group cohesion (Weilgart and Whitehead 1993). During these periods it is important to be able to recognize individuals and groups. Group identification, or to be more accurate, clan identification has been described as being performed through the use of different coda types (repertoire; Rendell and Whitehead 2003a). On the other hand, individual identification was suggested to occur due to individual temporal patterns of coda clicks of one coda type (5Reg; Antunes et al. 2011). Yet, our study provides evidence that individual identification is achieved by temporal patterns of coda clicks of more than one coda type, spectral features of coda clicks and the

size of the phonating animal (Chapter III). Thus, the function of coda clicks appears to be much more than unit or clan identification (Weilgart and Whitehead 1997; Rendell and Whitehead 2003a) and it is clear that they encode individual information, which is extremely important among these highly social animals. Besides the individual identification function of coda clicks, our study also suggests that the production of distinct coda types may vary individually with environmental context (depth) (Chapter III). If this can be confirmed with a large sample size in the future, it may bring new insights into the behavioural function of coda clicks.

Between foraging dives, sperm whales frequently gather with conspecifics at the surface and sometimes they even synchronize their dives (Whitehead 2003). We found that during this synchronized dives, sperm whales exchange coda clicks in the start of descents and in the end of ascents. Yet, they do not dive together to great depths but instead start spreading at about 550 m to forage individually (Chapter II).

During socializing periods, sperm whales communicate both acoustically and by touch. Besides the coda clicks production, they also seem to communicate with sounds produced by aerial displays, such as breaches (Whitehead 1985b, 2002). To accomplish these jumps out of the water, sperm whales need to perform shallow V-shaped dives up to 11-41 m depth for 13-31 s (Chapter IV). During the descent of a dive that precedes a breach, they frequent roll their bodies and fluke about 3 times to gain velocity and acceleration that will be used during the steep ascent. Ascents occur mainly by gliding, which seems to be favoured by their natural buoyancy (Miller et al. 2004b; Chapter IV).

After all these energetically demanding activities, sperm whales need to rest. As previously described, they seem to rest vertically either with their heads down or up (Miller et al. 2008). In the Azores, sperm whales also rest vertically, either heads up or down, and also horizontally, and these periods appear to occur mainly during nighttime (Chapter II).

When young males are between 3 and 15 years old they are observed in bachelor groups that gradually move to colder waters at higher latitudes (Gosho et al. 1984; Whitehead 2003). In the cold feeding grounds they seem to have a weak social organization (Whitehead et al. 1992; Whitehead 2003), but there are occasional records of clusters (Letteval et al. 2002). In our study we found that slow clicks appear to be communication signals among large males in high latitudes and are not related with prey debilitation (Norris and Møhl 1983; Gordon 1987b; Cranford 1999) as they were not correlated with buzzes. Moreover, they do not seem to be suitable for echolocation (Gordon 1987b; Mullins et al. 1988; Goold 1999; Tyack and Clark 2000; Jaquet et al. 2001), as the majority of these signals were produced at the surface and while ascending from a foraging dive (Chapter V; Oliveira et al. 2013). Additionally, these signals may encode individual and behavioural information,

extending the notion of the intraspecific relation between males in high latitude foraging grounds (Chapter V). When males grow older, they start migrating to breeding grounds where they search for females and, if successful, they mate (Gosho et al. 1984; Whitehead 2003). Fifteen to sixteen months after mating, a new sperm whale is born (Best et al. 1984; Whitehead 2003) and this whole cycle restarts.

Although the above description provides a standardized and uniform view of the behaviour and life cycle of the North Atlantic sperm whale, we found great variability among individual whales in most of the behavioural and ecological aspects investigated in this study. Besides differences in coda clicks (Chapter III), we also found individual differences in the acoustic behaviour while foraging (Chapter II), in the underwater dive behaviour before breaching (Chapter IV), in the positioning while resting (Chapter II), and in some repetitive patterns of slow clicks production (Chapter V). These differences may be related with individual physical characteristics, either related with their sound producing system (emission, reception and interpretation of acoustic signals) or with their body weight (and size), affecting their buoyancy and manoeuvrability. For the repetitive patterns of slow clicks there may be a type of "cultural" influence from what males have experienced with coda communication among social units at the breeding grounds.

Global threats affecting sperm whales

Sperm whales are protected by several legal tools. However, there are many anthropogenic sources of disturbance that may affect them in several ways (Richardson et al. 1995). Incidental collisions with sperm whales frequently cause great injuries or death (Laist et al. 2001; Jensen and Silber 2003; Carrillo and Ritter 2010). Sperm whales rely mostly on sound and the majority of their acoustic emissions (clicks) has energy centered between 2 and 25 kHz (Madsen et al. 2002a, b). Commercial shipping produces noise to the ocean mainly in the low-frequency band, but smaller vessels produce mostly in the mid-frequency band (Hildebrand 2009). The capacity of sperm whales to avoid ship collisions may be limited due to the maximum velocity of these animals at the surface (6-12 knots when frightened or alarmed, and 10-21 knots for brief periods when subject of extreme stress; Caldwell et al. 1966), and the need to breathe and recover at the surface, for several minutes, between foraging dives (Chapter II; Watwood et al. 2006). The avoidance of smaller vessels, such as whale watching boats, may be easily achieved but their presence may disturb sperm whales in other ways. Studies performed off Kaikoura, New Zealand revealed that sperm whales tended to reduce their surface periods, the number of blows, the intervals between blows and the frequency of dives

with raised flukes (indicative of foraging dives) while in the presence of boats (Gordon et al. 1992). Off the Azores, the presence of whale watching boats near sperm whales induced small changes in their speed and exhibition of aerial displays (Magalhães et al. 2002).

Contribution to reduce impacts on sperm whales at the study areas

Shipping has been growing worldwide and, consequently, the ambient noise has increased by as much as 12dB (Hildebrand 2009) over the past few decades. At present, both the Azores and Andøya Canyon are subject to intense ship traffic (Fig. VI.1) that may affect sperm whale populations locally, but have long-term impacts in the whole North Atlantic population, given the importance of these areas to both social units and sexually mature males. Even though ship strikes with sperm whales at the Azores and off northern Norway are not present in the referred literature (Laist et al. 2001; Jensen and Silber 2003; Carrillo and Ritter 2010), there are at least two cases of sperm whale mortality due to a collisions with ships in the Azores.

