Electrosensing in cetaceans: anatomy and implications

Natasha Savanna Mynett

A thesis submitted in fulfilment of the requirements of
Manchester Metropolitan University for the degree of
Master of Science by Research

Faculty of Science and Engineering
Department of Natural Sciences

2022

Abstract

Offshore wind developments are increasing the amount of artificial electromagnetic fields (EMFs) in the ocean, and these are known to have behavioural and physiological impacts on many marine species. A previous investigation on a cetacean (Guiana dolphin, *Sotalia guianensis*) found that an individual was able to electrosense accredited to their vibrissal follicles. However, it is not known whether this sensory modality is present in other cetaceans, or if they are affected by artificial EMFs. Therefore, the aim of this thesis is to evaluate the potential and impact of electrosensing in cetaceans by i) identifying potential electrosensory organs, ii) identifying cetacean species that may be able to detect electric and magnetic fields from ecological characteristics and phylogeny, and iii) reviewing the data on movement and interactions of cetaceans around windfarms. The vibrissal follicles of three species of foetal cetaceans were characterised here for the first time. Vibrissal follicles in two species, the harbour porpoise (*Phoconea phocoena*) and minke whale (*Balaenoptera acutorostrata*), displayed follicles like that of mechanosensory hair follicles observed in mysticetes. In contrast, the Atlantic white-sided dolphin (*Lagenorhynchus acutus)* had follicles that were closer to the electrosensing Guiana and the bottlenose dolphin (*Tursiops truncatus*). These delphinid species had follicles that had a characteristic innervation pattern around the base and sides of the follicle. Members of the Delphinidae are therefore of great interest to further study the effects of EMFs. Around the UK, sighting data are available for several species of cetacean. However, these records do not overlap with the dates and positions of windfarm sites, and it is therefore not possible to infer the effects of EMFs on cetacean distribution and behaviour in situ. Future work would need to survey cetacean distribution and behaviour at windfarm sites over the long-term. Anatomical studies and psychophysical studies of captive animals will complement the data in this study and provide a greater understanding of electrosensory form, function and sensitivity in cetaceans. Although the ability of both magneto- and electrosensing in cetaceans is not fully understood, these sensory modalities may be crucial in relation to detecting the increasing levels of EMFs from the increasing developments of offshore windfarms. Therefore, more information is needed to characterise the possible impacts of EMFs on cetacean physiology and behaviour.

Acknowledgements

Contents page

1. Chapter One: Literature Review

1.1. Introduction

Anthropogenic activities in the oceans have increased in recent years, including marine traffic (Erbe et al., 2019), overfishing (Sumaila and Tai, 2020), seabed mining (Thompson et al., 2018), pollution (Häder et al., 2020) and oil and gas extraction (Ragnarsson et al., 2017). The development of offshore renewable energy has also increased, particularly around the United Kingdom (UK) and the rest of Europe (Hutchison et al., 2020). There are concerns that these developments might be negatively impacting marine species (Dolman and Simmonds, 2010), particularly cetaceans (Gill et al., 2005; Madsen et al., 2006). Indeed, the construction and operation of windfarms is believed to interfere particularly with the sensory environment of many marine species (Nyqvist et al., 2020), since they produce noise, vibrations, and electromagnetic fields (EMFs) (Thompson et al., 2010). Whilst noise and vibrations tend to subside somewhat once the windfarms have been developed (Gill, 2005), EMFs from cabling will persist during the lifetime of the windfarm. Artificial EMFs have been reported to have both behavioural and physiological effects in a number of marine species (Tricas and Sisneros, 2004; Hutchison et al., 2018; Hutchison et al., 2020). Elasmobranchs, teleosts and crustaceans use electro- and magnetosensing to navigate, hunt and find a mate (Kalmijn, 1982; Krylov, 2014; Lohmann and Ernst, 2014; Hutchison et al., 2018), and may therefore be particularly sensitive to artificial EMFs. Cetaceans are also known to be sensitive to changes in the geomagnetic fields (Gill et al., 2012a). Investigations into a Guiana (*Sotalia guianensis;* Czech-Damal et al. 2012) and bottlenose dolphins (*Tursiops truncatus*; Huttner er al., 2021) identified that they are able to electrosense. Therefore, cetaceans may also be impacted by artificial EMFs. As charismatic species (Mazzoldi et al., 2019), which play important roles within ecosystems (Katona & Whitehead, 1988; Parsons et al., 2015), cetaceans are an important taxon to study and are therefore the focus of this thesis. The recent findings (Czech-Damal et al. 2012; Huttner er al., 2021) that two species of cetacean can electrosense, makes this a timely investigation.

The aim of this review is to synthesise the available literature in relation to cetacean ecology and conservation. It will start by reviewing the growth of the offshore windfarm sector, the technology that is involved in its operation and the data which are freely

sourced on cetacean sightings around the UK. It will summarise the current literature on magnetosensing and electrosensing abilities in many marine species and highlight the effects of anthropogenic EMFs on species that can either electro- or magneto-sense. It will also review threats faced by cetaceans and cover key ecological characteristics of cetaceans. The chapter will conclude by outlining the knowledge gaps and outline the remaining objectives of this thesis.

