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Declaração de autoria de trabalho

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Declaro ser o autor deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

(Esteban Iglesias Rivas)

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Abstract

High-resolution sound and movement recording tags (e.g. Dtags, Acousonde tags, A-tags) offer unprecedented views of the fine-scale foraging behaviour of cetaceans, especially those that use sound to forage, such as the sperm whale (*Physeter macrocephalus*). However, access to these tags is difficult and expensive, limiting studies of sperm whale foraging behaviour to small sample sizes and short time periods, preventing inferences at the population level. The development of accurate foraging indices from relatively inexpensive time-depth recorder (TDR) data would allow obtaining data from a larger number of individuals, and capitalizing on datasets already available, providing long-term analyses of foraging activity. In this study, data from high-resolution acoustic and movement recording tags from 8 sperm whales was used to build predictive models of the number of buzzes (i.e, indicative of prey capture attempts (PCA)) for dive segments of different lengths, using dive metrics calculated from time-depth data only. The number of buzzes per dive segments of 180s and 300s was best predicted by the average depth, depth variance, vertical velocity variance and number of wiggles. Model performance was best for 180s segments, accurately predicting the number of buzzes in 63% of the segments used to construct the model and in 58% of the segments for new individuals. Predictive accuracy reached 81%, when only presence or absence of buzzes in segments was assessed. These results demonstrate the feasibility of finding a reliable index of sperm whale foraging activity for time-depth data, when combining different dive metrics. This index estimates the number of buzzes over short dive segments (of 180s), enabling investigating and quantifying PCAs at very fine-scales. Finally, this work contributes to leverage the potential of time-depth data for studying the foraging ecology of sperm whales and the capacity of applying this approach to a wide range of cetacean species.

Keywords: Sperm whale, Dtag, time-depth data, foraging behaviour, buzz predictive model

Resumo

O cachalote (*Physeter macrocephalus*) é um dos mais conhecidos predadores marinhos, passando mais da metade da sua vida abaixo dos 500m de profundidade, onde se alimenta principalmente de lulas meso e bentopelágicas, embora também possam consumir outros cefalópodes, peixes profundos e invertebrados. Apresenta uma distribuição mundial e pode ser encontrado no arquipélago dos Açores durante todo o ano, perto da costa, razão pela qual os Açores foram uma das regiões baleeiras mais importantes.

O som desempenha um papel fundamental na vida dos cachalotes. Eles produzem sons enquanto estão a socializar e na procura e captura de alimento. Foram identificados pelo menos quatro tipos de cliques (cliques usuais, "buzzes", codas e "slow clicks"), dos quais os cliques usuais e os "buzzes" estão envolvidos no comportamento de alimentação. Os cliques usuais têm níveis sonoros elevados e são altamente direcionais, servindo como um biosonar para navegar pelo ambiente e eco-localizar presas. Os "buzzes", consistem em cliques de alta frequência e baixa amplitude, produzidos em intervalos rápidos. Por esta razão, têm um alcance mais curto do que os cliques usuais, fornecendo uma resolução mais alta e, portanto, informações mais detalhadas sobre o seu ambiente próximo e presas.

A observação direta é uma das ferramentas mais poderosas para estudar o comportamento animal, não obstante, no caso dos cachalotes é altamente limitada, consequência dos longos períodos que passam em profundidade. Por este motivo, os estudos sobre o comportamento do cachalote, e de outros predadores marinhos de mergulho profundo, dependem da utilização de diferentes ferramentas que permitem obter informações sobre o seu comportamento subaquático. Os hidrofones e as marcas colocadas em animais estão entre as ferramentas mais importantes para estudos sobre o comportamento dos cetáceos, permitindo o registo contínuo de sons produzidos debaixo de água e o seguimento, também contínuo, de movimento e outras variáveis de mergulho.

A incorporação de hidrofones em marcas para colocação em animais, como as marcas acústicas digitais ("Dtags"), marcas "Acousonde" ou "A-tags" revolucionou o estudo do comportamento dos cetáceos. Estas marcas fornecem dados de movimento tri-dimensional e acústicos de alta resolução, simultaneamente registando informação sobre

o comportamento do animal, possibilitando, por exemplo, a compreensão de como os cachalotes usam o som durante a alimentação. Estudos baseados na análise de dados de "Dtags" revelaram que a presença de picos de velocidade na parte mais profunda do mergulho e movimentos rápidos da mandíbula estavam relacionados com a produção de "buzzes". Consequentemente, foi sugerido que os "buzzes" são emitidos durante a fase terminal de captura de presas, a fim de obter informação de alta resolução sobre o alvo. Desde então, a produção de cliques tem sido usada como um indicador de esforço de alimentação e a produção de "buzzes", considerada como o melhor indicador de tentativa de captura de presas.

Não obstante, o acesso a estas marcas de alta resolução acústica e movimento é extremamente difícil e caro, limitando o estudo do comportamento de alimentação do cachalote a amostras pequenas e curtos períodos de tempo. Por esta razão, o desenvolvimento de um índice de esforço de alimentação exato, a partir de dados de mergulho 2D de dados de tempo-profundidade como os "time-depth recorders" (TDR), permitiria capitalizar um conjunto de dados de mergulho já disponíveis, analisando séries temporais de atividade de alimentação e avaliando alterações ligadas a mudanças climáticas ou antropogénicas.

No presente estudo, dados de alta resolução com informação acústica de oito cachalotes marcados com "Dtags" no arquipélago dos Açores foram usados para construir um modelo preditivo do número de "buzzes", baseado exclusivamente em dados profundidade-tempo e com resolução máxima de 1m de profundidade, correspondendo, portanto, às capacidades de registo de um TDR. O número total de "buzzes" por segmento foi modelado a partir de um conjunto de variáveis que descrevem a média e variabilidade de profundidade, tempo passado na fase profunda do mergulho, velocidade vertical, aceleração vertical e número de excursões verticais, usando um modelo linear generalizado misto (GLMM), com o indivíduo como um efeito aleatório.

De um total de 816 "buzzes" analisados, 95% apresentaram uma duração de 2 a 14 segundos. Portanto, inicialmente os mergulhos foram divididos em segmentos de curta duração. Porém, as primeiras análises demonstraram fracas capacidades preditivas e finalmente optou-se por usar segmentos de 180s e 300s.

Os melhores modelos de número de buzzes por segmento de 180s e 300s incluíram a profundidade média, a variância de profundidade, a variância da velocidade vertical e o

número de “wiggles” por segmento. Os segmentos de mergulho com “buzzes” apresentaram uma maior profundidade média, menor variância de profundidade, maior variância de velocidade e maior presença de “wiggles”, sendo a profundidade média a métrica mais relevante do modelo. Estes resultados confirmam que os “buzzes” ocorrem nas partes profundas do mergulho e sugerem que as várias tentativas de captura podem ocorrer numa extensão de profundidade limitada, demonstrado pela pequena variação de profundidade, maior variação de velocidade e presença de “wiggles”.

O desempenho do modelo foi melhor para segmentos de 180s, resultando em deteções corretas do número de “buzzes” em 63% dos segmentos usados para construir o modelo e em 58% dos segmentos para novos indivíduos usados para testar o modelo. Assim mesmo, o modelo resultou em 81% de deteções corretas quando avaliada apenas a presença ou ausência de “buzzes” nos segmentos. Apesar do nosso modelo ter algumas deficiências preditivas, os resultados preditivos são similares àqueles obtidos com modelos desenvolvidos anteriormente, para prever tentativas de captura de presas em conjuntos de dados 2D de baixa resolução em outras espécies. Porém, ao contrário desses modelos que previram tentativas de captura de presas na escala de mergulho ou, na melhor das hipóteses, em escalas de 30 minutos e de uma hora, o modelo desenvolvido neste estudo previu tentativas de captura de presas a cada 3 minutos.

Este é o primeiro estudo a desenvolver um modelo que prevê o número de tentativas de captura de presas e, consequentemente, o esforço de alimentação em cachalotes a partir de perfis de mergulho 2D. O presente método poderá ser aplicado a conjuntos de dados de profundidade de tempo já disponíveis, a fim de conduzir análises retrospetivas do comportamento de alimentação. Porém, o aumento do tamanho da amostra e uma análise de dados mais detalhada permitiria obter previsões mais precisas. Finalmente, a presente abordagem de estimativa de alimentação é baseada na previsão do número de “buzzes” e, portanto, poderia ser potencialmente aplicada a uma série de espécies de odontocetes, potencialmente permitindo estimativas mais precisas do esforço de alimentação, do que os índices grosseiros e gerais tipicamente derivados de perfis de mergulho 2D.

Palavras-chave: Cachalote, Dtag, dados tempo-profundidade, comportamento de alimentação, modelo preditivo de “buzzes”.

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CHAPTER II: Sperm Whale Foraging Behaviour: A Predicted Model Based On 3D Movement and Acoustic Data from Dtags

List of abbreviations

AICc – Akaike's information criterion

ARGOS – Advanced Research and Global Observation

ARS – area restricted search

Dtags – digital acoustic tags

GLMMs – generalized linear mixed models

ICI – inter-click interval

IPI – inter-pulse interval

PCA – prey capture attempt

TDRs – time depth recorders

VHF – very high frequency

Chapter I

General introduction

The Sperm Whale

The sperm whale (*Physeter macrocephalus*, Linnaeus 1758), the largest of all toothed cetaceans, is commonly recognized by its prominent and squarish head forming the hypertrophied nasal complex, which can make up to one-third of the animal's total length. As a consequence of its massive head, it is the animal with the biggest brain and spermaceti organ (Jefferson et al. 2011), which is strongly involved in sound production, contributing to the powerful and characteristic echolocation clicks of sperm whales (Whitehead 2018).

Adult females are up to 11m long and 15t weight, while adult males can reach and overpass 16m and 45t, making sperm whales the most sexually dimorphic of all cetacean species (Connor et al. 1998, Teloni et al. 2008, Jefferson et al. 2011, Whitehead 2018). The body is laterally compressed with a characteristically S-shaped blowhole offset to the left as a consequence of the skull's asymmetry (Whitehead 2018). The dorsal fin is thick, low and rounded and is located at approximately 2/3 of the body; the fluke is wide, flattened and triangular, and is usually used for photo-identification (Jefferson et al. 2011).

The body presents a dark coloration, ranging from black, dark bluish-gray to brown-grey, but the belly is lighter and often white (Gosho et al. 1984). In addition, tooth scars are frequently found in the head of mature males as a consequence of intra-sexual competition and/or prey fighting (Kato 1984, Jefferson et al. 2011). Between 20 to 26 pairs of conical teeth are present uniquely in the Y-shaped lower jaw (Gosho et al. 1984, Whitehead 2018).

Distribution and life history

Sperm whales are widely distributed across all oceans and seas, from the tropics to the pack-ice of both hemispheres. Their distribution is not homogenous but is associated with steep bottom topography, strong oceanographic fronts, and high productivity (Jefferson et al. 2011). Furthermore, sperm whale distribution varies with sex and maturity stage. Adult females, juveniles and calves of both sexes live in long-term stable social units, moving within tropical and temperate waters (Christal et al. 1998, Whitehead 2003). Young males disperse from their natal groups before puberty and

aggregate with other males in “bachelor herds”. As males grow older, they decrease in sociality and increase in migration range; after attaining sexual and social maturity, in their twenties, adult males turn solitary and gradually move to cold waters near the poles. The older the male, the further north it ventures, only coming back to warmer waters in their late twenties in order to mate (Gosho et al. 1984, Whitehead 2003, Jefferson et al. 2011, Whitehead 2018). During the mating season, adult males often associate with social units for short periods of time (Best 1979, Pinela et al. 2009, Ortega-Ortiz et al. 2012) (Figure 1.1).

The drivers of sexual segregation in sperm whales are not well understood but likely reflect different physiological, ecological and social needs of the sexes. Males may access high-latitude food sources to avoid competition from females and increase growth rates to attain competitive size, while calf thermoregulatory limitations may prevent social units from reaching colder waters. In addition, social units may avoid high-latitude waters to reduce predation risk of small calves (Whitehead 2003).

Sperm whales are “k-selected” species and as such are characterized by low reproductive rates, slow growth, high survival, and consequently longevity, presumably reaching over 50 years (Christal et al. 1998, Jefferson et al. 2011, Whitehead 2018). Females become sexually mature at around 9 years, and ~9m in length, and usually give birth every 5 years, although pregnancy rates slow down with age and may differ between locations. Adult males, on the other, reach sexual maturity at 25-27 years of age when they are most frequently from about 11.6 m upwards in size (Tarasevich 1967, Best 1979, Whitehead 2003). Sperm whales are polygamous; most births occur between the summer and after a gestation of 14 to 16 months, with newborns being around 4m long and weighting 1ton (Best et al. 1984).

Sources of natural mortality in sperm whales are poorly understood. Mass strandings are common in some regions but the causes and rates are unknown. Pitman et al. (2001) suggested that killer whale predation may be underappreciated in the evolution of sperm whale ecology, but no estimates have been provided.

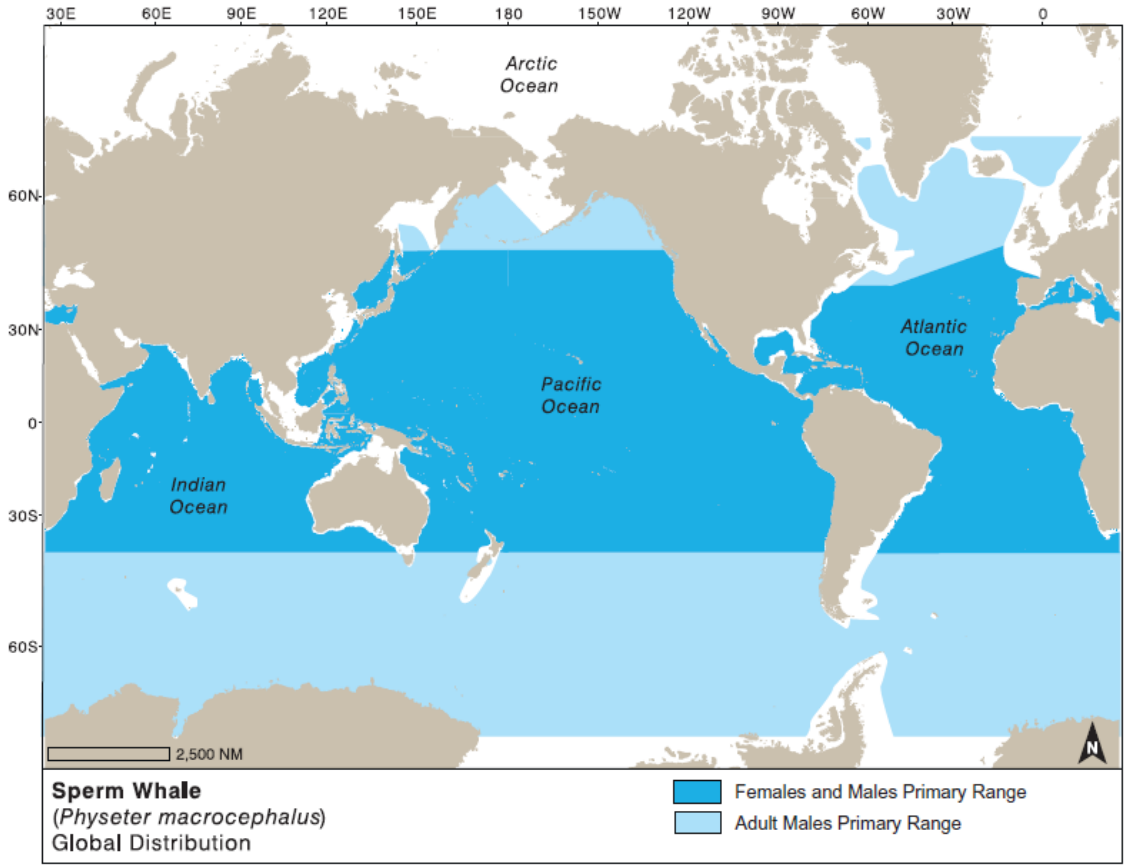

Figure 1.1. Sperm whale distribution map showing the sexual differences in habitat range between males and females (extracted from Whitehead et al. 2018).