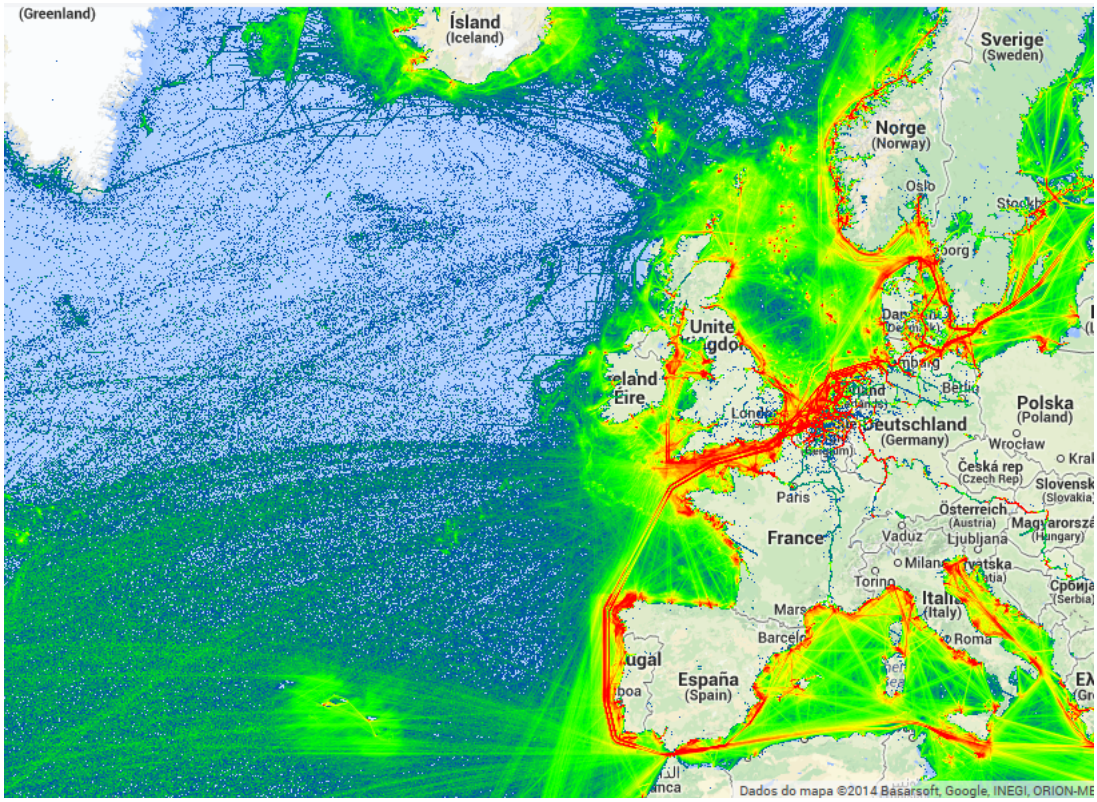


Figure VI. 1 – Map with the marine traffic from cargo vessels (green) and tankers (red) in an area that contains both study areas (Azores archipelago and Andøya Canyon, off northern Norway). Source: www.marinetraffic.com download on 25 June 2014.

Both study locations are known by their whale watching activity, mainly focused on sperm whales (Hoyt 2003; Nøttestad and Olsen 2004; Oliveira et al. 2007). In the Azores the whale watching activity has been increasing since 1993 (Oliveira et al. 2007). It is presently regulated by law order "DL 10/2003/A", that imposes a series of rules and restrictions to approaching and observing cetaceans (Oliveira et al. 2007). Norway has no legal regulations, but the whale watching operators are encouraged to follow guidelines (Hoyt 2003; Carlson 2011).

The present study provides novel information about sperm whale foraging behaviour and about their acoustic and "non-vocal" communication. We believe the results obtained in this study are useful to both researchers working with management and conservation, and whale watching operators. The former will find novel information that may help creating or improving conservation measures. Oliveira (2005) found that whale watching tourists in the Azores would like to receive much more information about the biology and ecology of cetacean species during their tour. Therefore, whale watching operators may find new information of sperm whale behavioural ecology and include it in the tour, complementing and improving the whole experience of the tourists.

Future research

Despite the fact that the present dissertation brought novel information about several aspects of the behavioural ecology of sperm whales, several gaps remain that we would like to address in future research.

The use of Dtags in this thesis provided substantial information on the animal movements and acoustics with a high level of detail. Yet, deployments used in this study were set to a maximum of 24 h and most of the times the tag released before that time. Most of the research presented here would have benefitted from extended deployments and tracking periods. We believe that, in the future, deployment periods should be longer to provide information on the activities of individuals over several days. This could be achieved without additional disturbance to the animals, as we found that they react more to the tagging procedures than to having the tag attached to the body. Although a continued tracking of the animals may also cause some disturbance of their natural behaviour, this could be performed from a sailboat, thus reducing the noise impact.

In order to respond to several informational gaps on the sperm whale behavioural ecology we suggest the use of Dtags to:

a) investigate if their foraging behaviour is similarly related with ocean bottom depths (due to location of their prey layer) in offshore areas beyond 2000 m;

b) investigate if the contexts in which different coda types are produced are just individual or also group-dependent;

c) study if the presence of small calves affects the foraging behaviour of the whales providing parental care (e.g. if they forage to the same prey layers and if they have similar acoustic behaviour as sperm whales that are not taking care of calves);

d) further investigate the underwater relation between synchronized foraging whales in units or groups; and

e) investigate the role of slow clicks “vocalizations” on mature male sperm whales while in breeding grounds.

Finally, all the suggested research on sperm whales would provide a better understanding of the reasons of the individual variability found in this dissertation.

References

Acevedo-Gutiérrez A. 2009. Group behavior In: Perrin WF, Würsig B and Thewissen JGM (eds) Encyclopedia of marine mammals. Second edition. Academic Press, Burlington, pp 511-520.

Aguilar Soto N, Johnson MP, Madsen PT, Díaz F, Domínguez I, Brito A and Tyack P. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). J Anim Ecol, 77: 936-947.

Akamatsu T, Matsuda A, Suzuki S, Wang D, Wang K, Suzuki M, Muramoto H, Sugiyama N and Oota K. 2005. New stereo acoustic data logger for free-ranging dolphins and porpoises. Mar Tech Soc J, 39(2): 3-9.

Amano M and Yoshioka M. 2003. Sperm whale diving behavior monitored using a suction-cup-attached TDR tag. Mar Ecol Prog Ser, 258:291-295.

Antunes R. 2000. Estudo do repertório de codas dos cachalotes (*Physeter macrocephalus*) dos Açores. Lic dissertation, Universidade do Algarve.

Antunes R. 2009. Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean. PhD dissertation, University of St. Andrews. 123 pp.

Antunes R, Schulz T, Gero S, Whitehead H, Gordon J and Rendell L. 2011. Individually distinctive acoustic features in sperm whale codas. Anim Behav, 81: 723-730.

Aoki K, Amano M, Mori K, Kourogi A, Kubodera T and Miyazaki N. 2012. Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. Mar Ecol Prog Ser, 444: 289-301.