1.2. Windfarms

Offshore wind projects are the leading technology in renewable energy, with more sites being developed than any other type of energy production, both non-renewable and renewable (Gill et al., 2012b). Positioning turbines offshore gives a higher wind to energy production ratio than those onshore (Díaz and Soares, 2020). Larger structures can be used offshore and due to their large turbine size and higher hub height, they encounter higher wind speeds (Aldersey-Williams et al., 2020). In the past two decades, the European offshore wind energy sector has developed rapidly. Between 2000-2004 the total number of operational windfarms in European countries increased by 42%, further increasing by 258% between 2005-2009 (Brown and Simmonds, 2009) and by finally has increased by 300% between 2010-2020 (The Wind Power, 2019). Much of this growth has been on the English East coast in the North Sea (Díaz and Soares, 2020; Figure 1.1), with the UK having more offshore windfarms than any other European country (Díaz and Soares, 2020). The first offshore wind turbines in the UK were installed in 2000 off the coast of Northumberland. There are currently thirty-two operational wind farms in the UK, with two more due to be commissioned shortly (Aldersey-Williams et al., 2020). On the 6th of October 2020, The UK Prime Minister Boris Johnson pledged £160 million towards the wind power sector with the aim that by 2030, offshore wind will power every home in the UK. This target requires offshore wind capacity to increase to 40GW (GOV.UK, 2020) – quadrupling the current total annual capacity. This further expansion of the offshore wind sector in the UK highlights the need to better understand how offshore wind farms impact marine organisms, including cetaceans.

Wind farm locations are freely available through KIS-ORCA (Kingfisher Information Service – Offshore Renewable & Cable Awareness; https://kis-orca.org/downloads/) and The Crown Estate (https://opendata-thecrownestate.opendata.arcgis.com). The data sets which were acquired included coordinate locations of detailed attributes such as substation points and turbine locations. Of the available data, 44 datasets were downloaded, this included 34 windfarms in UK waters. Data on the locations of subsea power cables were also freely available via The Crown Estate (https://opendata-thecrownestate.opendata.arcgis.com) in the form of a shapefile. Windfarm locations

and subsea power cables were mapped in QGIS version 3.18 Zurich (QGIS.org, 2022, QGIS Association, Zurich; figure 1.1).
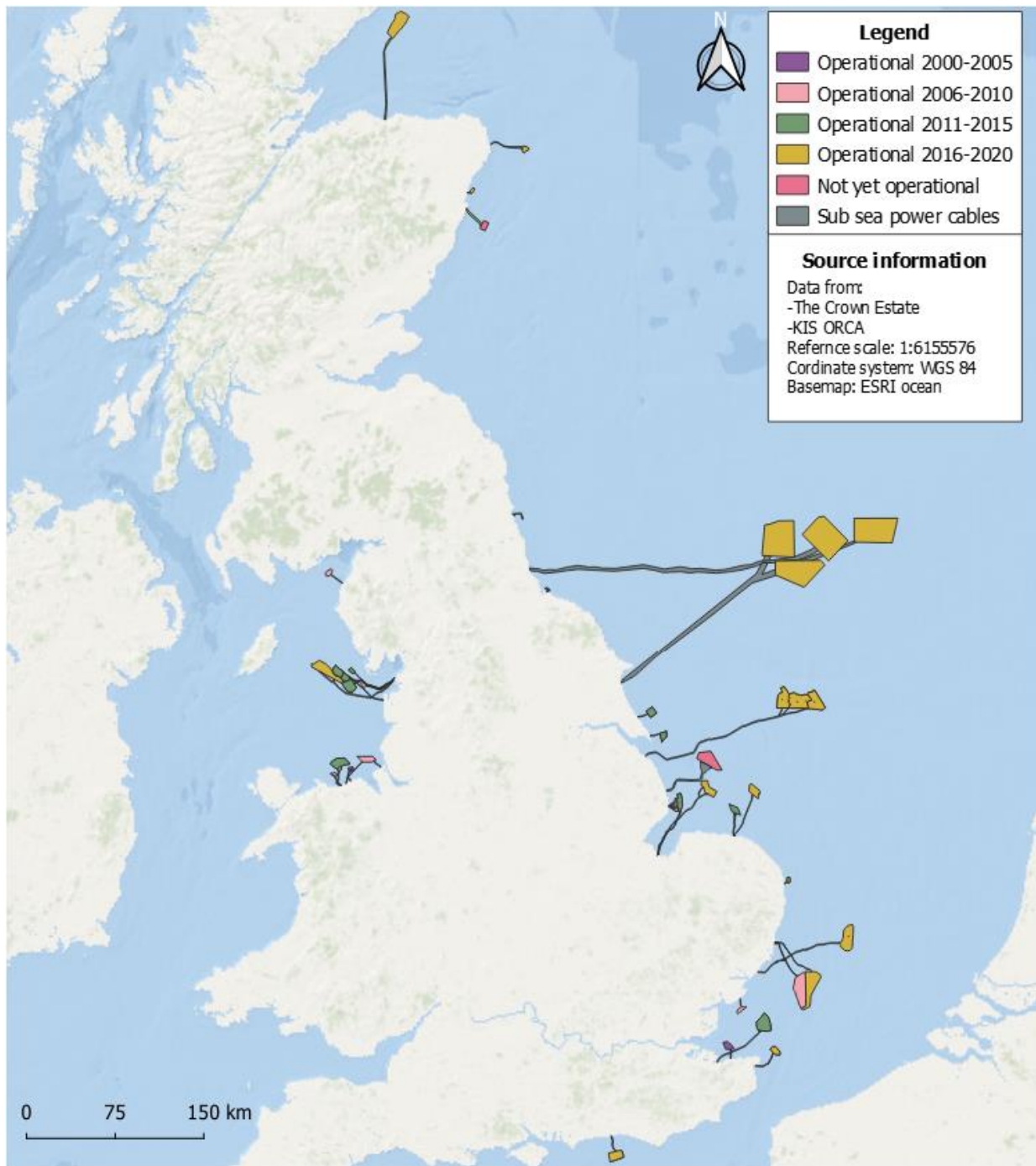