Sounds and sound production

Sounds play a fundamental role in the lives of cetaceans and sperm whales are no exception. Although sperm whales occasionally produce some low intensity tonal sounds (e.g., "squeals", "trumpets" and "pips") (Goold 1999, Teloni et al. 2005), clicks are the most frequent sound produced by sperm whales. Clicks are sharp-onset, broadband, impulsive vocalizations with energy ranging from 5 to 25 kHz (Madsen et al. 2002a, Madsen et al. 2002b). They are involved in foraging behaviour and social communication.

At least four kinds of clicks (usual clicks, buzzes, codas, and slow clicks) have been identified (Weilgart 1993, Jaquet et al. 2001, Miller et al. 2004). The usual clicks are the most common sound produced by sperm whales, and consist in long trains of regularly spaced clicks, often lasting for minutes and with an inter-click interval (ICI) of about 0.5-1.0s. Usual clicks are highly directional and have the highest biologically produced source levels ever recorded (Møhl et al. 2000). Usual clicks have a much longer

echolocation range than other click types (Madsen et al. 2002a) and are mostly used in echolocation, for scanning the environment, searching, locating and capturing prey (Jaquet et al. 2001, Madsen et al. 2002a, Miller et al. 2004). Buzzes, also termed "creaks", consist of high-frequency low amplitude clicks produced in rapid click trains with short ICI 15-100ms (Madsen et al. 2002a, Fais et al. 2016). Buzzes are produced at depth during foraging dives; they have shorter echolocation range than usual clicks, providing a higher resolution scan and therefore, more detailed information about their close environment. Several studies have linked the production of buzzes with bursts of swimming speed (Amano and Yoshioka 2003, Aoki et al. 2012) and fast jaw movements (Fais et al. 2016). For these reasons, it has been proposed that buzzes are emitted during the foraging terminal phase in order to provide high resolution echolocation of their target after being detected by their click scan and enable the capture of the prey, with the aid of fast jaw movements (Madsen et al. 2002a, Miller et al. 2004, Fais et al. 2015, Fais et al. 2016). Codas are stereotyped sets of 3 to 40 clicks lasting 0.2-5s, and are mostly produced within social units for communication (Rendell and Whitehead 2003). The slow clicks or "clangs" are composed of distinctively ringing and metallic clicks repeated every 5-8s (Madsen et al. 2002b). They have been reported only in adult males, and may be used for long range communication between males or with females, the function depending on the behavioural context in which they are produced (Weilgart and Whitehead 1988, Madsen et al. 2002b, Oliveira et al. 2013).

The sperm whale has a particularly complex sound production system integrated in the nasal complex, in which the spermaceti plays a determinant role (Møhl et al. 2000, Madsen et al. 2002a). The nasal complex is composed of a set of wax-filled cavities: the spermaceti organ; the "junk", a structure formed by several wax-filled cavities interspaced by connective tissue; two nasal passages extending through the nose; two air sacs diverting from the right nasal passage; and the monkey lips or "museau de singe", composed of connective tissue and surrounding the right nasal passage (Wahlberg et al. 2005) (Figure 1.2).

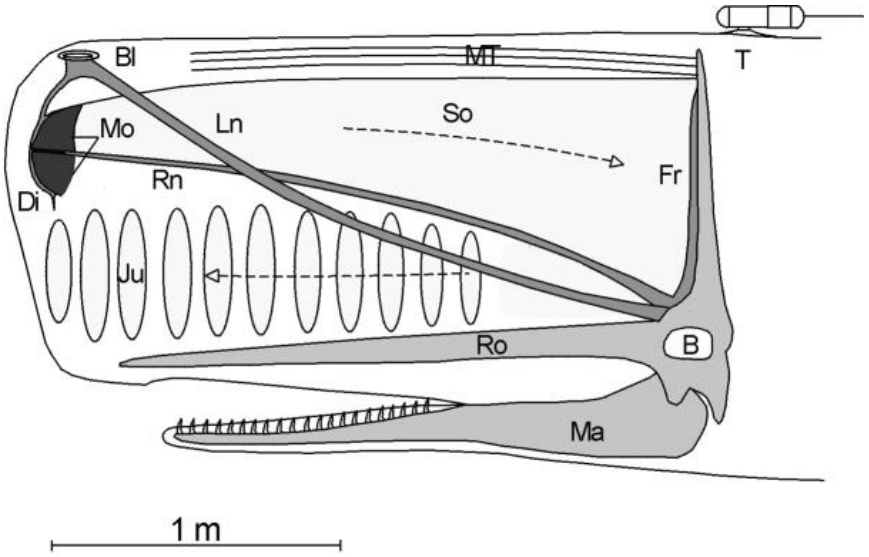

Figure 1.2. Cross section of the head of a sperm whale showing anatomical structures relevant for sound production: B, brain; Bl, blow hole; Di, distal air sac; Fr, frontal air sac; Ju, junk; Ln, left naris; Ma, mandible; Mo, monkey lips/museau de singe; MT, muscle/tendon layer; Ro, rostrum; Rn, right naris; So, spermaceti organ; T, tag. Arrows indicate the sound path according to Møhl, 2001. (Extracted from Madsen et al. 2002).

The sound production mechanism starts in the so-called monkey lips by pressurized air flowing from the right naris through the monkey lips, producing the initial sound pulse (Wahlberg et al. 2005). The majority of the click energy is redirected backward along the spermaceti and reflected in the frontal air sac. After this, part of the click signal is reflected into the junk, causing its emission towards the water, and the rest of the pulse is reflected back in the distal air sac and again in the frontal air sac, which leads to the formation of a second pulse redirected to water by the junk as well (Madsen et al. 2002a, Wahlberg et al. 2005). The successive repetition of these back and forth pulse reflections creates a loop resulting in the complex multipulsed structure of sperm whale clicks, where each inter-pulse interval (IPI) is proportional to the size of the spermaceti organ and, hence, of the individual whale (Gordon 1991, Rhinelander and Dawson 2004).

Foraging behaviour

Sperm whales present two clear and distinctive behavioural modes: foraging in the deep ocean versus resting and socializing in shallow waters (Whitehead 2003, 2018). Sperm whales are deep-diving predators, spending more than half of their lives below 500m depth, where they mainly target meso- and benthopelagic squids, although they may

also consume other cephalopods, deep-fishes and invertebrates (Madsen et al. 2002b, Aoki et al. 2007, Teloni et al. 2008, Thode et al. 2015). Moreover, sperm whale diet and foraging behaviour varies geographically (Martin and Clarke 1986, Clarke et al. 1993, Evans and Hindell 2004) and, more importantly between the sexes, possibly as a result of physiological needs and habitat characteristics.

Adult females and subadults display a stereotyped foraging behaviour, making 30-45 min long dives, to 600-1200 m depths (Amano and Yoshioka 2003, Watwood et al. 2006). Mature males target a higher proportion of deep-fishes than females and youngsters, although cephalopods still dominate their diet (Martin and Clarke 1986, Whitehead 2003, Isojunno and Miller 2018). Mature males also show a bimodal foraging mode, preying on highly mobile prey in shallow waters (14-500m), and on less mobile, more densely distributed and perhaps more predictable resources during deep dives (1000-1860m) (Isojunno and Miller 2018). The selection between shallow and deep foraging modes seems to be governed by the whale perception of the relative energetic profits in each depth layer (Teloni et al. 2008). Each foraging dive is followed by a resting period at the surface of approximately 9-10 min, or by shallow dives and behavioural displays (Watkins et al. 2002, Amano and Yoshioka 2003, Whitehead 2003).

In order to navigate in the environment and ultimately detect and capture prey, sperm whales use usual clicks and buzzes, whose echo give them information about their surroundings (Miller et al. 2004, Watwood et al. 2006). After leaving the surface for a deep foraging dive, adult females and subadults start making usual clicks at approximately 100-220 m depth (Madsen et al. 2002a, Watwood et al. 2006, Oliveira 2014). In the Azores archipelago, the foraging phase, the period between the first and last buzz within a dive, occurs between 700-1200 m and lasts around 25 min (Oliveira 2014). The first usual click of adult males from higher latitudes is produced between 4 and 218m and buzzes have been recorded between 17 and 1860m depth (Teloni et al. 2008).

How sperm whales actually locate and capture their prey has become and on-going debate since the first scientific studies of the species. Early in the 19th century, Beale (1835) proposed for the first time the “sit-and-wait strategy” by which sperm whales attract and capture their prey luring them with their white lips. This hypothesis was later

changed by the bioluminescence mucosa produced by squid prey that remains attached to the mouth of the whale (Gaskin and Cawthorn 1967) and by bioluminescent organisms that are stimulated with the whale's movement (Fristrup and Harbison 2002). Contrary to these passive foraging theories, Rice (1989) proposed that sperm whales may use an active search and pursue of prey while swimming randomly with their mouths open, and using tactile sense to detect their prey. However, after the discovery that sperm whale produce intense broadband pulses termed "clicks", most of the researchers supported the idea that sperm whales use an active foraging behaviour in which these clicks are involved (Worthington and Schevill 1957). Some investigators even hypothesized that these clicks were used to acoustically debilitate prey and enable their capture (Norris and Mohl 1983). The most accepted of these hypotheses was active searching and pursuing using echolocation (Norris and Harvey 1972, Whitehead and Weilgart 1991, Jaquet et al. 2001, Whitehead 2003).

However, it was not until the development of animal attached tags that some light was brought into this conjecture, confirming the previous hypothesis. The long bottom times and the variability both in depth and velocity with "bursts of speed" found by Amano and Yoshioka (2003) confirmed that sperm whales use an "active search-and-pursue strategy" while foraging, in which the clicks are used as a biosonar in order to echolocate prey (Madsen et al. 2002a, Madsen et al. 2002b, Møhl et al. 2003). Both clicks and buzzes are involved in the foraging behaviour of sperm whales for the detection and capture of prey items. Madsen et al. (2002a) showed the echolocation ranges of creaks (buzzes) were remarkably smaller than those of usual clicks. In fact, it has been suggested that usual clicks are used to scan the environment and detect prey, whereas buzzes are emitted before prey capture (Madsen et al. 2002a, Miller et al. 2004).This fact was later confirmed by Fais et al. (2016) who demonstrated strong acceleration ("jerks") approximately 5 seconds before the end of most buzzes, suggesting these jerks are triggered by "rapid movements in the gular region during strikes at prey".

They also seem to have developed "active auditory stream segregation", enabling the tracking of fast-moving prey in challenging reverberant conditions (Fais et al. 2015). Therefore, sperm whales adjust their sounds according to prey range: as sperm whales approach prey, they increase the click rates (shorter ICI) and reduce the source levels in order to provide high temporal and spatial resolution "image" of the prey in the last few

meters before capture. In addition, the ICI has also been related to the animal's size and manoeuvrability, as the distance to be covered by the sound increases with animal's size (Fais et al. 2015, Fais et al. 2016).

The finding of intact prey items in the stomach content, and the anatomy of the gular apparatus, point towards suction feeding (Fais et al. 2016). In addition, sperm whales start buzzing at a median distance of 24m from the prey (Tønnesen et al. 2020). Moreover, sperm whales rely upon information obtained in previous dives and preceding foraging events in order to decide where to invest their foraging effort (Fais et al. 2015).

Nevertheless, how prey items are echolocated in the last few meters of their capture, especially after being off from the sperm whales' sonar range, how they are finally captured and engulfed and the role of sound production in this final phase still remains an incognita.

Social behaviour and communication

Sperm whales are probably among the most social cetaceans, with a multilevel social structure: solitary adult males, young male associations, small tight familiar units, bigger group movements and socializing during different activities.

Female sperm whales spend their whole lives in the company of other females and their offspring, forming the so-called social or matrilineal familiar units, composed of around 7-12 members (Whitehead 2003), often genetically related (Christal et al. 1998, Pinela et al. 2009). Different units are frequently seen moving together for several hours or days forming aggregations of 20-30 individuals; aggregations of animals within a certain geographical area are most likely "clans" of animals which share similar coda vocalizations (Christal et al. 1998, Whitehead 2003, 2018).

The formation of groups is especially important for the protection of calves and youngsters against predators, "alloparental care" and most likely increased foraging success (Pitman et al. 2001, Whitehead 2003, 2018). When being attacked, most often by killer whales, sperm whales display the commonly known "marguerite formation", adults gather and may react aggressively with their flukes or jaws against predators, maintaining calves or injured individuals in the middle (Pitman et al. 2001, Jefferson et

al. 2011). Therefore, long-term relationships and alliances are critical for the survival and reproductive success of sperm whales. The communal care of the young, termed "alloparental care", ensures almost continuous protection and even nursing to calves by other females ("allosuckling"), while their mothers forage at the depths (Whitehead 1996a, Perrin et al. 2009). Although this might offer foraging advantages to adult females, the benefit of socializing to sperm whale foraging success is still unclear (Whitehead 1989).

The highest social level of sperm whale corresponds to the "vocal clans" or "coda clans", a group of whales or units that share a coda repertoire or dialect (Rendell and Whitehead 2003, Gero et al. 2016b, Amorim et al. 2020). As explained earlier, codas consist of three or more broadband clicks produced in stereotyped patterns exchanged at or near the surface to communicate (Watkins and Schevill 1977). Coda clans are not genetically distinct, and therefore, coda repertories or dialects are culturally transmitted through social learning (Rendell and Whitehead 2003). Different coda clans coexist sympatrically in the Pacific and Eastern Caribbean, while in the Atlantic codas may differ depending on the geographic area (Gero et al. 2016a, Gero et al. 2016b). Therefore, different coda dialects may segregate and establish the sperm whale society, as social units seem only to associate with each other if they share a dialect (Gero et al. 2016a). In addition, codas may encode individual and behavioural information in the form of fine variations in the click pattern and in the type of coda produced in a certain context (Antunes et al. 2011, Oliveira et al. 2016).

Male sperm whales, on the other hand, switch from a social to a solitary lifestyle. After leaving the natal social unit they usually aggregate in bachelor groups and become solitary with age (Whitehead 2003, Pinela et al. 2009). However several temporal clusters of mature males have been registered both in breeding grounds (Christal and Whitehead 1997) and feeding grounds (Lettevall et al. 2002). Besides, solitary mature males from higher latitudes have been identified to produce slow clicks, mainly at the surface and during ascents from foraging dives (Oliveira et al. 2013), in some sort of communication, as previously speculated by several authors (Madsen et al. 2002b, Whitehead 2003). The click interval and waveform of slow clicks plus the context in which they are produced point towards a potential long range communication in which individual encoded information might be transmitted (Oliveira et al. 2013).