Arnbom T, Papastavrou V, Weilgart LS and Whitehead H. 1987. Sperm whales react to an attack by killer whales. J Mamm, 68(2): 450-453.

Arranz P, Aguilar de Soto N, Madsen PT, Brito A, Bordes F and Johnson MP. 2011. Following a foraging fish-finder: Diel habitat use of Blainville's beaked whales revealed by echolocation. PLoS ONE, 6(12): e28353.

Au WWL. 2009. Echolocation In: Perrin WF, Würsig B and Thewissen JGM (eds) Encyclopedia of marine mammals. Second edition. Academic Press, Burlington, pp 348-357.

Au WWL and Hastings MC. 2008. Principles of Marine Bioacoustics. Springer Science. 679 pp.

Ávila de Melo AM. 1986. Trends of the summer abundance of sperm whales in Azorean waters, using sighting data and CPUE. Instituto Nacional de Investigação das Pescas: 1-13.

Backus RH and Schevill WE. 1966. Physeter clicks In: Norris KS (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, pp. 510-528.

Baird R. 1998. Studying diving behavior of whales and dolphins using suction-cup attached tags. Whalewatcher, 31(1): 3-7.

Baird RW, Borsani JF, Hanson MB and Tyack PL. 2002. Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. Mar Ecol Prog Ser, 237: 301-305.

Baird RW, Webster DL, Schorr GS, McSweeney DJ and Barlow J. 2008. Diel variation in beaked whale diving behavior. Mar Mamm Sci, 24(3): 630-642.

Balance LT. 2009. Cetacean ecology In: Perrin WF, Würsig B and Thewissen JGM (eds) Encyclopedia of marine mammals. Second edition. Academic Press, Burlington, pp 196-201.

Barale V and Zin I. 2000. Impact of continental margins in the Mediterranean Sea: Hints from the surface colour and temperature historical records. J Coast Conserv, 6(1): 5-14.

Barlow J and Taylor BL. 2005. Estimates of sperm whale abundance in the Northeastern Temperate Pacific from a combined acoustic and visual survey. Mar Mamm Sci, 21(3): 429-445.

Beale T. 1839. The Natural History of the Sperm Whale... to which is Added a Sketch of a South-Sea Whaling Voyage Etc. London, John Van Voorst.

Beasley I, Robertson KM and Arnold P. 2005. Description of a new dolphin, the Australian snubfin dolphin *Orcaella heinsohni* sp. N. (Cetacea, Delphinidae). Mar Mamm Sci, 21(3): 365-400.

Benoit-Bird KJ and Au WWL. 2001. Target strength measurements of Hawaiian mesopelagic boundary community animals. J Acoust Soc Am, 110(2): 812-819.

Benoit-Bird KJ and Au WWL. 2009. Cooperative prey herding by the pelagic dolphins, *Stenella longirostris*. J Acoust Soc Am, 125(1): 125-137.

Benoit-Bird K, Au WWL and Kastelein R. 2006. Testing the odontocete acoustic prey debilitation hypothesis: No stunning results. J Acoust Soc Am 120(2): 1118-1123.

Berzin AA. 1972. The sperm whale. NMFS-NOAA, Wahington, 394 pp.

Best PB. 1979. Social organization in sperm whales *Physeter macrocephalus* In Winn HE and Olla BL (eds) Behavior of marine animals, Vol 3, Plenum Press, New York, pp 227-289.

Best, P. B., Canham, P. A. S., and Macleod, N. 1984. Patterns of Reproduction in Sperm Whales, *Physeter macrocephalus*. Rep. Int. Whal. Comm. (Special Issue) 6: 51-79.

Bradbury JW and Vehrencamp SL. 1998. Principles of animal communication. Sinauer Associates Inc, 882 pp.

Breed MD and Moore J. 2012. Animal Behavior. Academic Press, Burlington, 496 pp.

Brennan B and Rodriguez P. 1994. Report of two orca attacks on cetaceans in Galápagos. Noticias Galápagos, 54: 28-29.

Burgess WC. 2000. The bioacoustic probe: A general-purpose acoustic recording tag. J Acoust Soc Am, 108: 2583.

Caldwell MC and Caldwell DK. 1965. Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). Nat, 207: 434-435.

Caldwell DK, Caldwell MC and Rice DW. 1966. Behavior of the sperm whale, *Physeter catodon* L. In Norris KS (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, pp. 677-717.

Carlson C. 2011. A review of whale watching guidelines and regulations around the world. Version 2011. ACCOBAMS. 209 pp.

Carrillo M and Ritter F. 2010. Increasing numbers of ship strikes in the Canary Islands: proposals for immediate action to reduce risk of vessel-whale collisions. J Cetacean Res Manag, 11(2): 131-138.

Chapman JL and Reiss MJ. 1999. Ecology: Principles and applications. 2nd edition. Cambridge University Press, Cambridge, United Kingdom. 330 pp.

Christal J, Whitehead H and Lettevall E. 1998. Sperm whale social units: variation and change. Can J Zool, 76: 1431-1440.

Clapham PJ and Mead JG. 1999. Megaptera novaeangliae Mammal Species, 604, 1-9.

Clarke MR. 1976. Observations on sperm whale diving. J Mar Biol Ass UK, 56: 809-810.

Clarke MR. 1978a. Physical properties of spermaceti oil in the sperm whale. J Mar Biol Ass UK, 58: 19-26.

Clarke MR. 1978b. Buoyancy control as a function of the spermaceti organ in the sperm whale. J Mar Biol Ass UK, 58:27-71.

Clarke MR, Martins HR and Pasccoe P. 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. Phil Trans R Soc Lond B, 339: 67-82.

Clarke R. 1954. Open boat whaling in the Azores: The history and present methods of a relic industry. Discovery reports, 26: 281-354.

Clarke R. 1956. A giant squid swallowed by a Sperm whale. Proc Zool Soc Lond, 126: 645.

Clarke R and Paliza O. 1988. Intraspecific fighting in sperm whales. Rep Int Whal Commn, SC/39/Sp1, 38: 235-241.

Clausen KT, Wahlberg M, Beedholm K, DeRuiter S and Madsen PT. 2010. Click communication in harbour porpoises *Phocoena phocoena.* Bioacoustics, 20: 1-28.

Collum LA and Fritts TH. 1985. Sperm whales (*Physeter catodon*) in the Gulf of Mexico. Southwest Nat, 30(1): 101-104.

Connor RC. 2000. Group living in whales and dolphins In Mann J, Connor RC, Tyack PL and Whitehead H (eds) Cetacean societies, University of Chicago Press, Chicago, pp 199-218.