Figure 1.1: **Map displaying operational windfarms around England, Scotland, and Wales 2000-2020.**

1.2.1. Subsea power cables and EMFs

Subsea power cables have spread across the globe since the 20th century (Hansson, 1954) and among other uses, they can be used to connect offshore marine renewable energy installations to the grid. These cables transmit either high voltage direct current (HVDC) or alternating current (HVAC). HVDC lines transmit more power than an HVAC line of the same length, but are more expensive (Öhman et al., 2007; Taormina et al., 2018). An HVAC cable is more frequently used for close transport, such as inter-turbine connections within grids or short connections with substations (Copping et al., 2013), as these reduce the power lost to the surrounding environment (Soares-Ramos et al., 2020). HVDC cable is more suitable for long distance transmission, e.g. transferring power from farm to shore (Soares-Ramos et al., 2020). The subsea power cables used for marine renewable energy installations emit electromagnetic fields (EMFs) (Gill et al., 2012b), which are made up of two types of field: electric (E-fields) measured in microvolts per metre (µV/m) and magnetic (B-fields) measured in microteslas (µT) (Slater et al., 2010; Taormina et al., 2018).

The characteristics of EMFs depend on their location, the type of cable, the type of power supply (HVDC vs HVAC) and if transmitting HVAC, the current, frequency and amplitude (CMAS, 2003; Öhman et al., 2007; Copping et al., 2013). The strength of both magnetic and electric fields increases with current flow and rapidly declines with distance from the cable (Gill and Taylor, 2001). Burial of the cable reduces the electric fields from the cable but does not reduce the magnetic field (CMAS, 2003). The emission of magnetic fields into the surrounding environment can produce an induced electric field (iE) by an object or organism moving through the alternating magnetic field (Gill et al., 2012b). However, there is a lack of agreement on the specific characteristics of EMFs emitted by subsea power cables, and this prevents researchers from precisely assessing the potential impacts of EMF emissions on marine organisms (CMAS, 2003). It is important to clearly identify the strength and type of EMFs emitted by subsea power cables to further investigate their effect on marine species.

1.2.2. Cetacean observational data around windfarms

Currently there is limited literature reviewed data on the abundance and distribution patterns of cetaceans around offshore marine structures in Europe. This lack of knowledge limits our understandings of how future expansions of marine renewables may affect distributions of cetaceans in European waters. Here I review open sourced data to investigate the scale and locations of potential impacts of cetacean abundance around marine renewable structures, specifically around the UK. Wind farms have been developed in UK waters since 2000. This provides the time frame for the sighting data that were required to be investigated. Pre-windfarm sightings are also required to set the base line to establish if there are differences from when the construction of windfarms began. Therefore, sighting data from 1990 onwards were also sought. In total 22 datasets of cetacean sightings were identified and collated (Table 1.1).

Table 1.1: **Overview of the datasets that were obtained for cetacean sightings in waters around the UK between 1990-2020**.