Sperm whales also perform a series of behavioural displays at the surface - breaching, flucking-up, spyhops, sideflucking- which have been associated to communication and social interactions, although the context and meaning of such displays remain unknown (Whitehead 2003, Dudzinski et al. 2009, Whitehead 2018).

Sperm whale in the Azores archipelago

Sperm whales can be found year round in the waters around the Azores archipelago (Silva et al. 2014). Groups of females and offspring –sometimes accompanied by large adult males- are present during the summer months, confirming that the Azores serves as a breeding and feeding ground for sperm whales (Clarke 1956, Matthews et al. 2001, Pinela et al. 2009). In addition, the year round presence of large males and their interaction with female groups (Pinela et al. 2009, Silva et al. 2014) suggests that mating may also occur in the archipelago.

Whaling in the Azores was one of the most important local industries during the 20th century. Prieto et al. (2013) estimated that between 1896-1987 a total of 23557 whales were hunted. This unsustainable catch had a huge impact on the population, from which it is still recovering. Based on the development of a multi-state open robust design model (MSORD) using opportunistic data, the sperm whale open population in the Azores has been estimated to 275 individuals for the year 2014 (Boys et al. 2019).

The sperm whales visiting the Azorean archipelago belong to a single genetically differentiated population with high genetic diversity and absence of inbreeding (Pinela et al. 2009). The sperm whale primary social units are mainly composed by members of the same family and are highly related with members of secondary social groups (union of primary social units) (Christal and Whitehead 2001, Whitehead 2003, Pinela et al. 2009). Immature males from the Azores archipelago have a significantly higher age at dispersal (16.6 years) than previously found, which could be consequence of the whaling era (Pinela et al. 2009).

While the Azorean sperm whale population is still recovering from the whaling era, an indirect but potentially harmful activity has been increasing in the region during the last decades. The whale watching industry in the Azores archipelago has the sperm whale as its main target species. While no clear short-term reaction pattern has been identified, a

continuous monitoring should be carried out in order to analyse the potential long-term effects of the whale watching industry for the Azorean sperm whale population (Magalhães et al. 2002).

Conservation

The presence of top-predators as sperm whales and other cetaceans has been identified as an excellent indicator of ecosystems' health and productivity (Katona and Whitehead 1988). However, sperm whale populations worldwide are still recovering from the declines caused by the commercial whaling, which hunted them to near extinction during the last centuries (Whitehead et al. 1997, Baker and Clapham 2004, Gero and Whitehead 2016). "Open-boat" whaling for sperm whales commenced in 1712 and peaked around 1830, continuing until the end of the 19th century and becoming one of the most important industries due to its precious oil for which it was hunted (Whitehead 2002, 2003). The development of engine-powered whaling vessels, harpoon guns and other technologies greatly triggered the intensification of the hunts. During the 1950-1960s the sperm whale hunt experimented the second peak after all the other whale populations have been drastically depleted and the sperm whale became the principal target (Whitehead 2002, Baker and Clapham 2004). Whitehead (2002) estimated the sperm whale global population in 360000 whales using a model that scales up the population from the 24% of sperm's whale global surveyed habitat.

Commercial whaling ceased in 1988 with the International Whaling Commission moratorium, although some native groups from Indonesia are still allowed a small quota (Whitehead 2018). However, even though sperm whales are not being hunted anymore they are currently facing an increasing number of threats from anthropogenic activities and possibly climate change (Magalhães et al. 2002, Whitehead 2003, Farmer et al. 2018). The most obvious of these threats are those causing direct mortality, including ship strikes, entanglement in fishing gear, ingestion of plastic debris or chemical pollution (Whitehead 2003). Nevertheless there are a series of other threats that can have adverse effects on individual health and ultimately on populations, like underwater noise (Whitehead 2003, Farmer et al. 2018).

Sperm whales depend on sound to forage, communicate, navigate and perceive threats, and high levels of noise can cause behavioural disturbances and potentially reduce

foraging and reproductive efficiency (Miller et al. 2009, Isojunno et al. 2016, Farmer et al. 2018). Most of the research on the consequences of noise to sperm whales have focused on occasional sources of intensive noise, such as military sonars and seismic surveys used for oil and gas exploration (Miller et al. 2009). Fewer have addressed the potential impact of chronic disturbance from vessel noise, including from the whale watching boats.

Therefore there is an important gap in our understanding about the potential long-term effects of permanent noise pollution that could lead to significant biological and ecological consequences for the population. This could be especially important in an area as the Azores archipelago, that constitutes an important feeding, calving and mating ground for sperm whales (Oliveira 2014, Silva et al. 2014).

Tools to study the foraging behaviour of sperm whales

Direct observation is one of the most powerful tools to study animal behaviour and it constitutes the base of the first behavioural studies of sperm whales. Nonetheless, direct observation of sperm whales is rather complicated by the fact that the animals spend most of their time underwater. For this reason, several tools have been developed during the last decades (e.g., depth sounders, hydrophones, animal-borne tags) enabling to study the behaviour of sperm whales at depth. Some of the most important tools are hydrophones and animal attached tags. Hydrophones are electronic instruments specifically designed for recording sounds produced underwater. They convert sound waves into electrical voltage by detecting pressure changes in the surrounding environment (Gordon and Tyack 2002, Romero Vivas and León López 2010). They allow the continuous monitoring of underwater sounds for long periods of time, allowing documenting the presence, movements and behaviour of vocalizing cetaceans, including sperm whales (Mann 1999, Gordon and Tyack 2002, Perrin et al. 2009).

Animal attached tags are capable of collecting location, movement, sounds, and even environmental data for periods ranging from hours to years (Mann 1999, Johnson and Tyack 2003). Depending on how the data are obtained and transmitted, there are two main types of tags: satellite tags and archival tags. Satellite tags allow tracking animals for long periods of time as the information is being transmitted directly while the animal is at the surface. However, satellite transmissions can only send small amounts of

compressed data at each uplink due to bandwidth and satellite limitations of the ARGOS system, resulting in low resolution data, and therefore are not suitable for fine-scale studies (Szesciorka et al. 2016, Palacios et al. 2019). Archival tags, on the other hand, have a high sampling rate, providing a high resolution dataset of different variables depending on the tag and included sensors, and therefore enable the detailed study of animal behaviour. These tags need to be recovered by using the incorporated VHF transmitter in order to obtain the data, and both their internal storage and attaching duration limit the total recording time, resulting in high resolution datasets over short periods of time, most frequently less than 24h (Szesciorka et al. 2016, Palacios et al. 2019).

Time-depth recorders (TDRs) are small size archival tags designed to study the diving and foraging behaviour of marine animals. They were first used in the late 60s and early 70s to study the diving patterns of Weddell seals (*Leptonychotes weddellii*) in the Antarctic, and have been commonly used since the 90s (Perrin et al. 2009). TDRs provide depth variation over time, therefore computing a 2D profile of the animal dive. Since its development, several models have been designed, reducing its size while increasing capacity and number of sensors. Most commonly, TDRs include a depth, temperature, light-level, and wet/dry sensors (Wildlife Computers) and most frequently they are attached to the animal's body with suction cups or barbs/hooks (Hooker and Baird 2001, Madsen et al. 2002a). TDRs datasets have been widely used to investigate the diving and foraging behaviour of several marine mammal species (Heerah et al. 2014), namely sperm whales (Amano and Yoshioka 2003).

As a consequence, most foraging behaviour studies using TDR tags use low resolution data and are based solely on depth data, relying on very "coarse" indices. As a matter of fact, U-shaped diving profiles with a clear "horizontal" bottom phase (Figure 1.3) have been widely interpreted and used as indicators of foraging activity for different deep diving predators (Thompson et al. 1991, Lesage et al. 1999).

The development that revolutionized the study of the foraging behaviour of cetaceans was the incorporation of hydrophones into animal attached archival tags (e.g., Dtags, Acousonde tags, A-tags). Among these, digital acoustic tags (Dtags) (Johnson and Tyack 2003) are small size archival tags that include one or two high resolution hydrophones.

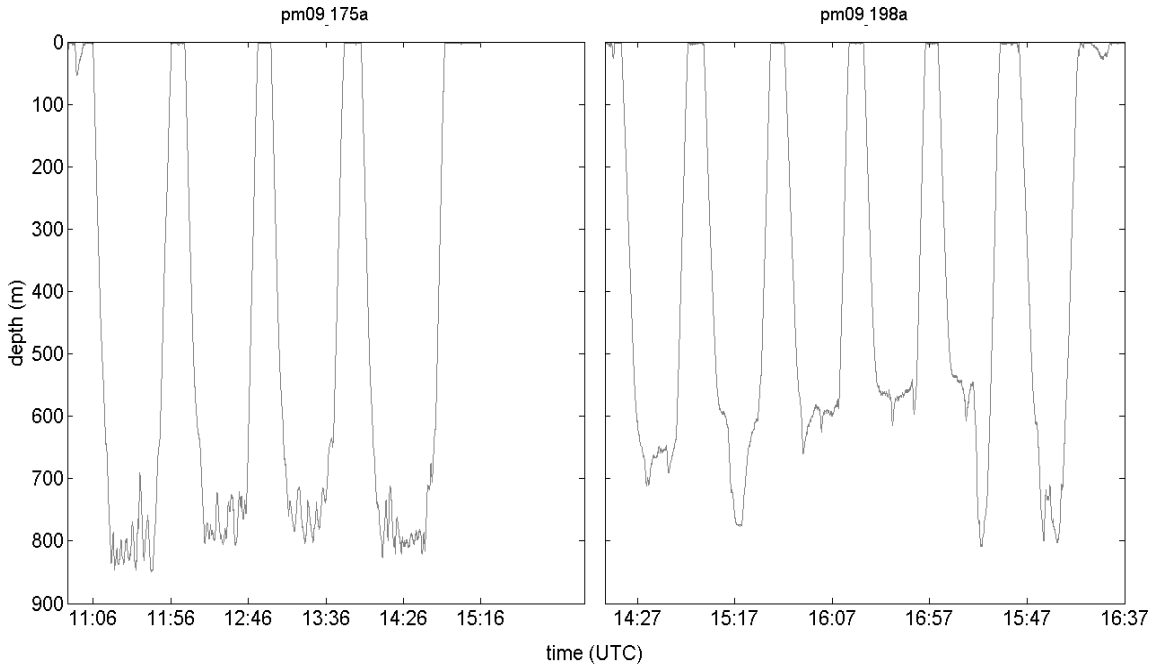

Figure 1.3. Sperm whale 2D dive profile (time-depth) from TDRs showing a series of U-shaped dives indicative of foraging activity.

Dtags record sounds produced by tagged individuals, as well as surrounding sounds, continuously through the dive cycle. In addition to hydrophones, Dtags contain sensors for pressure (depth), acceleration and magnetic field. Dtags are normally deployed with suction cups and, after a pre-programmed time, an electric conductor penetrating the suction cup is burnt off releasing the tag which floats to the surface. An integrated VHF transmitter allows the animal tracking and the recovery of the device after its release (Johnson and Tyack 2003).

Dtags provide high-resolution acoustic and 3D movement data of tagged animals and enabled understanding how sperm whales use sound during foraging (Miller et al. 2004, Watwood et al. 2006, Oliveira et al. 2013, Fais et al. 2015, Fais et al. 2016) (Figure 1.4). Some of these studies revealed that bursts of speed at the bottom of the dive were correlated with the production of buzzes; buzz production was thereafter considered as the best indicator of a prey capture attempt and used for the detailed examination of sperm whale foraging behaviour (Fais et al. 2015, Fais et al. 2016)

Notwithstanding, Dtags are not commercially available and can only be used through leasing contracts or under agreements with tag developers. This makes access to Dtags extremely difficult, expensive and unpredictable. Because of this, studies on foraging

behaviour using Dtag data are most often based on very small sample sizes, usually collected from a handful of animals in a single year, do not accounting for individual or environmental variability or the effect of gender or age class. Moreover, it is almost impossible to rely on Dtags to monitor changes in behaviour associated with anthropogenic activities, as these studies generally require sampling over multiple seasons and years.

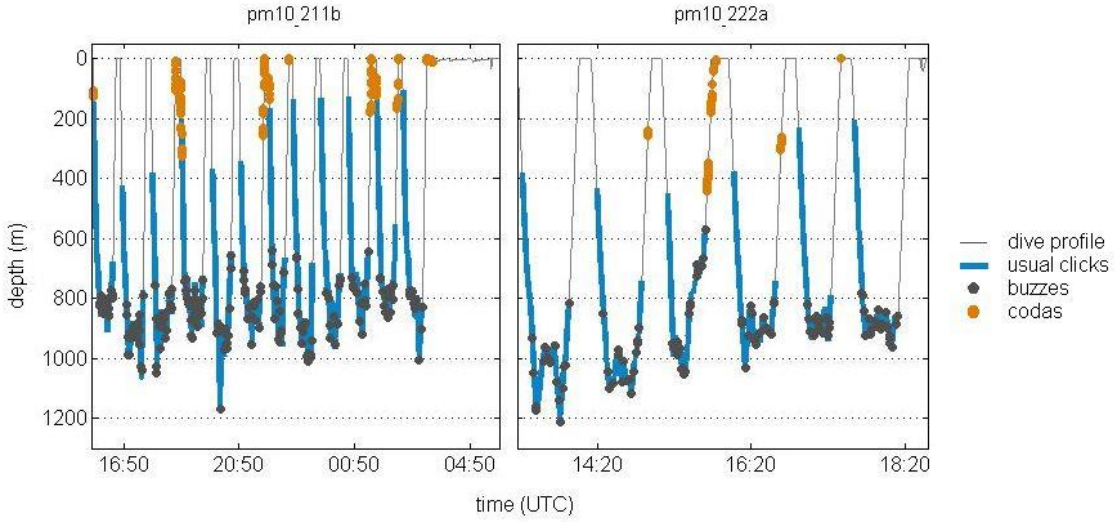

Figure 1.4. Sperm whale 2D dive profile (time-depth) from a Dtag showing acoustic production.

Motivation of the current study

While sperm whales are protected by several international agreements and legislation (e.g., The International Whaling Commission, the International Union for Conservation of Nature, the Convention of Biological Diversity, Habitats and Birds Directive, etc.) they face important and an increasing number of threats (Perrin et al. 2009). Several human activities (e.g., fisheries, shipping traffic, deep-sea mining, construction, etc.) are likely to alter species distribution, directly or indirectly through changes in prey availability and habitat alterations. Moreover, sperm whales rely heavily on sound to find and capture prey, and increasing human use of the oceans, with the consequent introduction of noise, can directly interfere with their ability to forage successfully (Whitehead 2003, Perrin et al. 2009, Jefferson et al. 2011). Therefore, knowledge of foraging behaviour is critical to identify important areas for sperm whale conservation, as well as to evaluate and monitor the potential impacts from human activities.

While time-depth recorders provide valuable information about the diving behaviour of marine species, the lack of acoustic data imposes obvious limitations to study the foraging behaviour of those marine species that use sound to search and capture prey items, as the sperm whale (Madsen et al. 2002b, Miller et al. 2004, Watwood et al. 2006). On the other hand, the use of high resolution movement and acoustic recording tags is extremely difficult and pricey, and as a consequence, studies on sperm whale foraging behaviour based on these tags are generally limited by small sample sizes and short sampling periods.