Cranford TW. 1999. The sperm whale's nose: sexual selection on a grand scale? Mar Mamm Sci, 15(4):1133-1157.

Cranford TW, Amundin M and Norris KS. 1996. Functional morphology and homology in the Odontocete nasal complex: Implications for sound generation. J Morph, 228.3: 223-285.

Darling JD and Bérubé M. 2001. Interactions of singing humpback whales with other males. Mar Mamm Sci, 17(3): 570-584.

Davis RW, Fargion GS, May N, Leming TD, Baumgartner M, Evans WE, Hansen LJ and Mullin K. 1998. Physical habitat of cetaceans along the continental slope in the North-Central and Western Gulf of Mexico. Mar Mamm Sci, 14(3): 490-507.

Douglas LA, Dawson SM and Jaquet N. 2005. Click rates and silences of sperm whales at Kaikoura, New Zealand. J Acoust Soc Am 118(1): 523-529.

Drouot V, Gannier A and Goold JC. 2004. Diving and feeding behaviour of sperm whales (*Physeter macrocephalus*) in the Northwestern Mediterranean Sea. Aq Mamm, 30(3): 419-426.

Dudzinski KM, Thomas JA and Gregg JD. 2009. Communication in Marine Mammals In: Perrin WF, Würsig B and Thewissen JGM (eds) Encyclopedia of marine mammals. Second edition. Academic Press, Burlington, pp 260-269.

Dunlop RA, Cato DH and Noad MJ. 2008. Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*). Mar Mamm Sci 24(3): 613-629.

Endres W, Bambach W and Flösser G. 1971. Voice spectrograms as a function of age, voice disguise, and voice imitation. J Acoust Soc Am 49(6), Part 2: 1842-1848.

Fish FE, Nicastro AJ and Weihs D. 2006. Dynamics of the aerial maneuvers of spinner dolphins. J Exp Biol, 209: 590-598.

Frantzis A and Alexiadou P. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. Can J Zool, 86: 62-75.

Fristrup KM and Harbison GR. 2002. How do sperm whales catch squids? Mar Mamm Sci, 18(1): 42-54.

Gannon WL, Sikes RS, The Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal, 88: 809-823.

Gaskin D E 1964. Recent observations in New Zealand waters on some aspects of behaviour of the sperm whale (*Physeter macrocephalus*). Tuatara 12(2): 106-114.

Gero S, Engelhaupt D and Whitehead H. 2008. Heterogenous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. Behav Ecol Sociobiol, 63: 143-151.

Gero S, Gordon J and Whitehead H. 2013. Calves as social hubs: dynamics of the social network within sperm whale units. Proc R Soc B, 280: 1-9.

Gillespie D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the *RSV Aurora Australis*. Rep Int Whal Commn, 47: 897-907.

Goldbogen JA, Calambokidis J, Friedlaender AS, Francis J, DeRuiter SL, Stimpert AK, Falcone E and Southall BL. 2013. Underwater acrobatics by the world's lasgest predator: 360º rolling manoeuvres by lunge-feeding blue whales. Biol Lett, 9: 20120986.

Goold JC. 1999. Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. J Mar Biol Assoc UK, 79: 541-550.

Gordon JCD. 1987a. Sperm whale groups and social behaviour observed off Sri Lanka, Rep Int Whal Commn SC/38/Sp7, 37:205-217.

Gordon JC. 1987b. Behaviour and ecology of sperm whales off Sri Lanka. PhD dissertation, University of Cambridge, Cambridge, UK.

Gordon JC. 1991a. Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. J Zool, 224(2): 301-314.

Gordon JC. 1991b. The World Wildlife Fund's Indian Ocean sperm whale project: an example of cetacean research within the Indian Ocean Sanctuary. Mar Mamm Tech Rep, 3: 219-239.

Gordon J and Steiner L. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus,* in the Azores. Rep Int Whal Commn SC/42/Sp7, 42: 561-565.

Gordon J and Tyack P. 2001. Sound and cetaceans In: Evans PGH and Raga JA (eds) Marine mammals, Biology and Conservation, Kluwer Academic, New York, pp 139-196.

Gordon J, Leaper R, Hartley FG and Chappell O. 1992. Effects of whale-watching vessels on the surface and underwater acoustic behaviour of sperm whales off Kaikoura, New Zealand. Sci & Res, Ser 52, NZ Dept Conserv, Wellington.

Gordon JCD, Matthews JN, Panigada S, Gannier A, Borsani JF and Notarbartolo di Sciara G. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. J Cetacean Res Manag, 2(1): 27-36.

Gosho ME, Rice DW and Breiwick JM. 1984. The sperm whale, *Physeter macrocephalus.* Mar Fish Rev, 46(4): 54-64.

Gregory PR and Rowden AA. 2001. Behaviour patterns of bottlenose dolphins (*Tursiops truncates*) relative to tidal state, time-of-day, and boat traffic in Cardigan Cay, West Wales. Aq Mamm, 27.2: 105-113.

Hain JHW, Carter GR, Kraus SD, Mayo CA and Winn HE. 1982. Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the Western North Atlantic. Fish Bull, 80(2): 259-268.

Herman LM and Tavolga WN. 1980. The communication systems of cetaceans In: Herman LM (ed) Cetacean behavior: Mechanism and functions. John Wiley and Sons Inc, pp 149-209.

Hildebrand JA. 2009. Anthropogenic and natural sources of ambient noise in the ocean. Mar Ecol Prog Ser, 395: 5-20.

Hooker SK and Baird RW. 1999. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). Proc R Soc Lond B, 266: 671-676.

Hooker SK and Baird RW. 2001. Diving and behaviour of odontocetes: a methodological review and critique. Mamm Rev, 31(1): 81-105.

Hoyt E. 2003. The best whale watching in Europe, A guide to seeing whales, dolphins and porpoises in all European waters. WDCS, Unterhaching. 60 pp.

Hrbek T, da Silva VMF, Dutra N, Gravena W, Martin AR and Farias IP. 2014. A new species of river dolphin from Brazil or: how little do we know our biodiversity. PLoS ONE, 9(1): e83623.

Jaquet N, Dawson S, and Douglas L. 2001. Vocal behavior of male sperm whales: Why do they click? J Acoust Soc Am, 109(5): 2254-2259.

Jensen AS and Silber GK. 2003. Large whale ship strike database. US Department of Commerce. NOAA Technical Memorandum NMFS-F/OPR 25. 37 pp.

Johnson MP and Tyack PL. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J Ocean Eng, 28(1): 3-12.

Johnson M, Madsen PT, Zimmer WMX, Aguilar de Soto N and Tyack PL. 2004. Beaked whales echolocate on prey. Proc R Soc B, 271: S383-S386.

Johnson M, Madsen PT, Zimmer WMX, Aguilar de Soto N and Tyack PL. 2006. Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. J Exp Biol, 209: 5038-5050.