Dataset	Years covered	Reference
Données du Réseau d'observateurs des mammifères marins en mer de la Manche	1990-2012	Inventaire National du Patrimoine Naturel N (2020)
iNaturalist Research-grade Observations	1990-2019	iNaturalist contributors, iNaturalist (2020)
Incidental sightings of marine mammals	1990-2015	Hartvedt, 2020.
Inventaire des Mammifères marins de France (métropole et outre-mer)	2000-2016	Inventaire National du Patrimoine Naturel N (2020)
JNCC Seabirds at Sea data	1990-2000	Camphuysen et al., 2004
Marine mammal monitoring from coastal sites in Cardigan Bay	2004-2009	Allan, 2011
NBIS records to December 2016	1990-2016	Norfolk Biodiversity Information Service (2017)
NE Scotland marine mammal records	1990-2011	North East Scotland Biological Records Centre (2017)
Observation.org, Nature data from around the World	1990-2020	de Vries and Lemmens M (2021)
Observations du Grand dauphin du Golfe normand-breton	2012-2016	Inventaire National du Patrimoine Naturel N (2020)
ORCA sightings	2006-2019	ORCA, 2019
SCANS I cetacean sightings	1994	Lacey, 2015
SCANS II cetacean sightings on primary platform of vessel surveys 2005	2005	Lacey, 2014
SCANS II cetacean sightings on tracker platform of vessel surveys 2005	2005	Lacey, 2014
SCANS II cetacean sightings from aerial surveys	2005	Lacey, 2014
Seatrust Cetacean Records West Wales	2004-2015	West Wales Biodiversity Information Centre (2018)
Belgian Marine Mammals database	2001-2019	Haelters and Vandenberghe (2019)
UK Royal Navy Marine Mammal Observations	1991-2003	Maughan, B. and K. Arnold. 2010
United Kingdom National Whale Stranding Database	1990-2008	Officer, 2011.
Visual sightings from Song of the Whale	1993-2013	Boisseau et al., 2020
walvisstrandingen_nl	1990-2019	Keijl and Creuwels (2020)
WDC Shorewatch Sightings	2005-2018	Whale and Dolphin Conservation (2021)

These datasets contained the latitude and longitude of sightings of individuals or groups of cetaceans. A total of 81,433 sightings were obtained but the data have considerable issues. This limited their suitability for reviewing the abundance of cetaceans over three decades and therefore the impacts of operational windfarms on cetaceans. There was major bias in the number of sightings recorded between the decades and is probably indicative of more sighting effort and legislation on the monitoring of cetaceans in more recent decades (Hammond et al., 2013). Records were not equally distributed over time, with over four times more sightings in the most recent decade compared to 1990-2000 (1990-2000: 11,742; 2001-2010: 18,527; 2011-2020: 51,164; Figure 1.2). This reduces the effectiveness of any baseline data for detecting changes in abundance and distribution.
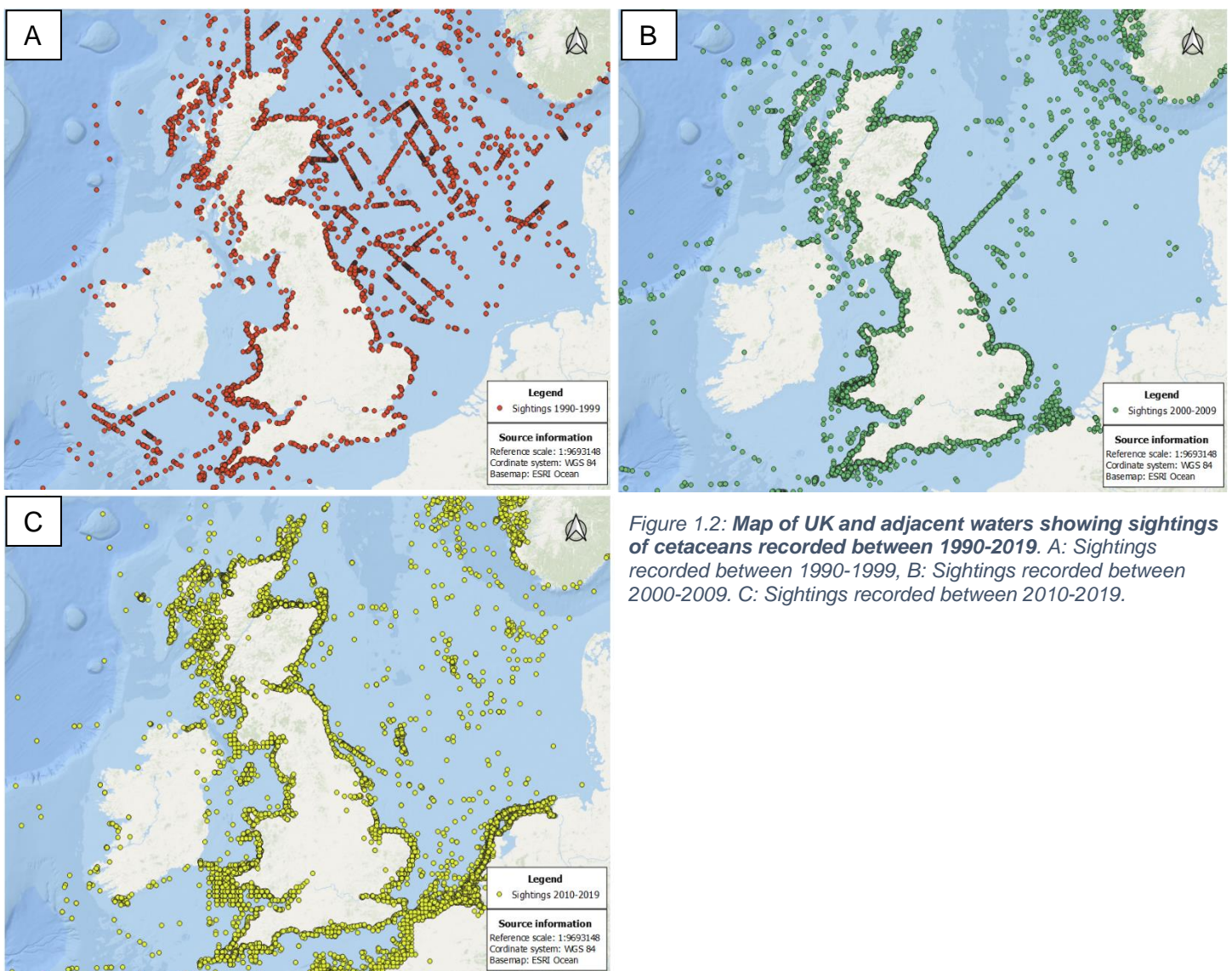
Figure 1.2: **Map of UK and adjacent waters showing sightings of cetaceans recorded between 1990-2019**. A: Sightings recorded between 1990-1999, B: Sightings recorded between 2000-2009. C: Sightings recorded between 2010-2019.