The development of accurate, high-resolution foraging indices from 2D dive profiles, would allow maximizing the use of already available and future datasets obtained from cheap and widely available TDRs. Improved predictions of foraging events in the TDR data would allow the re-interpretation of extensive datasets available for many geographic areas, and provide much needed information on the sperm whale foraging behaviour. Finally, analysing time-series datasets of diving activity would allow the identification of potential changes in the foraging behaviour, in response to climate or anthropogenic changes which could have caused biological and ecological population effects.

Previous research on foraging indices from low-resolution 2D dive data

Measuring the actual foraging effort and foraging success of deep divers still remains a complex objective due to the fact that there is no way of actually verifying the foraging activity at great depths. For this reason, the study of the foraging behaviour of deep diving predators relies on the identification of proxies or indices capable of estimating the foraging effort (Dragon et al. 2012, Vacquié-Garcia et al. 2015). The most traditional methods analysed the animal dive profile and estimated the foraging effort based on the time at depth or breaking up the dive in the classical 3 phases: ascent, bottom, descent; from which the bottom time and the U-diving profiles were used as the foraging time (Thompson et al. 1991, Lesage et al. 1999, Bailleul et al. 2007, Dragon et al. 2012).

Heerah et al. (2014) demonstrated the possibility of developing an accurate method for the detection and quantification of foraging effort in low resolution diving data. The method is based on the identification of diving parameters which correlate with the

foraging effort found in the high resolution data and capable of being detected in the low resolution data (Heerah et al. 2014, 2015, Heerah et al. 2019). Despite the fact that this method was developed for southern elephant seals (*Mirounga leonina*) and Weddell seals (*Leptonychotes weddellii*) it clearly highlights the possibility of doing the same for other deep diving predators if a proper species specific index is identified.

Objectives

The principal aim of this master thesis is to develop a method to accurately identify and quantify the foraging effort and prey capture attempts of sperm whales in 2D dive profiles from TDRs datasets, when no concurrent acoustic information is available. In order to achieve this, a subset of high-resolution movement and acoustic data collected from tags with 3D movement and acoustic sensors (Dtags) were analysed in order to identify and calculate a set of candidate 2D movement parameters associated with buzz production, indicative of prey capture attempts.

These movement parameters were then combined into a model to predict prey capture attempts in a 2D dive profile. Model performance was assessed by applying it to a second subset of novel Dtag data, for which presence of buzzes was used to confirm foraging events. If successful, this model could be extremely useful to identify foraging behaviour in TDR data, thereby increasing the potential of this tool in future studies and maximizing the application of an extensive and already available dataset.

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Chapter II

Sperm Whale Foraging Behaviour: A Predicted Model Based On 3D Movement and Acoustic Data from Dtags

Sperm Whale Foraging Behaviour: A Predicted Model Based On 3D Movement and Acoustic Data from Dtags

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Abstract

High-resolution sound and movement recording tags (e.g. Dtags, Acousonde tags, A-tags) offer unprecedented views of the fine-scale foraging behaviour of cetaceans, especially those that use sound to forage, such as the sperm whale (*Physeter macrocephalus*). However, access to these tags is difficult and expensive, limiting studies of sperm whale foraging behaviour to small sample sizes and short time periods,

preventing inferences at the population level. The development of accurate foraging indices from relatively inexpensive time-depth recorder (TDR) data would allow obtaining data from a larger number of individuals, and capitalizing on datasets already available, providing long-term analyses of foraging activity. In this study, data from high-resolution acoustic and movement recording tags from 8 sperm whales was used to build predictive models of the number of buzzes (i.e, indicative of prey capture attempts (PCA)) for dive segments of different lengths, using dive metrics calculated from time-depth data only. The number of buzzes per dive segments of 180s and 300s was best predicted by the average depth, depth variance, vertical velocity variance and number of wiggles. Model performance was best for 180s segments, accurately predicting the number of buzzes in 63% of the segments used to construct the model and in 58% of the segments for new individuals. Predictive accuracy reached 81%, when only presence or absence of buzzes in segments was assessed. These results demonstrate the feasibility of finding a reliable index of sperm whale foraging activity for time-depth data, when combining different dive metrics. This index estimates the number of buzzes over short dive segments (of 180s), enabling investigating and quantifying PCAs at very fine-scales. Finally, this work contributes to leverage the potential of time-depth data for studying the foraging ecology of sperm whales and the capacity of applying this approach to a wide range of cetacean species.

Introduction

Efficiency at foraging is crucial for predators so that enough energy is left for the remaining life-history traits, ensuring growth, reproductive success and ultimately, individual survival (Charnov 1976, Krivan 1996). Consequently, foraging activity constitutes one of the most important drivers of populations' dynamics (Robinson et al. 2012). For this reason, the study and quantification of foraging effort over long time series represents one of the most powerful tools to assess populations' health and the impact linked to climatic or anthropogenic changes (McIntyre et al. 2011, Bost et al. 2015, Nabe-Nielsen et al. 2018).

For the vast majority of marine diving predators, foraging occurs at depth, and consequently direct observation of foraging activity is, at least, challenging. As a result, the first studies on the foraging behaviour of diving predators (e.g., northern elephant

seal (*Mirounga angustirostris*) (Morejohn et al. 1970); ringed Seal (*Phoca hispida Schreher*) (McLaren 1958) and various cetaceans (Fitch and Brownell Jr 1968)) were based in occasional direct observations and the examination of stomach contents. Through the analyses of stomach contents of whaled or stranded individuals, Clarke (1955) revealed that sperm whales (*Physeter macrocephalus*) are deep-diving predators, that feed primarily on bathypelagic and demersal prey. These studies also provided the first estimates of daily food consumption of individual animals (Lockyer 1981, Clarke et al. 1993). Later, observations of defecation by fluking whales were used to infer feeding success and investigate variations with behavioural context and oceanographic conditions (Clarke 1955, Whitehead 1996b).

Advances in animal-attached biologging devices allowing the continuous tracking and recording of movements and behaviour of animals at sea, revolutionized the study of foraging behaviour of marine predators (Mann 1999). Some of the first biologging devices collect only vertical movement data (i.e., depth), usually at sampling frequencies of 1 second or more (Kooyman et al. 1976, LeBoeuf et al. 1986). Data collected by time-depth recorders (TDRs) enable reconstructing the 2D dive profile and have been widely used to calculate different dive metrics to infer foraging activity (Watkins et al. 2002, Amano and Yoshioka 2003). Numerous studies have separated dives into different phases - descent, ascent, bottom, and surface – to discriminate and quantify time spent transiting, foraging, and resting (Hindell et al. 1991), and used dive shape to separate foraging (U-shaped) from exploratory (V-shaped) dives (Thompson et al. 1991, Lesage et al. 1999). Several studies have used dive duration, time spent at the bottom of a dive, the number of wiggles (vertical excursion with a certain extent) or vertical sinuosity as indirect measures of foraging effort or success in several pinniped (Dragon et al. 2012, Gallon et al. 2013, Heerah et al. 2014) and cetacean species (Watts and Draper 1986, Baird 1994, Croll et al. 2001, Calambokidis et al. 2007)**.** Use of these metrics is based on the assumption that diving predators increase vertical sinuosity and reduce vertical speed once prey are encountered, in order to remain in depth layers with higher density of prey and thus maximize foraging efficiency (Dragon et al. 2012). This is analogous to a behaviour known as area restricted search (ARS) (Kareiva and Odell 1987), but in the vertical dimension. Evidence for a link between ARS behaviour measured from surface tracks and foraging activity has come from studies on different taxa (Kuhn et al. 2010, Dragon et al. 2012). Nevertheless, the complexity in the diving

behaviour of most marine predators later revealed by high resolution movement tags, highlighted the need to refine this approach and to develop and validate species-specific proxies to estimate foraging effort from time-depth data (Heerah et al. 2014, 2015, Vacquié-Garcia et al. 2015).

The use of the first animal attached tags and underwater acoustic recording tools (e.g., hydrophones) provided new insights into the foraging behaviour of marine predators, especially those that use sound to forage as the sperm whale (Weilgart 1993, Jaquet et al. 2001). Sperm whales produce sharp-onset, broadband, impulsive vocalizations with energy ranging from 5 to 25 kHz commonly known as "clicks" (Madsen et al. 2002a, Madsen et al. 2002b), from which at least four kinds (usual clicks, buzzes, codas, and slow clicks) have been identified (Weilgart 1993, Jaquet et al. 2001, Miller et al. 2004). Codas are stereotyped sets of 3 to 40 clicks lasting 0.2-5s, and are mostly produced within social units for communication (Rendell and Whitehead 2003). Slow clicks are composed of distinctively ringing and metallic clicks repeated every 5-8s (Madsen et al. 2002b), only produced by adult males for long range communication (Weilgart and Whitehead 1988, Madsen et al. 2002b, Oliveira et al. 2013). Usual clicks are the most common, and consist in long trains of regularly spaced clicks, often lasting for minutes and with an inter-click interval (ICI) of about 0.5-1.0s. (Møhl et al. 2000). They are highly directional and have the highest biologically produced source levels ever recorded, suggesting its use in habitat scanning and echolocation and enabling the search, location and capture of prey (Jaquet et al. 2001, Madsen et al. 2002a, Miller et al. 2004). Buzzes consist of high-frequency low amplitude clicks produced in rapid click trains with short ICI 15-100ms, therefore providing a higher resolution but shorter echolocation range (Madsen et al. 2002a, Fais et al. 2016).

The development of more sophisticated tags incorporating high-resolution tri-axial accelerometers and hydrophones (e.g., Dtags, Acousonde tags, A-tags) enabled unprecedented views of the 3D fine-scale diving behaviour of cetaceans and the correlation of movement and acoustic data (Watwood et al. 2006, Teloni et al. 2008). Amano and Yoshioka (2003), and later Aoki et al. (2012), demonstrated that sperm whales spent long periods of time at the bottom of the dives with great variability in depth and velocity, and occasional bursts of speed, suggesting an active-pursuit hunting foraging strategy. Using digital acoustic recording tags (Dtags) (Johnson and Tyack 2003), Miller et al. (2004) demonstrated that buzzes occurred most often at the bottom

phase of sperm whale dives, and were associated with increased manoeuvring. Later, the existence of strong and sudden changes in acceleration were found to occur near the end of the buzzes (Fais et al. 2016). For these reasons, click and buzz production have been widely used as proxies for sperm whale prey searching and capture attempts respectively (Miller et al. 2004, Watwood et al. 2006, Teloni et al. 2008, Miller et al. 2009, Fais et al. 2016).

Unfortunately, the wide-scale and long-term use of the aforementioned tags is severely constrained by their high cost and reduced availability, limiting data collected to a few animals and hours (rarely more than 24 h), and making it difficult to assess within or between individual variations in foraging behaviour. The development of a reliable index of sperm whale foraging activity from time-depth data alone, could offer the possibility of using relatively inexpensive, widely available TDRs to investigate different aspects of sperm whale foraging behaviour. This would not only enable increasing the sample size and duration of studies but also conducting retrospective analysis of existing diving datasets to assess changes in foraging behaviour over longer time scales.

Several studies have succeed in developing methods capable of predicting foraging effort and prey capture attempts (PCA) in low resolution diving datasets of several marine species: Antarctic fur seals (*Arctocephalus gazella*) (Viviant et al. 2014), southern elephant seals (*Mirounga leonine*) and Weddell seals (*Leptonychotes weddellii*) (Heerah et al. 2014, 2015), and Australian fur seals (*Arctocephalus pusillus doriferus*) (Volpov et al. 2016).

Viviant et al. (2014) modelled Antarctic fur seals PCA at the dive scale based in the ascent and descent rates, and concluded that vertical transit rates are between the most important parameters in predicting foraging success in a marine predator. Heerah et al. (2014) developed a more robust method that uses a broken stick algorithm in order to summarize each dive in the best number of broken stick points (inflection points), from which those highly sinuous segments were found to indicate foraging activity of both southern elephant seals and Weddell seals. Volpov et al. (2016) showed that the most accurate diving parameters in predicting Australian fur seal foraging activity in time-depth datasets were bottom time and ascent rate. However, both Viviant et al. (2014)

and Volpov et al. (2016) agreed that accuracy of diving predictor variable differs depending on the data resolution.

While the aforementioned studies were quite successful in developing reliable proxies of foraging activity that could potentially be applied to several pinnipeds, there have been no attempts to develop similar indices for large toothed whales, including sperm whales. The objective of this study was to develop a predictive model of foraging effort in sperm whales from low-resolution time-depth data. To do this, we used high-resolution movement and sound data from eight sperm whales instrumented with Dtags in the Azores archipelago during 2017-2019 to extract time-depth values with a sampling frequency of 1 s and detect buzzes (considered to represent PCA). These dataset was then used to calculate a suite of diving metrics at different time scales and to use these metrics to develop models predicting the number of buzzes. Finally, we tested the predictive performance of the best model by applying it to an independent time-depth dataset derived from four other sperm whales fitted with Dtags, to compare predicted and observed buzzes.

Material and methods

Tagging data

Data used in this study were from sperm whales tagged by the Azores Whale Lab group (http://whales.scienceontheweb.net/) during 2017-2019 around the islands of Faial and Pico, in the Azores archipelago (38ºN, 28ºW).

The tags used were digital acoustic recording tags (Dtag, version 3) (Johnson and Tyack 2003) that record 2-channel acoustic data (96 kHz sampling frequency, 16 bit resolution), and collect pressure, 3-axis accelerometer and 3-axis magnetometer data at 50 Hz (16 bit). Tags were attached to the backs of surfacing whales with four suction cups using a 11m cantilevered pole from a 9m long rigid-hulled inflatable boat (RHIB), or a 6m handpole from a 5m long RHIB. Tags were located and recovered by radio tracking after being released from the whale, naturally or after a programmed maximum deployment time that varied across sampling years.

Sperm whale tagging was conducted under research permits 37/2016/DRA, 80/2017/DRA and SAI-DRA/2018/3602 issued by the Regional Government of the Azores.

Data processing

Dtag data from 12 sperm whales were available for analysis in this study. Dtag data from eight of these whales were used for data exploration and to calculate dive metrics to be included in the models predicting the number of buzzes. Data from the remaining four whales were used to test model predictions (Table 2.1).

The first dive of all animals was removed to eliminate potential effects from the tagging operation (Miller et al. 2009). In order to exclude resting periods at the surface and shallow submersions from further analysis, only dives deeper than 25m (i.e., about two body lengths, Teloni et al. (2008)) were analysed. A foraging dive was defined as being deeper than 25m and including at least one buzz (Isojunno and Miller 2015).

Table 2.1. Summary of the sperm whale tagging, diving and acoustic data used in this study.