Kenney RD and Winn HE. 1987. Cetacean biomass densities near submarine canyons compared to adjacent shelf/slope areas. Cont Shelf Res, 7(2): 107-114.

Kiefte M. 1999. Discriminant Analysis Toolbox version 0.3. http://www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=189 . Accessed 8 October 2013.

Kostianoy AG, Nihoul JCJ and Rodionov VB. 2004. Physical oceanography of frontal zones in the subarctic seas. Elsevier Oceanography series 71. Amsterdam, The Netherlands. 316 pp.

Kot BW, Zbinden D and Sears R. 2013. Aerial behavior by the fin whale (*Balaenoptera physalus*) in the wake of a freighter and near other boats. Mar Freshw Behav Physiol, 46(4): 267-272.

Krebs JR and Davies NB. 1997. Behavioural ecology: An evolutionary approach. 4th edition. Blackwell Publishing, Malden United States of America. 464 pp.

Laberg JS, Vorren TO, Dowdeswell JA, Kenyon NH and Taylor J. 2000. The Andøya Slide and the Andøya Canyon, north-eastern Norwegian-Greenland Sea. Mar Geol, 162:259-275.

Laberg JS, Vorren TO, Kenyon NH, Ivanov M and Espen S. 2005. A modern canyon-fed sandy turbidite system of the Norwegian continental margin. Norwegian Journal of Geology, 85: 267-277.

Laist DW, Knowlton AM, Mead JG, Collet AS and Podesta M. 2001. Collisions between ships and whales. Mar Mamm Sci, 17(1): 35-75.

Legendre P and Legendre L. 1998. Numerical Ecology, 2nd edition, Elsevier, New York, pp 671-672.

Lettevall E, Richter C, Jaquet N, Slooten E, Dawson S, Whitehead H, Christal J, and Howard PM. 2002. Social structure and residency in aggregations of male sperm whales. Can J Zool, 80(7): 1189-1196.

Lockyer C. 1981. Estimates of growth and energy budget for the sperm whale, *Physeter catodon*, In Mammals in the Seas, vol III, FAO Series 5: 489–504.

Lockyer C. 1997. Diving behaviour of the sperm whale in relation to feeding. Bull Kon Belg Inst Natuurwet Biologie, 67(suppl): 47-52.

Madsen PT, Wahlberg M, and Møhl B. 2002a. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. Behav Ecol Sociobiol, 53: 31-41.

Madsen PT, Payne R, Kristiansen NU, Wahlberg M, Kerr I and Møhl B. 2002b. Sperm whale sound production studied with ultrasound time/depth recording tags. J Exp Biol, 205: 1899-1906.

Madsen PT, Carder DA, Au WW, Nachtigall PE, Møhl B and Ridgway SH. 2003. Sound production in neonate sperm whales. J Acoust Soc Am 113(6): 2988-2991.

Magalhães S, Prieto R, Silva MA, Gonçalves J, Afonso-Dias M and Santos RS. 2002. Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. Aq Mamm, 28.3: 267-274.

Magalhães S, Silva MA, Prieto R, Quérouil S, Pinela A and Santos RS. 2005. Spatial and temporal patterns of Sperm whale groups in the Azores archipelago In European Research on Cetaceans – 19 Proc. 19th Ann Conf ECS, La Rochelle, France, 2-7 April 2005. European Cetacean Society, France.

Martin AR. 1982. A link between the sperm whales occurring off Iceland and the Azores. Mammalia, 46(2): 259-260.

Martin AR and Reeves RR. 2002. Diversity and zoogeography In: Hoelzel AR (ed) Marine mammal biology: An evolutionary approach. Blackwell Publishing, Malden, pp 1-37.

Matthews JN, Steiner L and Gordon J. 2001. Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-id data from the Azores (1987-1995). J Cetacean Res Manag, 3(3): 219-226.

McComb K, Reby D, Baker L, Moss C and Sayialel S. 2003. Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav, 65: 317-329.

Melendez KV and Feng AS. 2010. Communication calls of little brown bats display individual-specific characteristics. J Acoust Soc Am, 128(2): 919-923.

Miller PJO, Johnson MP, and Tyack PL. 2004a. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. Proc R Soc Lond B, 271: 2239-2247.

Miller PJO, Johnson MP, Tyack PL and Terray EA. 2004b. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. J Exp Biol, 207: 1953-1967.

Miller PJO, Aoki K, Rendell LE and Amano M. 2008. Stereotypical resting behaviour of the sperm whale. Curr Biol, 18(1): R21-R23.

Moore KE, Watkins WA and Tyack PL. 1993. Pattern similarity in shared codas from sperm whales (*Physeter catodon*). Mar Mamm Sci, 9(1): 1-9.

Morton B, Britton JC and Martins AMF. 1998. Ecologia Costeira dos Açores. Sociedade Afonso Chaves. Associação de Estudos Açoreanos. Ponta Delgada.

Mullins J, Whitehead H and Weilgart LS. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Can J Fish Aq Sci, 45: 1736-1743.

Møhl B. 2001. Sound transmission in the nose of the sperm whale *Physeter catodon.* A post mortem study. J Comp Physiol A, 187: 335-340.

Møhl B, Wahlberg M, Madsen PT, Miller LA and Surlykke A. 2000. Sperm whale clicks: Directionality and source level revisited. J Acoust Soc Am, 107(1): 638-648.

Møhl B, Wahlberg M and Madsen PT. 2003. The monopulsed nature of sperm whale clicks. J Acoust Soc Am 114(2): 1143-1154.

Norris KS and Harvey GW. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.) In: Galler SR, Schmidt-Koenig K, Jacobs GJ and Belleville RE (eds) Animal orientation and navigation, NASA, Washington, D. C. pp 397-417.

Norris KS and Møhl B. 1983. Can odontocetes debilitate prey with sound? Am Nat, 122(1): 85-104.

Nøttestad L and Olsen E. 2004. Whales and seals: Top predators in the ecosystem In: Skjoldal HR (ed) The Norwegian Sea Ecosystem. Tapir Academic Press, Trondheim, pp 395-434.

Oliveira C. 2005. A actividade de observação turística de cetáceos no arquipélago dos Açores: Contribuição para o seu desenvolvimento sustentável. MSc dissertation. Universidade dos Açores. 90 pp.

Oliveira C, Filla G, Gonçalves J, Silva MA, Prieto R, Magalhães SM and Santos RS. 2007. A social-economic perspective of the whale watching activity in the Azores. Report of the Scientific Committee of the International Whaling Commision, SC/59/WW8. 8 pp.