The spatial coverage of the cetacean data is also rather limited, with large amounts of the sightings from specific locations including coastal sightings and on ferry routes (figure 1.2). A majority of these sightings therefore do not overlap with windfarm locations. The majority of windfarms are too far from the coast to spot any mammals in their vicinity. Whilst ferry routes are problematic due to the fact boat routes are not consistent between time periods (Hassel et al., 2017). This is in order to navigate around an increased number of marine structures to prevent collisions (Yu et al., 2019). This can be observed in the ferry routes taken between 1990-1999 across the North sea (figure 1.2.A) and the reduction of these in the latter two decades, especially figure 1.2.A-B. This may indicate that monitoring has had to adapt spatially to the growth of offshore structures and with the view of further growth in offshore renewable energy these constant changes will persist. Additionally, a large number of records consist of strandings which are not a direct representation of population numbers. The combination of these factors makes it impossible to compare historical sighting data between time periods of specific cetacean abundance and distribution.

1.3. Effect of electromagnetic fields on animals

Prior to the development, and during the construction phase, marine mammal and seabird populations are monitored on windfarm installation sites (Kaiser et al., 2006, Perrow et al., 2006, Perrow et al., 2011). With monitoring as a legal requirement for all windfarm installations in the UK and Europe. However, there is no legal stipulation to monitor these installations in the long-term once the windfarms are operational. Therefore, the effect of windfarm operation and EMFs are less understood. A previous study has tried to characterise subsea cable EMF levels in the field (Dhanak et al., 2016). The subsea cable was energised numerous times with both DC power (2 – 2.4 Amps) and AC power (0.98 - 1.59 A at 60 Hz). When DC power was used, the presence of an electric field was not identified, although this was expected due the shielding of this cable. However, a magnetic field was emitted, and was present within 3 m of the cable, recording levels greater than the Earth's natural magnetic field. The measured induced electric field when AC was used resulted in ranges exceeding 200 μV/m, which is likely to be detected by marine species, especially elasmobranchs (Gill and Taylor, 2002). Other studies have used the literature to model the estimated EMFs produced from subsea cables (e.g. CMACS, 2003; Tricas and Gill, 2011; Sutton et al., 2017), which has highlighted that specific details about the cables are needed, including cable design, burial depth, and cable loading, in order to accurately model them.

It is predicted that species which can magnetosense are most likely to be impacted from DC cables and species which electrosense may be impacted by both AC and DC (Gill et al., 2009; Tricas and Gill, 2011; Dhanak et al., 2016). The majority of studies that have investigated the effect of a range of EMFs on marine species were conducted *ex situ*, specifically, observing behavioural and physiological effects (Gill et al., 2009; Tricas and Gill, 2011; Hutchison et al., 2018; Gill and Desender, 2020; Nyqvist et al., 2020). As EMFs contain both electric and magnetic fields (Slater et al., 2010; Taormina et al., 2018) identifying species that magnetosense and/or electrosense may allow us to understand which species are likely to be affected by EMFs produced from subsea cables. Species that dive deeply in open water, or inhabit shallow coastal waters are also more likely to come in to contact with EMFs (Wilson et al., 2012).