	Animal	Frequency (Hz)	Tagging date	Duration (hh:mm)	Nº Dives	Nº of Dives Analysed	Nº Foraging Dives	Nº of Buzzes
Model development	sw17_194a	20	13 July 2017	8:57	10	8	8	135
	sw18_170a	25	19 June 2018	4:22	6	5	4	34
	sw18_172a	25	21 June 2018	5:04	6	5	5	94
	sw18_177a	25	26 June 2018	6:21	5	4	4	87
	sw19_137a	25	17 May 2019	9:28	18	16	9	134
	sw19_158a	25	07 June 2019	7:51	9	8	6	67
	sw19_160a	25	09 June 2019	25:45	31	28	22	180
	sw19_163a	25	12 June 2019	13:54	18	17	11	85
Total				**81:42**	**103**	**91**	**69**	**816**
Model evaluation	sw17_203a	20	22 July 2017	17:13	8	8	8	85
	sw18_173a	25	22 June 2018	3:13	4	3	3	12
	sw18_292a	25	19 October 2018	6:35	10	10	5	70
	sw19_088a	25	29 March 2019	23:17	25	25	24	360
Total				**50:18**	**47**	**46**	**40**	**527**

Depth data collected by Dtags at 20-25 Hz were downgraded into 1Hz to match the best resolution of the TDR data (1 second sampling rate). Acoustic data had been previously analysed by Azores Whale Lab group for the 12 sperm whales using MATLAB 2007b and 2016b (Mathworks, Inc., Natick, MA) with a custom spectrogram (512 sample FFT block size, 15 s segments with 2 s overlap) and dive depth display, to identify usual clicks and buzzes. Clicks produced by the tagged whale were identified based on their higher received acoustic level, angle-of-arrival to tag hydrophones (Johnson et al. 2006)

and temporal characteristics (Zimmer et al. 2005). Following Isojunno and Miller (2018), the start time of a buzz was defined as a change in amplitude and/or spectral content of clicks before a fast run (click rate >5 Hz); buzz end time was defined as the start of a pause before the next usual click train, exceeding the ICI of the subsequent usual clicks, or start of a pause before the next surfacing. In the absence of a clear pause, the end time of a buzz was identified as a change in amplitude and/or spectral content of clicks. The time between the end of one buzz and the start of the following was defined as the inter-buzz interval (IBI).

Approach to select the time scale of analysis

Following Fais et al. (2016), that showed the occurrence of "strong and sudden changes in acceleration *near the end* of the buzzes", we attempted to identify the duration of these moments to choose the time scale for subsequent analyses. First, the duration of buzzes and of inter-buzz intervals (IBI) was calculated. Based on these results, dives from all eight whales (Table 2.1) were divided into segments of different lengths, with and without overlap, by applying a moving window, with package 'zoo' (Zeileis and Grothendieck 2005) in R (R Core Team, 2016).

A second approach was to automatically divide sperm whale dives into segments of different length, by applying an optimized broken stick algorithm (Heerah et al. (2014). This method iteratively selects a series of inflexion points for individual dives, and calculates a suite of summaries that is used to automatically select the number of inflexions that best summarised the dive shape. These inflections define the start and end of each segment along the dive. While this method has shown promising results in the analysis of pinniped dives (Heerah et al. (2014), segments generated in the sperm whale dives analysed in this study were nonsensical, despite many efforts to adjust algorithm parameters (although it might be possible to refine the algorithm). Therefore, outputs from the broken stick algorithm are not shown here and this approach was abandoned.

Dive metrics

A set of candidate dive metrics were calculated for different dive segment lengths, based on knowledge of the species' foraging behaviour (Amano and Yoshioka 2003, Watwood et al. 2006, Aoki et al. 2007, Teloni et al. 2008, Aoki et al. 2012, Fais et al. 2016, Isojunno and Miller 2018) and their potential to predict buzzes (Table 2.2). All dive metrics were calculated from time-depth data with 1s of temporal resolution and 1m of depth resolution. For each dive segment, the total number of buzzes and the total buzz duration were calculated.

Sperm whales produce more buzzes and show increased manoeuvring, changes in body orientation and dive inflections during the bottom phase of their dives (Miller et al. 2004). To attempt to capture these behaviours in 2D dive data, for each dive segment we calculated a series of parameters potentially indicative of foraging at depth (average depth, sum depth, maximum depth), and of changes in depth resulting from increased manoeuvring along the vertical axis (variance and standard deviation of depth). As pointed out by Heerah et al. (2014), foraging during the bottom phase of the dive does not necessarily mean that foraging occurs at the maximum depth of the dive. Therefore, for each segment of a given dive, bottom times were calculated as the percentage of time of that segment spent at more than 60%, 70%, 80% and 90% of the dive maximum depth.

In sperm whales, the production of buzzes is associated with strong bursts of speed and changes in acceleration (Fais et al. 2016). Although time-depth data cannot be used to calculate swimming speed and acceleration, it can be used to detect changes in the vertical component of animal motion. Vertical velocity was calculated as the depth difference between time t+1 and time t, and vertical acceleration was defined as the difference in vertical velocity between consecutive time intervals. Average, total sum, variance and standard error of the selected diving metrics per segment were also calculated and tested for its capacity to predict buzz production.

Inflection points were defined as those moments in time t in which depth was higher or lower than depth at $t+1$ and time $t-1$. Following Aoki et al. (2007), a wiggle was defined as an inflection point with a difference in depth > 20m to the subsequent infection point. Steady points reflect the time spent at the same depth, and can be indicative of prey chasing along the horizontal axis (Aoki et al. 2012). Sequences of points at the same

depth (i.e. steady points) were common within our data, and therefore the total number of steady points and the number of steady point sequences per segment were calculated. The degree of vertical sinuosity is believed to be an indication of ARS behaviour during an animal's dive and was found to be the best proxy of prey capture attempts in southern elephant seals and Weddell seals (Heerah et al. 2015). In this study, the vertical sinuosity (hereafter, sinuosity) was calculated for each dive segment, as the ratio between the vertical distance swum in a linear path (i.e., the absolute depth difference between the start and end of the segment) and the sum of all the vertical distances the whale has actually swum in that segment (Heerah et al. 2015). A segment with a sinuosity of 1 expresses a straight path during this part of the dive; any deviation from a straight path decreases the sinuosity towards 0.

Prior to constructing the model, all candidate variables were tested for collinearity using the Pearson's correlation coefficient. Only those variables with a Pearson's coefficient < 0.7 were selected (Dormann et al. 2013) (Figure A3.1 of the annex).

Table 2.2. Description of dive metrics calculated for each dive segment.

Dive metrics	Definition	Calculation	Unit
Individual	Whale individual ID		
DiveID	Dive number per individual		
Total Nº Buzzes	Total Nº of Buzz	Summed	No unit
Total Buzz duration	Total Nº of seconds during which there is a buzz occuring	Summed	No unit
Steady points	Point X with = depth to the previous second (X-1)	Summed	No unit
Start steady points	Start point of a sequence of steady points	Summed	No unit
End steady points	End point of a sequence of steady points	Summed	No unit
Inflections	Point X in which depth (X-1)>X and (X+1)>X or (X-1)<X and (X+1)<X	Summed	No unit
Wiggles	Inflection point with more than 20m difference with the following inflection point	Summed	No unit
Depth			
Average depth	Averaged depth	Averaged	m
Sum depth	Summed depth	Summed	m
Maximum depth	Maximum depth	Maximum	m
Variance depth	Depth variance	Variance	m
Standard error depth	Depth standard error	Standard dev.	m
Depth difference	Absolute depth difference between start-end of the segment	Difference	m
Bottom time 60% max. Depth	Ratio 0-1 of the % of time spent at more than 60% of the dive's maximum depth	$sum(t_z)/t$	Ratio 0-1
Bottom time 70% max. Depth	Ratio 0-1 of the % of time spent at more than 70% of the dive's maximum depth	Formula	Ratio 0-1
Bottom time 80% max. Depth	Ratio 0-1 of the % of time spent at more than 80% of the dive's maximum depth	Formula	Ratio 0-1
Bottom time 90% max. Depth	Ratio 0-1 of the % of time spent at more than 90% of the dive's maximum depth	Formula	Ratio 0-1
Vertical velocity	Absolute depth difference between time *t+1* and time *t*		$m\ s^{-1}$
Average vertical velocity	Vertical velocity averaged over segment duration	Averaged	$m\ s^{-1}$
Sum vertical velocity	Vertical velocity summed over segment duration	Summed	$m\ s^{-1}$
Variance vertical velocity	Vertical velocity variance over segment duration	Variance	$m\ s^{-1}$
Standard error vertical velocity	Vertical velocity standard error over segment duration	Standard dev.	$m\ s^{-1}$
Vertical acceleration	Absolute vertical velocity difference between time *t+1* and time *t*		$m\ s^{-2}$
Average vertical acceleration	Vertical acceleration averaged over segment duration	Averaged	$m\ s^{-2}$
Sum vertical acceleration	Vertical acceleration summed over segment duration	Summed	$m\ s^{-2}$
Variance vertical acceleration	Vertical acceleration variance over segment duration	Variance	$m\ s^{-2}$
Standard error vertical acceleration	Vertical acceleration standard error over segment duration	Standard dev.	$m\ s^{-2}$
Sinuosity	Absolute depth difference / Sum vertical velocities over segment duration	$\|\Delta z\|$ / sum (v)	Ratio 0-1

t_z = time at depth greater than x; t = segment duration; Δz = depth difference; v = vertical velocity

Time scale for modelling

As buzzes were short and IBIs were long, dive metrics were initially calculated for dive segments of 5s, 10s, 15s, 20s, 25s, 30s, and 60s, with and without overlap, and models were built with these metrics. However, although some dive metrics were significant, they showed weak prediction capacity of the number of buzzes, possibly explaining the poor fit and small proportion of variance explained by all models developed (not shown here).

Model development and evaluation

Sperm whale foraging behaviour exhibits important differences between the sexes, most likely as a result of distinct physiological needs and habitat characteristics (Watwood et al. 2006, Teloni et al. 2008, Isojunno and Miller 2018). In addition, depth range targeted seems to be governed by the whale perception of the relative energetic profits in each depth layer (Teloni et al. 2008), which could induce differences in diving depth between whales tagged at different times and in different areas. For these reasons, the relationship between the number of buzzes and the candidate dive metrics was investigated using generalized linear mixed models (GLMMs), with individual whale as a random effect (package 'lme4' (Bates et al. 2007) in R) . Models were fitted with a Poisson family distribution and maximum likelihood of Laplace Approximation. Separate models were built for each segment length. The initial models contained all dive metrics with Pearson's correlations <0.7. Models were ranked based on the corrected Akaike's information criterion, AICc (Burnham and Anderson 2004), and the model with the lowest AICc was selected.

The predicted number of buzzes per segment was estimated based on the best fitting GLMM, and compared to the observed number of buzzes. Model predictive performance was first evaluated with the train data, to test the model ability to predict the number of buzzes for the dataset used to construct the model. Then, the model performance was assessed by fitting the model to a new dataset, collected from four other sperm whales (Table 2.1), and comparing predicted and observed buzzes per dive segment. This procedure was applied only to dive segments of 180s and 300s, which were the ones yielding the best modelling results (see Results). Modelling results were

compared between segment lengths to identify the best temporal scale for future analyses, and across individual sperm whales.

Results

Buzz duration and IBI

The eight sperm whales performed a total of 101 dives during the tag deployments. After removal of the first dive of all whales and of incomplete dives (due to tag release or malfunction), the dataset analysed contained information on 91 dives (Table 2.1). Of these, 69 (76%) were classified as foraging dives, during which 816 buzzes were detected (Table 2.1). Buzz duration ranged between 2 and 50s but most buzzes were substantially shorter, lasting only 4-6 s (Figure 2.1). Buzzes of 2-14s represented 95% of all buzzes identified. Over 95% of all IBI recorded fell within the 0-500s range (Figure 2.1).

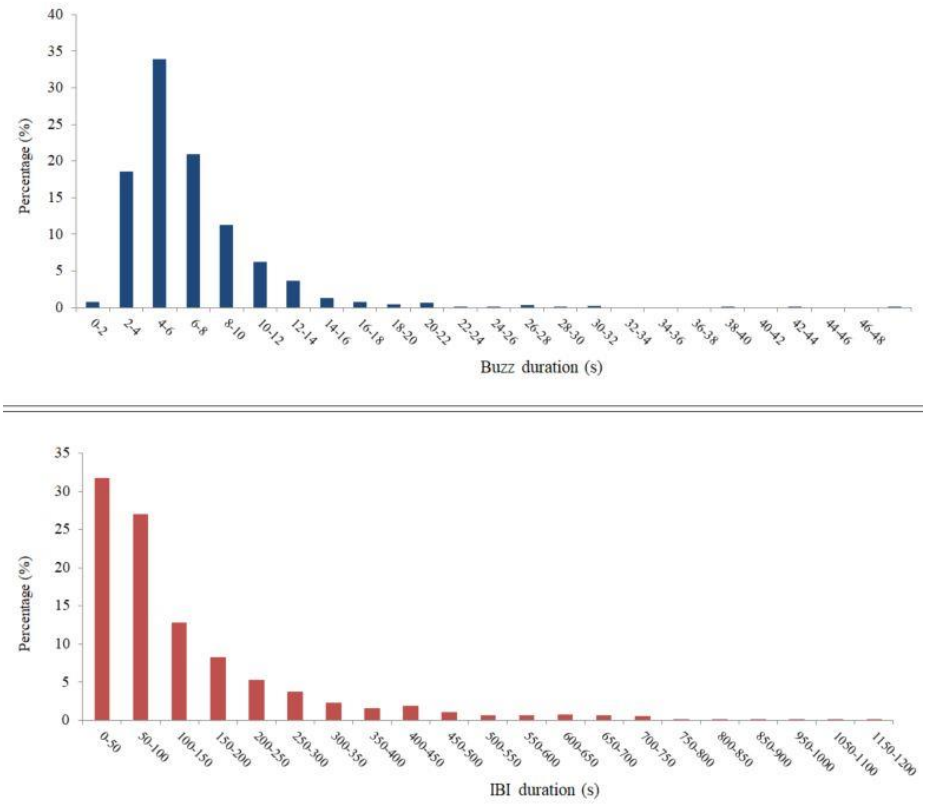


Figure 2.1. Distribution of the duration of buzzes (top) and of the inter-buzz-interval (IBI) (bottom) for the 12 sperm whales analysed in this study.

An exploratory analysis of dive metrics calculated for longer dive segments, of 180s and 300s of duration, strongly suggested that these could yield satisfactory results. Therefore, the following sections present the results obtained for dive segments of 180s and 300s.

The dives of the eight whales analysed were slit into 1115 segments of 180s and 653 segments of 300s of duration (Figure 2.2). Number of buzzes per segment ranged from 0-5 and 0-6 for 180s and 300s, respectively. About 43% (n=484) of the 180s segments and 58% (n=380) of the 300s segments contained at least one buzz.