Oliveira C, Wahlberg M, Johnson M, Miller PJO and Madsen PT. 2013. The function of male sperm whale slow clicks in a high latitude habitat: Communication, echolocation or prey debilitation? J Acoust Soc Am, 133(5): 3135-3144.

Page B, McKenzie J, Hindell MA and Goldsworthy SD. 2005. Drift dives by male New Zealand fur seals (*Arctocephalus forsteri*). Can J Zool, 83: 293-300.

Panigada S, Pesante G, Zanardelli M and Oehen S. 2003. Day and night-time diving behavior of fin whales in the Western Ligurian Sea. Oceans 2003 Proceedings IEEE, 1: 466-471.

Papastavrou V, Smith SC and Whitehead H. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. Can J Zool, 67: 839-846.

Perrin WF, Würsig B and Thewissen JGM. 2009. Encyclopedia of marine mammals. Second edition. Academic Press, Burlington, 1316 pp.

Pinela AM, Quérouil S, Magalhães S, Silva MA, Prieto R, Matos JA and Santos RS. 2009. Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. Can J Zool, 87: 802-813.

Pitman RL, Ballance LT, Mesnick SJ and Chivers SJ. 2001. Killer whale predation on sperm whales: observations and implications. Mar Mamm Sci, 17(3): 494-507.

Pompa S, Ehrlich PR and Ceballos G. 2011. Global distribution and conservation of marine mammals. PNAS, 108(33): 13600-13605.

Pryor K. 1986. Non-acoustic communicative behavior of the great whales: origins, comparisons, and implications for management. Reports of the International Whaling Commission, 8: 89-95.

Reeves RR, Smith BD, Crespo EA and Notarbartolo di Sciara G. 2003 Dolphins, whales and porpoises: 2002-2010 Conservation Action Plan for the World's Cetaceans. Vol 58, IUCN, Cambridge, 139 pp.

Reidenberg JS and Laitman JT. 2007. Discovery of a low frequency sound source in Mysticeti (baleen whales): Anatomical establishment of a vocal fold homolog. Anatom Rec, 290: 745-759.

Rendell L and Whitehead H. 2003a. Vocal clans in sperm whales (*Physeter macrocephalus*). Proc R Soc Lond B 270: 225-231.

Rendell L and Whitehead H. 2003b. Comparing repertoires of sperm whale codas: A multiple methods approach. Bioacoust 14(1): 61-81.

Rendell L and Whitehead H. 2004. Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement. Anim Behav, 67: 865-874.

Rendell L and Whitehead H. 2005. Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects. Anim Behav, 70: 191-198.

Rhinelander MQ and Dawson SM. 2004. Measuring sperm whales from their clicks: Stability of interpulse intervals and validation that they indicate whale length. J Acoust Soc Am, 115(4): 1826-1831.

Rice DW. 1989. Sperm whale – *Physeter macrocephalus* Linnaeus, 1758 In: Ridgway SH and Harrison SR (eds) Handbook of Marine Mammals, vol 4: River dolphins and the larger toothed whales, Academic Press, London, pp 177-233.

Richardson WJ, Greene Jr. CR, Malme CI and Thomson DH. 1995. Marine mammals and noise. Academic Press, California, 576 pp.

Santos RS, Hawkins S, Monteiro LR, Alves M and Isidro EJ. 1995. Marine research, resources and conservation in the Azores. Aquatic Conservation: Mar Freshw Ecosyst, 5: 311-354.

Sayigh LS, Tyack PL, Wells RS and Scott MD. 1990. Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behav Ecol Sociobiol, 26: 247-260.

Schack HB, Malte H and Madsen PT. 2008. The responses of Atlantic cod (*Gadus morhua* L.) to ultrasound-emitting predators: stress, behavioural changes or debilitation? J Exp Biol, 211: 2079-2086.

Schreer JF and Kovacs KM. 1997. Allometry of diving capacity in air breathing vertebrates. Can J Zool, 75: 339-358.

Schulz T, Whitehead H, Gero S and Rendell L. 2011. Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. Mar Mamm Sci, 27(1): 149-166.

Sibly RM, Nott HMR and Fletcher DJ. 1990. Splitting behaviour into bouts. Anim Behav, 39: 63-69.

Silva M, Prieto R, Magalhães S, Cabecinhas R, Cruz A, Gonçalves JM and Santos RS. 2003. Occurrence and distribution of cetaceans in waters around Azores (Portugal), Summer and Autumn 1999-2000. Aquat Mamm, 29(1): 77-83.

Silva MA, Magalhães S, Prieto R, Quérouil S, Pinela A, Seabra MI and Santos RS. 2006. Ecologia e estrutura populacional dos roazes e cachalotes nos Açores: Relação com as características do habitat. Arquivos DOP _ Série Estudos 4. Horta, Portugal: University of the Azores. 19 pp.

Silva MA, Prieto R, Cascão I, Seabra MI, Machete M, Baumgartner MF and Santos RS. 2014. Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. Mar Biol Res, 10(2): 123-137.

Simon M, Johnson M and Madsen PT. 2012. Keeping momentum with a mouthful of water: behaviour and kinematics of humpback whale lunge feeding. J Exp Biol, 215: 3786-3798.

Slater PJB and Lester NP. 1982. Minimising errors in splitting behaviour into bouts. Behav, 79(2/4): 153-161.

Smith WHF and Sandwell DT. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Sci, 277: 1956-1962.

Soltis J, Leong K and Savage A. 2005. African elephant vocal communication II: rumble variations reflects the individual identity and emotional state of callers. Anim Behav, 70: 589-599.

Steiner L, Lamoni L, Plata MA, Jensen SK, Lettevall E and Gordon J. 2012. A link between male sperm whales, *Physeter macrocephalus,* of the Azores and Norway. J Mar Biol Ass UK: 1-6.

Teloni V. 2005. Patterns of sound production in diving sperm whales in the Northwestern Mediterranean. Mar Mamm Sci, 21(3): 446-457.

Teloni, V, Zimmer WMX, Wahlberg M and Madsen PT. 2007. Consistent acoustic size estimation of sperm whales using clicks recorded from unknown aspects. J Cetacean Res Manag, 9(2): 127-136.

Teloni V, Johnson, MP, Miller PJO and Madsen PT. 2008. Shallow food for deep divers: Dynamic foraging behaviour of male sperm whales in a high latitude habitat. J Exp Mar Biol Ecol, 354: 119-131.

Thode A, Mellinger DK, Stienessen S, Martinez A and Mullin K. 2002. Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico. J Acoust Soc Am, 112(1): 308-321.

Tibbetts EA and Dale J. 2007. Individual recognition: it is good to be different. Trends Ecol Evol, 22(10): 529-537.

Townsend CH. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica, 19(1): 1-50.