1.3.1. Magnetosensing and effects of EMFs

Three mechanisms are currently considered for magnetosensing: i) magnetic-particle-based magnetoreception; ii) radical-pair mechanisms and iii) induced electric field detection (Mouritsen, 2018). Species respond to cues of the direction, magnitude and/or the inclination of the Earth's geomagnetic field. Geomagnetic orientation is the method of magnetosensing most commonly observed (Wiltschko and Wiltschko, 1995; Lohmann et al., 2007). This has been reported in all of the migratory salmonid species (Nyqvist et al., 2020), some crustacean species, such as the Atlantic spiny lobster (*Panulirus argus*;Lohmann et al., 1995; Hutchison et al., 2018) and suggested in some species of cetacean (Torres, 2017; Zapetis and Szesciorka, 2018; Nyqvist et al., 2020). Indeed, long distance migrations in aquatic species might be indicative of the ability to magnetosense utilising the Earths geomagnetic field (Walker et al., 2002; Taormina et al., 2018).

The increased presence of anthropogenic EMFs in many marine habitats may affect magneto-sensing species, especially in species that use naturally occurring geomagnetic fields to migrate over long distances, and in those species who migrate in specific cardinal directions (Wiltschko and Wiltschko, 1995; Wiltschko and Wiltschko, 2005; Johnsen and Lohmann, 2005; Lohmann et al., 2007). While the specific characteristics of EMFs emitted from subsea power cables are unknown (Section 1.2.1), many studies have evaluated the effects of a range of magnetic fields on the behaviour and physiology of marine species. Table 1.3 reports some of these studies. Studies were chosen to cover varying strength exposure of magnetic fields (0.2 µT-40,000 µT) to observe different types of impacts across different species.

Table 1.3: **Observed effects of magnetic fields on marine species**. The frequency of the electric field if present has been reported alongside the exposed magnetic field strength (If DC current, the frequency in the cable is 0Hz). The threshold value is the reported value at when a response was seen from the species in question. (B – behavioural effect, P –physiological effect, U/K – unknown).

Species	Effect	Location	Field strength exposure (Frequency of electric field)	Threshold (if known)	Reference
Antarctic amphipod (Gondogeneia antarctica)	Disorientation (B)	Ex situ	0.2 µT (976Hz)	0.02 µT	Tomanova and Vacha (2016)
Rainbow trout (Oncorhynchus mykiss)	Disorientation (B) Embryonic development impairment (P)	Ex situ	10 µT (50Hz)	5 µT	Formicki and Winnicki (1998)
Cetacea: Sperm whale (Physeter macrocephalus) and fin whale (Balaenoptera physalus	Stranding occurrences (B)	In situ	<50 µT natural fields	U/K	Nyqvist et al. (2020)
European eel (Anguilla anguilla)	Route deviation (B)	In situ	50µT (DC)	U/K	Westerberg and Begout-Anras, (2000)
Little skate, (Leucoraja erinacea)	Attraction and attacking (B)	Ex situ	65 µT (60Hz)	14 µT	Hutchison et al. (2018)
European sheatfish (Silurus glanis)	Biomass decrease (P)	Ex situ	600 µT (DC)	U/K	Krzemieniewski et al. (2004)
Edible crab (Cancer pagurus)	Attraction (B)	Ex situ	40,000 µT (DC)	2,800 µT	Scott et al. (2018)

In an *in situ* experiment, the presence of an electric cable that induced magnetic fields of 5µT caused European eels (*Anguilla anguilla*) to change their migratory path, although they corrected their route after about 30 minutes (Westerberg and Begout-Anras, 2000). It has been reported that fin whales (*Balaenoptera physalus*) orientate their migratory routes to pass through geomagnetic valleys (Walker et al. 1992) and their migration could therefore be impacted by artificial EMFs since it suggests that they rely on geomagnetic cues. It is also worth noting that records of mass strandings in sperm whales (*Physeter macrocephalus*) in the North Sea are associated with disruptions and changes in the Earth's magnetic field, such as during the occurrence of solar storms (Vanselow et al., 2017). This implies that an influx of artificial EMFs could increase these occurrences.

The majority of investigations of responses to EMFs have been conducted *ex situ*. The little skate (*Leucoraja erinacea*) increased feeding behaviour, with increases in the distance moved, the speed travelled and turning frequency (Hutchison et al., 2018), when exposed to laboratory-produced EMFs (51.6-65.3 µT). The scalloped hammerhead (*Sphyrna lewini*), sandbar sharks (*Carcharhinus plumbeus*; Meyer et al., 2005), and short tail stingrays (*Dasyatis brevicaudata;* Walker et al., 2003), were able detect the presence of an artificial magnetic field. Crustaceans have also been reported to be impacted by EMFs. The edible crab (*Cancer pagurus*) increased sheltering behaviour when exposed to a magnetic field for a 24-hour period (2,800-40,000 µT; Scott et al., 2018). Presence of magnetic fields varying from 20-200µT disrupted the orientation of the amphipod (*Gondogeneia antarctica*). Upon release, the amphipods were able to move in a seaward direction of the home beach, but when exposed to magnetic fields this movement was disrupted (Tomanova and Vacha, 2016).