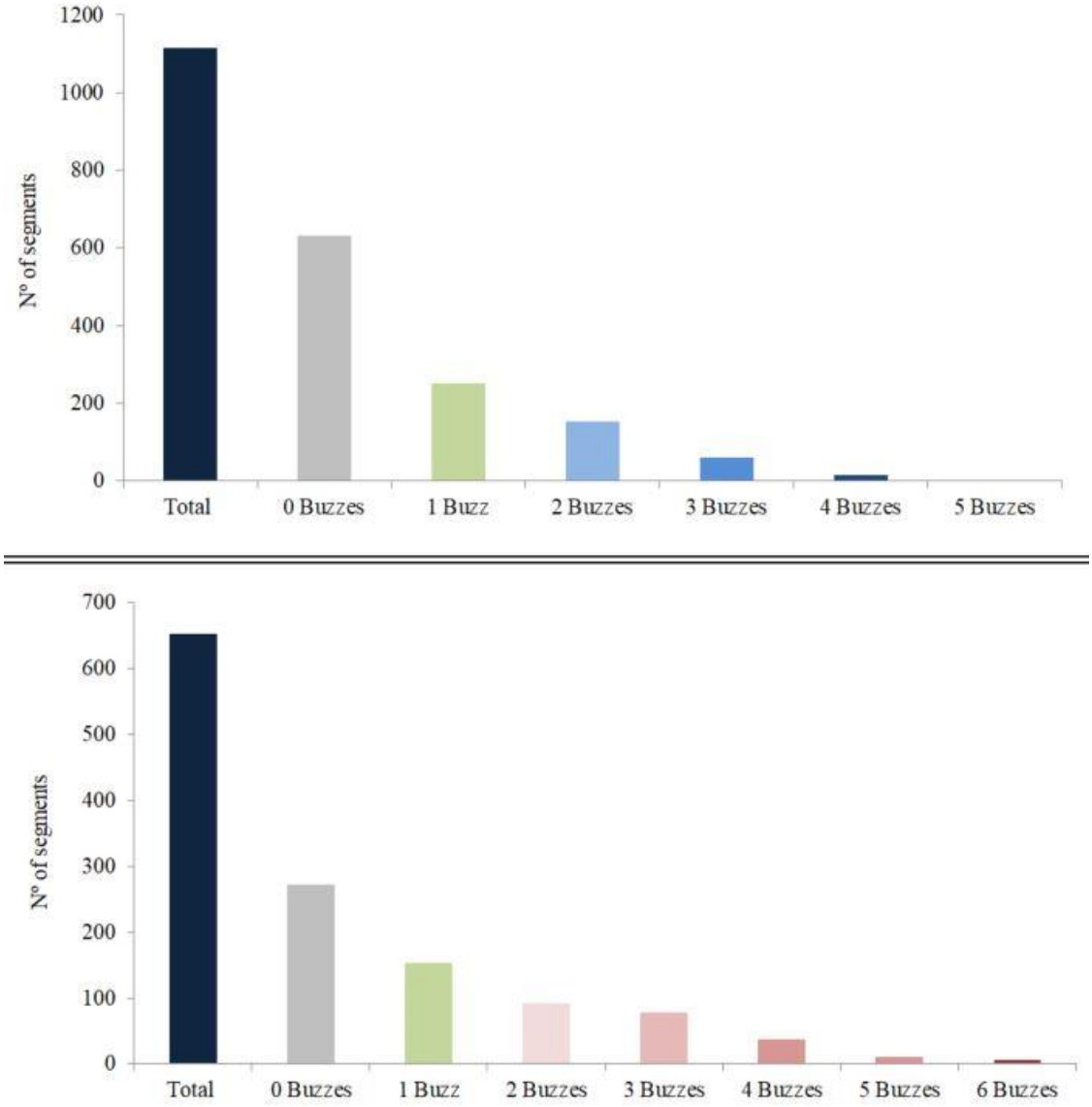


Figure 2.2. Number of segments as a function of the number of buzzes for segments of 180s (top) and of 300s (bottom).

Relationship between buzz production and diving behaviour

The best fitting GLMM for the number of buzzes per segments of 180s and 300s included the same dive metrics: average depth, variance of depth, variance of vertical velocity, and wiggles, and individual whale as a random effect (whale ID). The summary of the modelling output is included in Table 2.3.

Table 2.3. Summary of the best GLMMs of the number of buzzes per segment, for segments of 180s and 300s.

	180s Segments			300s Segments		
Random effects	Variance	SD		Variance	SD	
ID	0.04886	0.221		0.05314	0.2305	
Fixed effects	Estimate	SE	p-value	Estimate	SE	p-value
Intercept	-0.86679	0.1017	< 0.001	-0.19049	0.1008	0.0588
avg_depth	0.94089	0.06899	0.114	0.80268	0.069	0.0142
var_depth	-0.36236	0.07215	< 0.001	-0.31804	0.07689	< 0.001
var_vel	0.22038	0.02697	< 0.001	0.15613	0.03467	< 0.001
wiggles	0.04326	0.02734	< 0.001	0.07303	0.02979	< 0.001

Average depth and variance of depth were, respectively, the first and second most important predictors of the number of buzzes for both segments lengths (Table 2.3). In general, relationships between dive metrics and number of buzzes were very similar for the 180s and 300s segments. Dive segments with buzzes were deeper than segments without buzzes (Figure 2.3). The number of buzzes increased with increasing average depth for segments with 1-3 buzzes, but segments with 3-5 buzzes occurred at similar depths. Variance of depth was higher in segments without buzzes and in segments with the maximum number of buzzes (n=5), than in the segments containing 1 to 4 buzzes (Figure 2.3). Variance of vertical velocity was higher in segments with buzzes than without buzzes, and the number of buzzes increased with increasing vertical velocity variance (Figure 2.3). No wiggles were found in segments with 1 buzz and in segments without buzzes. Occurrence of wiggles was higher but similar in segments with 2-4 buzzes and highest in segments with the maximum number of buzzes (n=5) (Figure 2.3).

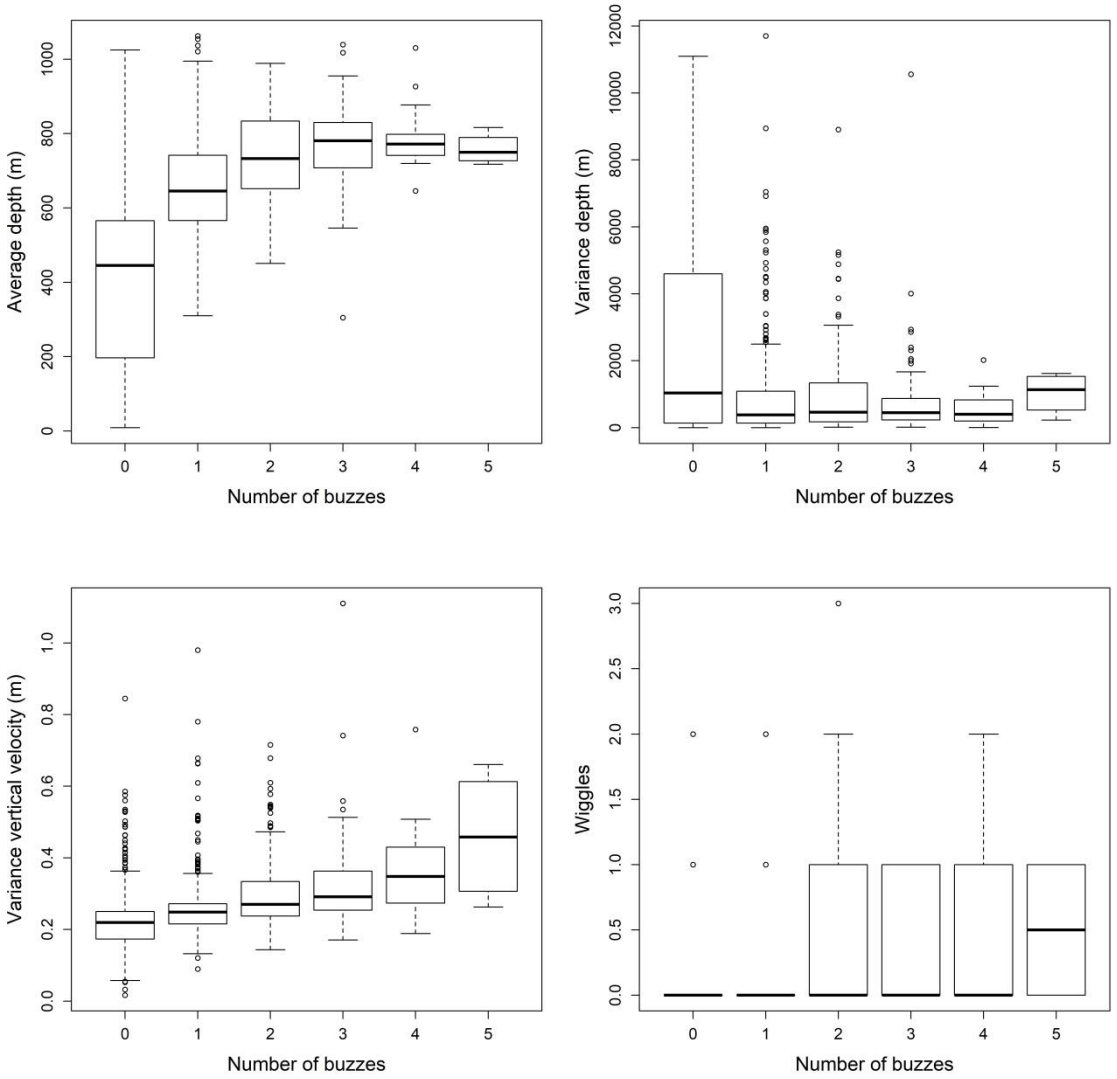


Figure 2.3. Boxplots of dive metrics for segments of 180s with different number of buzzes. Boxplots for segments of 300s were very similar and are not presented. The horizontal line represents the median, the box represents the 25th and 75th percentiles and the whiskers represent the extreme values within 1.5 times the length of the box. Outliers are plotted as points.

Predictive ability of the models

The model capacity to predict the number of buzzes per segment was compared between segments of 180s and 300s using train and test data (Table 2.4). As expected, the ability of models to correctly detect the number of buzzes per segment was higher in the train data than in the test data. Also, the model for the 180s was substantially better at predicting the number of buzzes than the model for the 300s segments. The model for the 180s accurately predicted the exact number of buzzes in 63% of the segments for the

train data and 58% of the segments for the test data, compared with the 51% (train data) and 41% (test data) of the model for the 300s (Table 2.4).
Both models were very good at discriminating between segments with and without buzzes (Table 2.4). In fact, model accuracy for both segment lengths and data types ranged from 80% to 82%, where the highest percentage of correct detections was with the model for the 300s segments on the train data.

Table 2.4. Predictive performance of the best fitting GLMMs for segments of 180s and 300s. The percentage of correct detections is shown both for the number of buzzes and for the presence/absence of buzzes per segment.

	180s Segments		300s Segments	
	Train data (8 individuals)	Test data (4 individuals)	Train data (8 individuals)	Test data (4 individuals)
Number of segments	1115	621	653	330
Percentage of correct predictions of number of buzzes per segment	63%	58%	51%	41%
Percentage of correct predictions of presence/absence of buzzes per segment	81%	81%	80%	82%

As the model for the 180s segments was better at predicting the number of buzzes, a more in-depth analysis of its predictive performance was carried out, in order to contribute to future model improvements.

Differences between the number of buzzes observed and predicted per segments of 180s for both train and test data are shown in Figure 2.4 and Table 2.5. Overall, the model tended to predict fewer buzzes per segment than those observed, especially in the test data (Table 2.5). In the majority of these cases (75% for the train data and 67% for the test data), the model predicted only one buzz less than what was observed (Figure 2.4). Similarly, 85% of the segments that were overpredicted by the model showed a difference of one buzz. However, in a few segments of the test data, overpredictions were of >5 buzzes, and in one instance the model predicted 11 buzzes in a segment with only 2 buzzes present (Figure 2.4).

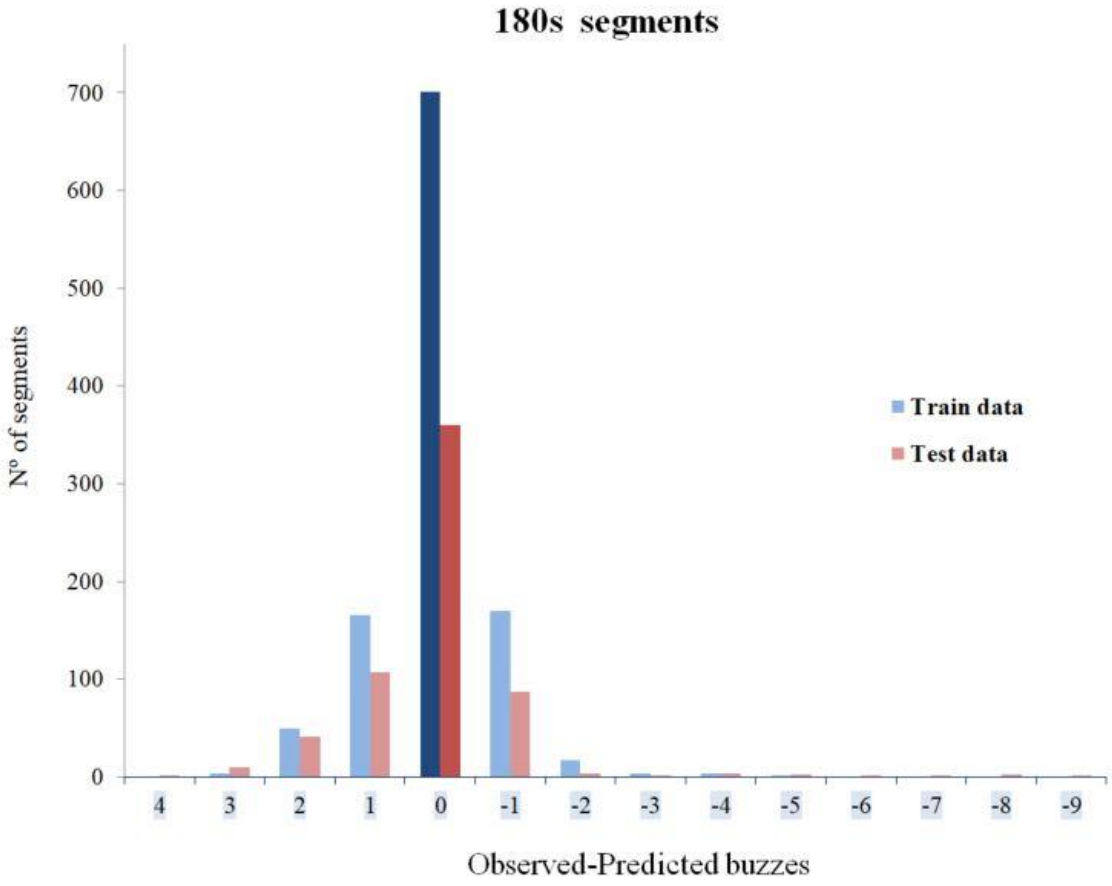


Figure 2.4. Differences in the number of observed and predicted buzzes per segment for train and test data, using outputs from the model of 180s segments. Dark colours indicate the number of segments with no difference in the number of predicted and observed nº of buzzes.

Table 2.5. Differences in the number of observed and predicted buzzes for segments of 180s for both train and test data. The percentage of correct prediction of the number of buzzes is shown for both train and test data.

Diff (Observed-Predicted) total Buzz events 180s segments					
Train data 1115 segments			Test data 621 segments		
Negative diff	Positive diff	diff = 0	Negative diff	Positive diff	diff = 0
194 (17%)	220 (20%)	**701 (63%)**	102 (16%)	159 (26%)	**360 (58%)**

Predictive ability of the models across individuals and within dives

The performance of the model (for 180s segments) at predicting the number of buzzes per segment was similar among individual whales, for both the train and test data (Figure 2.5A and C). For nearly all individuals, the distribution of observed-predicted values was centred about zero, suggesting a balance between over and underpredictions. In addition, the mean of observed-predicted values was very close to zero and most

values were within -2 to +2 range. Still, in one case (individual sw19_088a) the model performed considerably worse, predicting fewer buzzes in approximately 50% of the segments and overpredicting from 3 to 9 buzzes in other segments.