Tyack P and Clark CW. 2000. Communication and acoustic behavior of whales and dolphins In Au WWL, Popper AN and Fay RR (eds) Hearing in whales and dolphins. Handbook on Auditory Research, Springer, Berlin Heidelberg, New York, pp 156-224.

Tyack PL and Miller EH. 2002. Vocal anatomy, acoustic communication and echolocation In Hoelzel AR (ed) Marine Mammal Biology: an Evolutionary Approach, pp 142-184.

Tyack PL, Johnson M, Aguilar Soto N, Sturlese A and Madsen PT. 2006. Extreme diving of beaked whales. J Exp Biol, 209: 4238-4253.

Wahlberg M. 2002. The acoustic behaviour of diving sperm whales observed with a hydrophone array. J Exp Mar Biol Ecol, 281: 53-62.

Waring GT, Fairfield CP, Ruhsam CM and Sano M. 1993. Sperm whales associated with Gulf Stream features off the north-eastern USA shelf. Fish Oceanogr, 2(2): 101-105.

Waters S and Whitehead H. 1990. Aerial behaviour in sperm whales. Can J Zool, 68: 2076-2082.

Watkins WA and Schevill WE. 1977a. Spatial distribution of *Physeter catodon* (sperm whales) underwater. Deep Sea Res, 24: 693-699.

Watkins WA and Schevill WE. 1977b. Sperm whale codas. J Acoust Soc Am, 62: 1485-1490.

Watkins WA and Tyack P. 1991. Reaction of sperm whales (*Physeter catodon*) to tagging with implanted sonar transponder and radio tags. Mar Mamm Sci, 7(4): 409-413.

Watkins WA, Daher MA, Fristrup KM, Howald TJ and Notarbartolo di Sciara G. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. Mar Mamm Sci, 9(1): 55-67.

Watkins WA, Daher MA, DiMarzio NA, Samuels A, Wartzok D, Fristrup KM, Gannon, DP, Howey PW and Maiefski RR. 1999. Sperm whale surface activity from tracking radio and satellite tags. Mar Mamm Sci, 15(4): 1158-1180.

Watkins WA, Daher MA, DiMarzio NA, Samuels A, Wartzok D, Fristrup KM, Howey PW and Maiefski RR. 2002. Sperm whale dives tracked by radio tag telemetry. Mar Mamm Sci, 18(1): 55-68.

Watwood SL, Miller PJO, Johnson M, Madsen PT and Tyack PL. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). J Anim Ecol, 75: 814-825.

Weilgart L and Whitehead H. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*) Can J Zool, 66: 1931-1937.

Weilgart L and Whitehead H. 1993. Coda communication by sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. Can J Zool, 71: 744-752.

Weilgart L and Whitehead H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behav Ecol Sociobiol, 40: 277-285.

Weilgart L, Whitehead H and Payne K. 1996. A colossal convergence. Am Sci, 84(3): 278-287.

Whitehead H. 1985a. Humpback whale breaching. Investigations on cetacea, 17: 117-155.

Whitehead H. 1985b. Why whales leap. Sci Am, 252: 84-93.

Whitehead H. 1989. Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. Can J Zool, 67: 2131-2139.

Whitehead H. 1993. The behaviour of mature male sperm whale on the Galápagos Islands breeding grounds. Can J Zool, 71(4): 689-699.

Whitehead H. 1996. Babysitting, dive synchrony, and indication of alloparental care in sperm whales. Behav Ecol Sociobiol, 38: 237-244.

Whitehead H. 2002. Breaching In: Perrin WF, Würsig B and Thewissen JGM (eds) Encyclopedia of Marine Mammals, pp 162-164.

Whitehead H. 2003. Sperm whales: Social Evolution in the Ocean. The University of Chicago, Chicago, 431 pp.

Whitehead H. 2009. Sperm whale *Physeter macrocephalus* In: Perrin WF, Würsig B and Thewissen JGM (eds) Encyclopedia of marine mammals. Second edition. Academic Press, Burlington, pp 1091-1097 pp.

Whitehead H and Weilgart L. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour, 118(3/4):275-296.

Whitehead H, Brennan S and Grover D. 1992. Distribution and behaviour of male sperm whales on the Scotian shelf, Canada. Can J Zool, 70(5): 912-918.

Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D and Rendell L. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why are they so different? Int J Primatol, 33: 1142-1164.

Wilson M, Hanlon RT, Tyack PL and Madsen PT. 2007. Intense ultrasonic clicks from echolocating toothed whales do not elicit anti-predator responses or debilitate the squid *Logilo pealeii*. Biol Lett, 3: 225-227.

Winn HE and Winn LK. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. Mar Biol, 47: 97-114.

Würsig B, Dorsey EM, Richardson WJ and Wells RS. 1989. Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, summering in the Beaufort Sea. Aquat Mamm, 15(1): 27-37.