In addition to behavioural responses, physiological changes have also been observed upon the exposure to magnetic fields that are greater than those found naturally (natural ranges are between 60 µT at the poles and drop down to 30 µT at the equator). Krzemieniewski et al. (2004) found that the total mass of a group of 1200 European sheatfish larvae *(Silurus glanis)* decreased, and mortality increased when exposed to a constant magnetic field (400-600µT). Nishi et al. (2004) found that Japanese eels (*Anguilla japonica*) responded to both electric and magneto-sensitive conditioning, which was characterised by a decreased heart rate. Effects on the reproduction have also been observed. Exposure to a magnetic field slowed down the embryonic development of brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) and altered the circulation motion in the embryos in both pike (*Esox lucius*) and carp (*Cyprinus carpi*o; Formicki and Winnicki, 1998). The presence of a distorted magnetic field during the development phase of loggerhead sea turtles (*Caretta caretta*) and rainbow trout resulted in poor magnetic orientation along their normal migratory route in accordance with their known cardinal navigation directions and identifying naturally occurring distinctive magnetic field markers (Fuxjager et al., 2014; Putman et al., 2014).

1.3.2. Electrosensing and effects of EMFs

Species which are capable of electrosensing can detect electric and induced electric fields that are emitted by prey, conspecifics, and potential predators (Taormina et al., 2018). Such species include elasmobranchs (e.g. Kajiura & Holland, 2002; Kajiura 2003; Gill et al., 2009), crustaceans (e.g. Love et al., 2015), teleost fishes (e.g. Westerberg and Lagenfelt, 2008) and two species of cetacean (Czech-Demal et al., 2012; Huttner et al., 2021). Many studies have assessed the behavioural effects of a range of electric fields on marine organisms and will be discussed below. Table 1.4 presents a summary of some of these studies that have been conducted across a range of field strength exposure (12 µV/m-18,000,000 µV/m) to observe different types of effects across different species.

Table 1.4: **Observed effects of electric field presences on some marine species**. AC currents were used at frequency's ranging 50-60Hz (those generally reported in subsea cables). The threshold value is the reported value at when a response was seen from the species in question (B – behavioural effect, U/K – unknown)

Species	Effect	Location	Field strength exposure	Threshold (if known)	Reference
Thornback ray (Raja clavata)	Attraction and orientation (B)	In situ	12 µV/m	U/K	Gill et al., (2009)
Free-swimming spurdog (Squalus acanthias)	Attraction and orientation (B)	In situ	12 µV/m	U/K	Gill et al., (2009)
Small-spotted catshark (Scyliorhinus canicula)	Avoidance (B)	In situ	100 µV/m	1 µV/m	Gill and Taylor, (2001)
Freshwater sawfish (Pristis microdon)	Attraction and attacking (B)	Ex situ	80 µV/m	15 µV/m	Wueringer et al. (2012)
Guiana dolphin (Sotalia guianensis)	Attraction and perception (B)	Ex situ	900 µV/m	460 µV/m	Czech-Damal et al. (2012)
Bottlenose dolphin (Tursiops truncatus)	Detection of presence of electrical stimuli (B)	Ex situ	1500 µV/m	At least 500 µV/m	Huttner et al., 2021
Leopard shark (Triakis semifasciata)	At threshold head twitch responses and attraction, at max exposure retreat (B)	Ex situ	max exposure: 18,000,000 µV/m	4,000,000 µV/m	Marcotte and Lowe (2008)

One of the highest sensitivities to electric fields which has been recorded in literature are elasmobranchs. Emissions that range between 0.5–100 $\mu V/m$ have been identified to attract some species, while those over 100 $\mu V/m$ tending to repel them (Gill and Taylor, 2002, Tricas and Gill, 2011). Two species of elasmobranch, the thornback ray *(Raja clavata)* and the spurdog (*Squalus acanthias*), were attracted to EMF stimuli from buried subsea power cables in situ. The EMFs which were created presented a magnetic field of 12µT and an induced electric field of 36µV/m (Gill et al., 2009). This study also indicated that, based on the scale of responses of the species in this experiment and modelling estimates, electrosensitive marine organisms would encounter fields at or above the lower limit of their detection threshold at up to 300m from the cable. This strongly suggests that a range of species may be susceptible to the EMFs which can emitted from some subsea cables.