To further investigate the causes of the poor predictivity of the model, the distribution of the differences between observed and predicted buzzes were examined as a function of two model variables: the average depth and the variance of the vertical velocity (Figure 2.5B and D). For both the train and test data, the higher differences were found at the greatest depths and higher vertical velocities. This suggests that the model is unable to predict well at the upper end of the data range of both predictors.

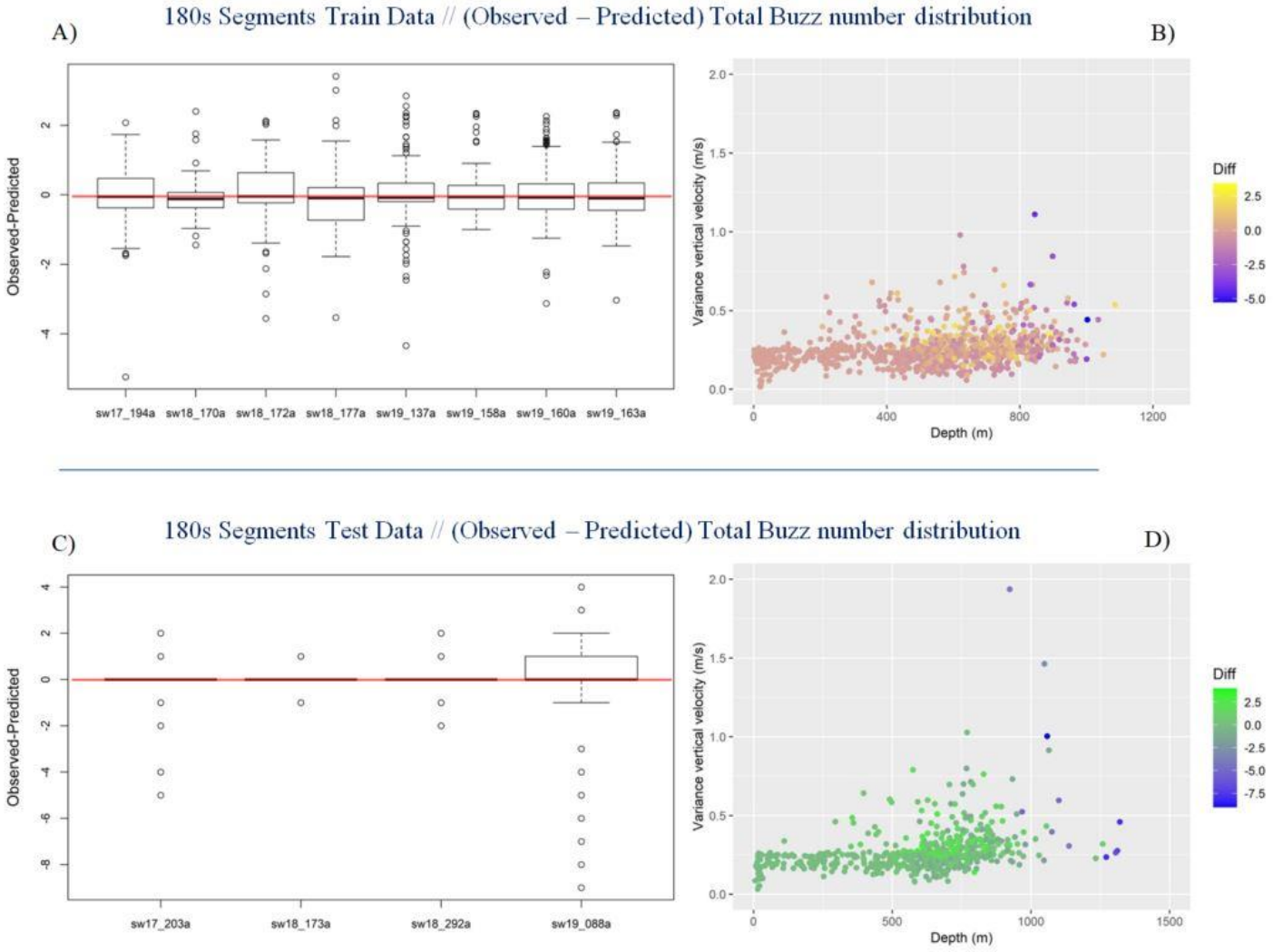


Figure 2.5. Differences in the number of observed and predicted buzzes per segment for individual sperm whales (A and C) and as a function of average depth (m) and variance of vertical velocity (m/s) (B and D). Predictions were made with train data (top) and test data (bottom). The horizontal line represents the median, the box represents the 25th and 75th percentiles and the whiskers represent the extreme values within 1.5 times the length of the box. Outliers are plotted as points.

The prediction accuracy of the total number of buzzes per individual whale was remarkably high for both train and test data, varying from 80% to 100% (Table 2.6). The only exception was individual sw18_173a which had the lowest number of buzzes, and for which the model overpredicted buzz production.

Table 2.6. Model prediction performance of the total number of buzzes for individual whales, in the train and test data.

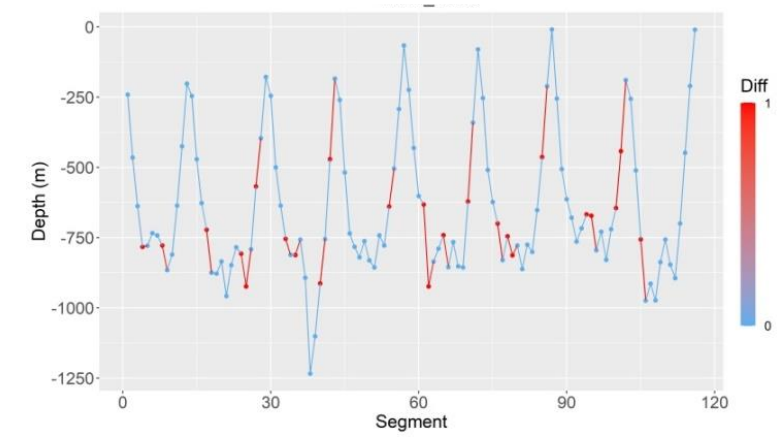
Total Buzz events per Individual

	Animal	Observed	Prediction	Prediction accuracy
Train data	sw17_194a	135	135	100%
	sw18_170a	34	35	97%
	sw18_172a	94	87	93%
	sw18_177a	87	87	100%
	sw19_137a	134	126	94%
	sw19_158a	67	58	87%
	sw19_160a	180	157	87%
	sw19_163a	85	83	98%
Total		**816**	**768**	**94%**
Test data	sw17_203a	85	93	91%
	sw18_173a	12	17	58%
	sw18_292a	70	65	93%
	sw19_088a	360	287	80%
Total		**527**	**462**	**83%**

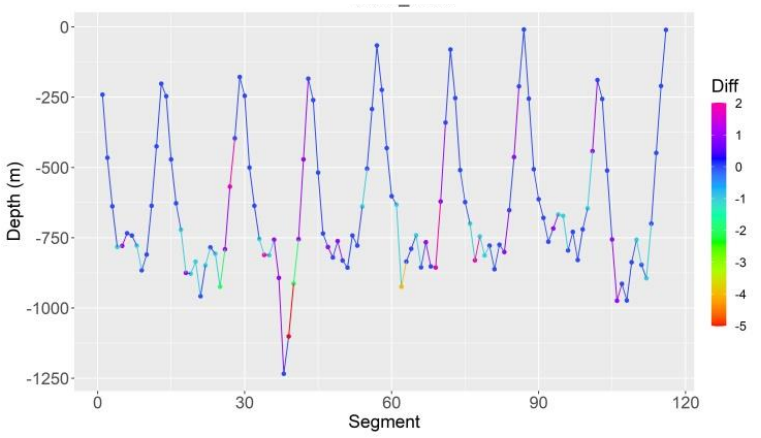
Figure 2.6 presents the differences in the absence/presence and number of buzzes observed and predicted by the model for the 180s segments along the dive profile of two sperm whales from the test data. Most of the incorrect predictions occurred in segments located during the ascent phase of the dives, followed by those located nearby depth peaks. Interestingly, most of the errors within the deep peaks corresponded to an overestimation of the actual number of buzzes, while most errors in the ascent phase were underpredictions of buzzes.

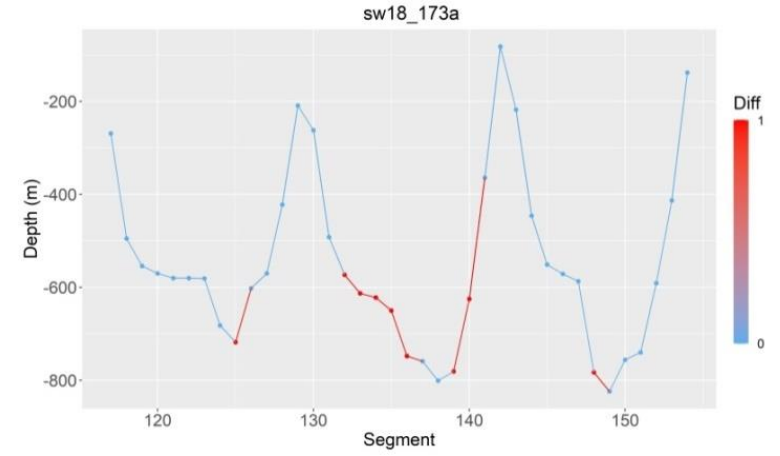
180s Segments (Observed – Predicted)

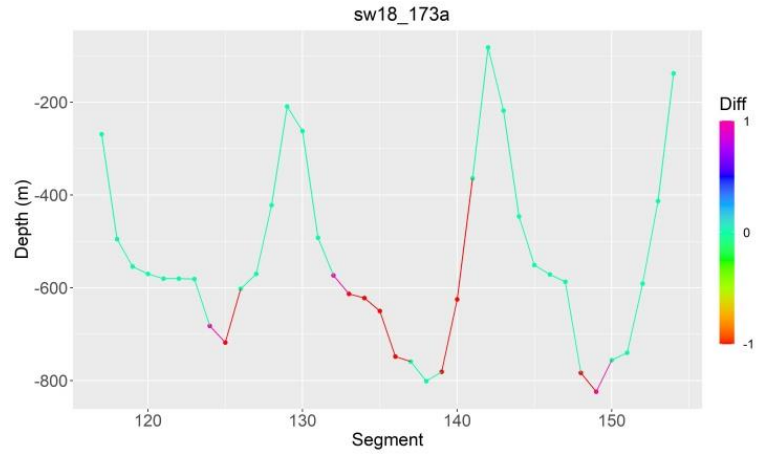
Buzz Absence/Presence

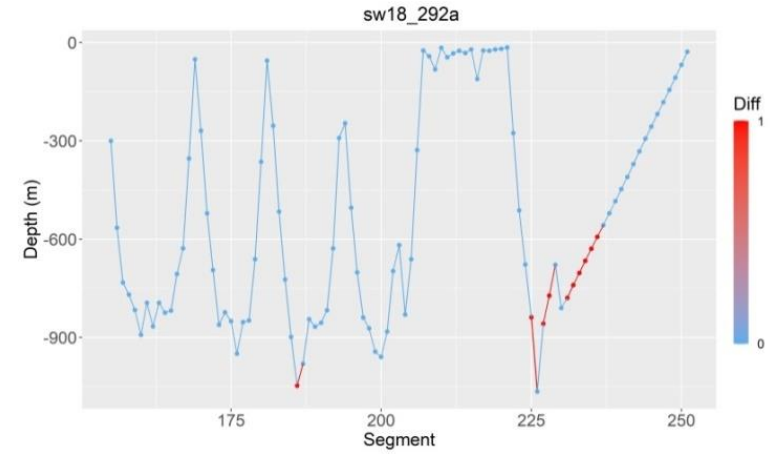


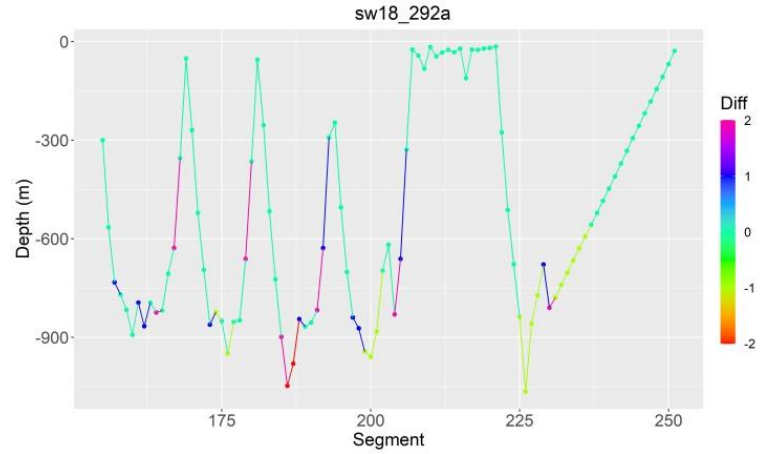
Total nº of Buzzes

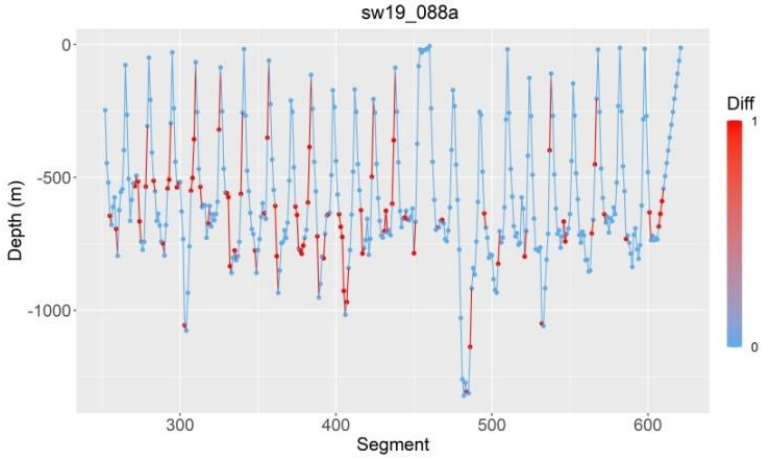












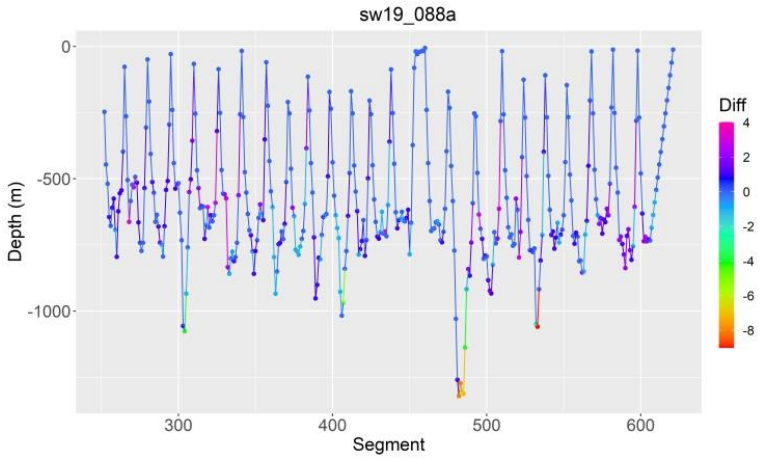


Figure 2.6. Location within the dive profile of differences in the presence/absence (left) and in the number (right) of buzzes observed and predicted by the models for 180s segments for four new individual whales (test data).