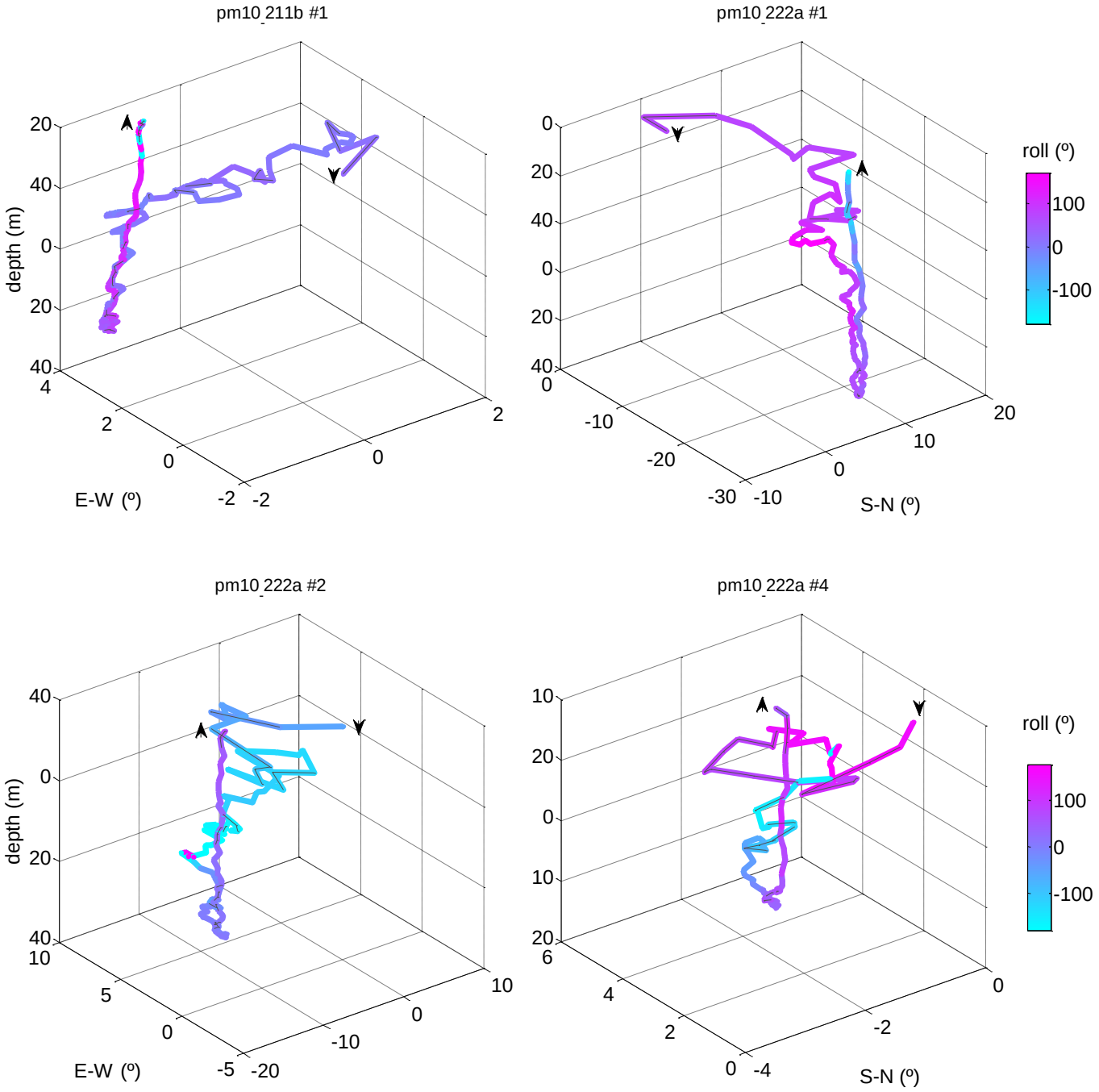
Ydenberg RC and Clark CW. 1989. Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. J Theor Biol, 139: 437-449.

Zimmer WMX, Johnson MP, D'Amico A and Tyack PL. 2003. Combining data from a multisensor tag and passive sonar to determine the diving behaviour of a sperm whale (*Physeter macrocephalus*). IEEE J Ocean Eng, 28(1): 13-28.

Zimmer WMX, Tyack PL, Johnson MP and Madsen PT. 2005a. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. J Acoust Soc Am 117(3): 1473-1485.

Zimmer WMX, Madsen PT, Teloni V, Johnson MP and Tyack PL. 2005b. Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. J Acoust Soc Am 118(5): 3337-3345.

Annex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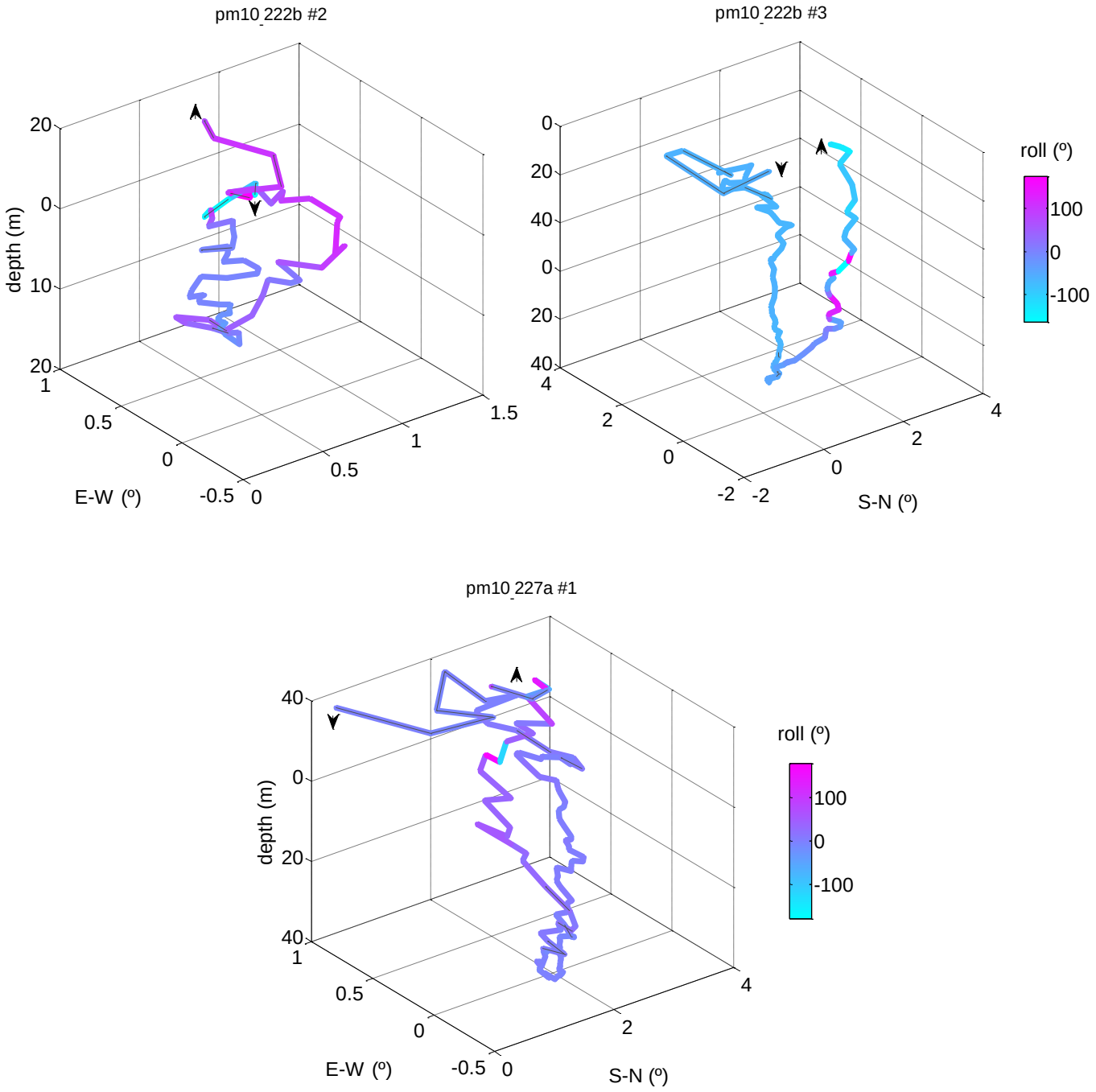

Annex of Figure IV. 5 – Pseudotracks of the descent and ascent before breaching, of the remaining breaches. Body rolling is shown as a color gradient, with positive values meaning the animal is turned to its right side and negative values to its left side.