Discussion

Sperm whales use echolocation clicks to find and track prey (Watwood et al. 2006, Teloni et al. 2008, Fais et al. 2016, Tønnesen et al. 2020). The association of fast click trains or buzzes with increased manoeuvring of sperm whales, supports the hypothesis that buzzing plays a role in prey acquisition (Miller et al. 2004). Hence, production of echolocation clicks has been widely used as a proxy of foraging activity and effort in the species, with buzzes indicating prey capture attempts (Fais et al. 2015, Fais et al. 2016, Isojunno et al. 2016).

We developed a model to detect the number of buzzes within sperm whale dive segments, when no concurrent acoustic information is available and solely based in dive metrics derived from low-resolution (at 1Hz and 1m) 2D dive profiles. Previous studies have developed similar methods to predict foraging activity for other diving predators, namely pinnipeds, in low-resolution datasets (Heerah et al. 2014, 2015). However, to the best of our knowledge, this is the only method capable of predicting prey capture attempts by sperm whales at the scale of a few minutes, along the entire dive. The model developed here was able to detect the presence and number of buzzes within dive segments of new individuals with good accuracy, despite of inter-individual variability in behaviour. This model, therefore, constitutes a powerful tool to estimate sperm whale foraging activity in time-depth data, representing a significant improvement over previous approaches without acoustic information (e.g., surface time (Watkins et al. 1999); dive duration, surface interval and distance travelled during a dive cycle (Jaquet et al. 2000);

Effect of time scales on model performance

The fine scale analysis of foraging behaviour obviously requires measurements at short temporal resolutions, ideally at the scale of individual capture events. The majority of buzzes detected were 2-14s long, in accordance with previous studies reporting a median buzz duration of 9.1s (Fais et al. (2016). For this reason, the initial analyses

focused in segments of short duration; however estimations from these segments provided disappointing results. Although a detailed investigation of the causes is beyond the scope of this work, these results suggest that, over time scales of <60s, vertical movements during prey capture attempts are not substantial, and that increased manoeuvring (Miller et al. 2004) occurs mostly while the whale is swimming horizontally.

The models based on segments of 180s and 300s provided good fits to the data. Both models showed a very high accuracy (80-82%) at predicting presence and absence of buzzes in segments. However, segments of 300s contained more buzzes than those of 180s, and the model of 300s was considerably worse in predicting the number of buzzes per segment (41% of segments of new individuals correctly predicted, compared to 58% of the model for 180s). Thus, in the case of this dataset, 180s was considered the most suitable time scale for modelling the number of buzzes. With a longer dataset and a more extensive analysis, it might be possible to refine the models or find a set of other parameters capable of detecting prey capture attempts in shorter segments. A model predicting presence/absence of a buzz could then be applied to obtain data for every capture attempt.

Dive metrics used to detect buzzes

In the Azores archipelago, the sperm whale foraging phase, the period between the first and last buzz within a dive, mainly occurs between 700m and 1200m depth (Oliveira 2014), explaining why average depth was an important predictor in the model. The fact that foraging activity occurs within a restricted, well-defined depth range also contributes to the excellent ability of the model in discriminating between segments with and without buzzes, and to the better model performance for segments with an average depth < 500m.

In addition, sperm whales produce higher buzz rates during the bottom phase of the dives and with increased bottom duration (Oliveira 2014). None of the metrics used in this study to measure time spent at the bottom phase of the dive was retained in the final models. However, the number of buzzes per segment was found to be an increasing but decelerating function of the average depth of the segment (Figure 2.3). For segments

deeper than ~800m, a higher average depth did not imply a higher number of buzzes per segment, resulting in great overlap in average depth for segments ranging from 3 to 5 buzzes. This partly explains why differences between the number of observed and predicted buzzes increased with depth (Figures 2.5B and D). On top of this, the dataset used to develop the model included few dives deeper than 1000m and model accuracy in the deepest segments was substantially reduced.

The presence of buzzes was associated with reduced depth variance, most likely because the majority of segments without buzzes occur during the descent and ascent phases of the dive. Average vertical velocity during the descent and ascent phases of dives for sperm whales in the Azores is 1.35±0.21 ms^{-1} and 1.60±0.19 ms^{-1} (Oliveira 2014). This means that changes in depth between the start and end of segments located in the descent and ascent phases of the dive can surpass 200m, so the variance in depth within these segments is high. Conversely, results from this study showed that during the bottom phase of the dives, where most buzzes are produced, variations in depth over time scales of a few minutes are substantially smaller and variance in depth within 180s segments is lower than during descents and ascents. Variance in depth during the foraging phase possibly results from the occurrence of vertical excursions, which has been previously defined as ARS behaviour and linked to foraging activity (Dragon et al. 2012, Heerah et al. 2014, 2015). Although variance in depth was a good predictor of the presence and absence of buzzes, it did not increase with increasing number of buzzes, suggesting that consecutive prey capture attempts concentrate in a restricted depth range.

The emission of buzzes by sperm whale is linked to strong bursts of speed (Amano and Yoshioka 2003, Fais et al. 2016). In order to try to detect the vertical component of these bursts, we calculated the average vertical velocity (i.e, change in depth between time t and t+1) and average vertical acceleration (i.e, change in vertical velocity between consecutive time intervals) of dive segments, as well as other statistics describing the amount of variation in these metrics within segments. Only variance in vertical velocity had a significant effect on the number of buzzes per segment. Buzzes occurred in segments with higher variance in vertical velocity, in accordance with the bursts of speed previously reported (Amano and Yoshioka 2003, Fais et al. 2016). Increased variance in vertical velocity may be the consequences of sudden accelerations

during active prey chases, followed by slowdowns after prey has been captured (Fais et al. 2016).

Vertical excursions are necessarily linked to a change in vertical direction in animal movement and are consequently, linked to the presence of inflection points and wiggles (Dragon et al. 2012). In fact, vertical sinuosity quantified by wiggles, has been previously related to successful prey capture in cetaceans and other deep diving predators (Goldbogen et al. 2006, Calambokidis et al. 2007, Heerah et al. 2019). For this reason, and in base that buzzes are emitted prior to a prey capture attempt (Fais et al. 2016), the presence of wiggles was selected as a predictable variable. The number of wiggles proved to be a significant predictor in the final model. Nonetheless, the small number of wiggles detected within our dataset resulted in difficulties for this variable to predict the number of buzzes per segment, and consequently considerable lower predictivity than that of the other variables. These results suggest that the definitions used to calculate both wiggles and inflection points (the latter was not retained in the final model), used to calculate the former, might have not been the most appropriate. The reduced number of inflection points was due to both to the depth resolution and the selected time interval (*t-1*, *t+1*). Thus, we strongly believe that the presence of wiggles and inflection points, could improve buzz prediction if a longer time interval is used to account both the lower depth resolution and large body size of the species for the wiggle definition.

Model predictive performance and potential application for population inference

Overall, the best fitting model developed for the analysis of 180s dive segments correctly detected the presence or absence of buzzes in 81% of new observations, from the four sperm whales used in the test data. In 58% of these new segments, the model was able to accurately predict the number of buzzes. The performance of this model is similar to that of models developed to predict prey capture attempts in 2D low resolution datasets of southern elephant seals and Weddell seals using a different approach (Heerah et al. 2014, Viviant et al. 2014, Heerah et al. 2015). Unlike these models that predicted prey capture attempts at the dive scale (Heerah et al. 2014, 2015) or, at best, at 30 minutes and hourly scales (Viviant et al. 2014), the model developed in this study predicted prey capture attempts every 3 minutes.

Hence, the model developed in this study shows great potential to estimate prey capture attempts at very fine scales in low-resolution 2D sperm whale dive profiles. Nonetheless, some problems still remain that deserve further work.

Perhaps the most important problem was that, for all dive metrics included in the final model, there was a large overlap in the distribution of values for different numbers of buzzes. This was especially evident for the variance in depth, the number of wiggles, and for the average depth in segments ranging between 3 and 5 buzzes. This largely explains why the model performance at predicting presence/absence of buzzes was substantially better that at predicting the exact number of buzzes, given presence. The increasing but decelerating relationship between average depth and number of buzzes is also believed to have been responsible for the overestimations observed in the dive segments that peaked in depth (Figure 2.6), leading to lower model performance in the deepest parts of the dive.

The underestimation in segments during the ascent phase of the dive is more difficult to explain, when compared to the model remarkable accuracy for segments in the descent phase. We did not conduct a detailed analyses of these segments but, in general, the buzzes detected in the ascent and descent parts of the dive occurred in segments that were shallower, characterized by a high variance in depth but low variance in vertical velocity, as swimming speed is more or less constant. Therefore, it is not surprising that the model had difficulty in predicting the presence or the accurate number of buzzes in these segments. What is surprising was the huge difference in model performance between the ascent and descent phases. Fais et al. (2015) showed that, in deep dives, sperm whales produced around 17% of the buzzes while ascending, and that some of these buzzes might represent opportunistic prey capture attempts, while the whales continuously echolocate to obtain information for subsequent dives (Fais et al. 2015, Fais et al. 2016).

The goal of developing a model to predict prey capture attempts from time-depth data was then to apply this model to different individuals, tagged in different locations and periods of time. To account for the individual, spatial and temporal variability in diving and foraging behaviour, the model was developed using data from different months and years, and including individual whales as a random effect. As expected, the random

factor was significant in all models, confirming there was high inter-individual differences in behaviour.

Despite some of the shortcomings discussed above, the model performed reasonably well when applied to data from new individuals. In three out of four whales, the model predicted the true number of buzzes in the majority of dive segments, and the errors in the remaining segments were usually small (varying between -2 to +2). There was one individual, however, where the model performed substantially worse. This individual produced an average of 4 buzzes per dive, whereas the average number of buzzes per dive for all the other whales (both test and train data) varied from 7.8 to 21.8. Although the reasons for this difference are unknown, the model was unable to account for this variability, emphasizing the importance of adding data from more individual whales to refine and test the model.

Recommendations for model improvement

The segments in the ascent and deepest part of the dive, which accounted for most predictive errors, represent the most important limitations and, if improved, could greatly increase the performance of the model. The inclusion of the diving phase in a conditional model could discriminate between “ascent buzz segments” and the rest, potentially enabling a better prediction of buzzes in the ascent phase and in the whole dive. Additionally, standardizing or normalizing the dive metrics, or finding other dive metrics that better expain the number of buzzes could help improve model accuracy. Generalized additive mixed models should also be tried.

Another important improvement for our method would be to reduce the length of the dive segments for which buzzes are predicted. A successful model predicting the number of buzzes or the presence/absence in shorter segments would, most likely, increase the model prediction accuracy and give more precise information about when the buzzes are being produced. However, this requires a more exhaustive data analysis, increasing the sample size and the re-assessment of more diving metric candidate parameters.

Conclusion

This is the first study to develop a model that predicts the number of prey capture attempts, and consequently foraging effort, in low-resolution time-depth data for sperm whales. The model showed good predictive performance at short-time scales (3 minutes) for whales tagged in different times and locations, and therefore has huge potential to investigate the fine-scale foraging activity of sperm whales. We believe that the present method could already be applied to available time-depth datasets, in order to conduct retrospective analyses of the foraging behaviour of the species. However, we also identified a number of issues in the models. These issues could be solved with an increased sample size, and by a more detailed data analysis in order to obtain more accurate predictions. Moreover, further research is needed to understand whether all the buzzes are produced within a foraging context, and if not, to identify those that represent prey capture attempts.

The present foraging estimation approach is based on the prediction of the number of buzzes and, therefore, could potentially be applied to a number of odontocete species, potentially enabling more accurate estimations of foraging effort than the coarse and general foraging indexes typically derived from 2D dive profiles.

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Annex

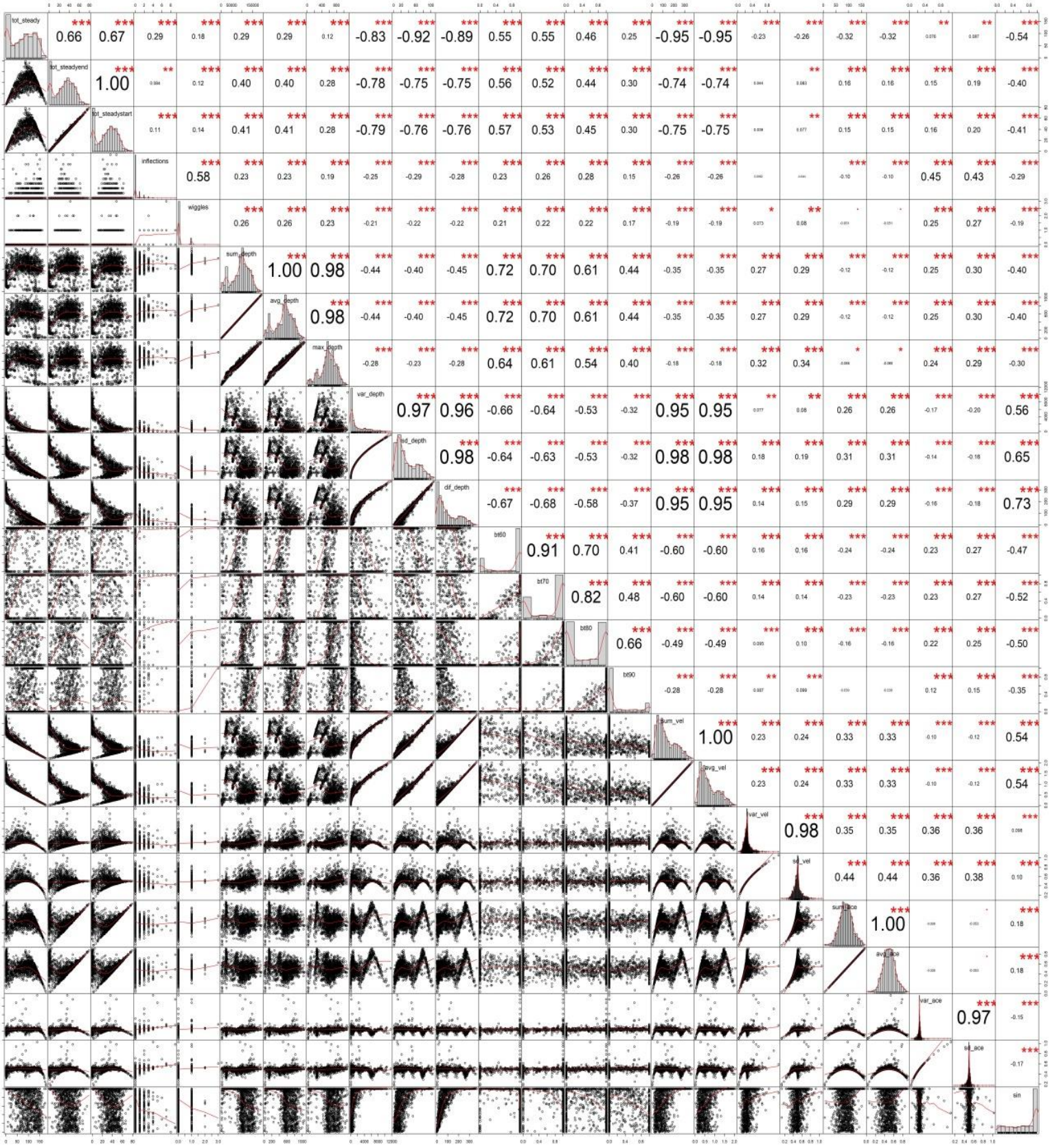

Figure A3.1: Pearson's correlations diagram of all dive metrics.