Under laboratory conditions, male Atlantic stingrays (*Hypanus sabinus*) were able to detect the location of plastic model females, which were buried under sediment using electric cues emitted from the model (Tricas et al., 1995). Kalmijn (1982) explored electric detection in a range of elasmobranch fishes using the presence of artificial electric fields that were similar to those of ocean currents. Stingrays (*Urolophus helleri*) were able to orientate themselves relative to these. Additionally, two species of shark, smooth dogfish (*Mustelus canis*) and blue sharks (*Prionace glauca*), were attracted to a bait dipole source and exhibited bite attack responses whilst ignoring the visual stimulus. Kajiura (2003) also reported that bonnethead sharks (*Sphyrna tiburo*) exhibited vigorous biting on active dipoles releasing prey stimulus fields. Interestingly, two-thirds of behavioural responses were observed to fields of less than 10 μV/m, however, positive reactions declined drastically once the stimulus was greater than 10 μV/m. This supports the fact that, once electric field stimuli reach a certain threshold, they can repel individuals (Tricas and Gill, 2011). The sharks also never engaged on inactive dipoles and stopped the attack on the dipole as soon as it was switched off. Furthermore, the scalloped hammerhead and sandbar sharks demonstrated attack responses to fields less than 10 μV/m (Kajiura and Holland, 2002). Bite responses were also initiated in the Atlantic stingray with a median stimulus threshold of 0.6 μV/m in the saltwater population (McGowan and Kajiura, 2009).

Electroreceptive responses have also been reported in two species of cetacean. Czech-Damal et al. (2012) demonstrated that the Guiana dolphin can detect an electric fields with a stimulus below 10 μV/m. They determined the absolute detection threshold of 460 μV/m from a 50% hit rate, which was determined by interpolating the percentage of correct go responses to stimuli. Huttner et al. (2021) demonstrated that four bottlenose dolphins could be taught cross sensory perception and that the dolphins presented above an 80% hit rate on the perception of an electric stimuli. A threshold value was not established but is currently being studied further. The studies conducted by Czech-Damal et al. (2012) and Huttner et al. (2021), will be further discussed in section 2.2.2. As little is known about the responses of cetaceans to electric fields, this is an area open for investigation. The presence of electroreception is also hypothesised in other species of cetacean (Czech-Damal et al., 2012).

1.3.3. Conclusions

Many studies presented here have not been conducted in the field. The majority were carried out in the laboratory under variable conditions, making it challenging to compare findings between studies. The range of sensitivity values presented in literature (Tables 1.1 and 1.2) is large and it is hard to identify if these values are species-specific or depend on the exact experimental conditions. In situ EMFs may present different characteristics to those in ex situ conditions, and we do not know enough about subsea cable EMFs to be able to design representative conditions in the laboratory. Variations in current, cable length and cable requirements for farm outputs can all affect the strength. While laboratory experiments might not be wholly realistic, it must not be ignored that some marine species (e.g. some of those in Tables 1.1 and 1.2) are likely to be affected by EMFs from subsea cables in their natural habitats. These studies indicate that exposure to EMFs likely leads to both behavioural and physiological implications. This may include impacts in navigation, feeding behaviours, social interactions, reproduction and growth. It is imperative that we understand more about EMFs in the marine environment and their effect on marine species.

Furthermore, the ability to identify which species may be sensitive to EMFs is also important so that they can be targeted in future studies. This is especially true of cetaceans, where recent work has suggested that some species rely on magnetosensing for migration and may be impacted by the presence of magnetic fields. In addition, with the findings of electrosensing capabilities in two species of dolphin, it is likely that more cetacean species can electrosense. Thus, cetaceans may be a species which may be impacted by EMFs in some way.

1.4. Ecology and conservation of cetaceans

Cetaceans play vital roles in helping to maintain the integrity and health of ecosystems (Katona & Whitehead, 1988; Bowen, 1997; Sergio et al., 2008). By acting as distributors of nutrients and generators of material flux in the ocean via the so called the whale pump (Roman and McCarthy, 2010) cetaceans can increase species richness in ecosystems (Buesseler & Boyd, 2003; Lavery et al., 2010; Roman et al., 2014). Whales bring key nutrients, such as iron and nitrogen, from the depths and defecate near the surface (Lavery et al., 2010). This redistribution of nutrients increases plankton productivity and fish population growth (Roman and McCarthy; 2010; Roman et al., 2014). The influx of iron from deep-diving cetaceans is a crucial fertiliser, which stimulates blooms of phytoplankton and causes considerable drawdown of CO_2 from the atmosphere to the deep ocean (Blain et al., 2007; Pollard et al., 2009). Lavery et al. (2010) suggest that these drawdowns could result in the removal of at least 200,000 tons C yr^{-1} from the atmosphere above the Southern Ocean, contributing to the reduction of greenhouse gases (Roman et al., 2014). As well as improving nutrient cycling, cetaceans also play important roles in oceanic food webs (Spitz et al., 2018). Changes in abundance and distribution of predatory cetaceans can shift the composition of prey communities, which can affect ecosystems (Baum and Worm, 2009) occasionally resulting in trophic cascades (Pace et al., 1999). Therefore, cetaceans help to regulate and maintain natural species compositions within habitats (Katona & Whitehead, 1988).

Cetaceans also provide economic benefits. Cetaceans are charismatic and are a popular taxon among the human population (Mazzoldi et al., 2019). Globally, the whale watching industry is worth over 1 billion US dollars annually over the past twenty years (Hoyt, 2001; O'Connor et al., 2009; Pace et al., 2015), with over ten million people partaking in whale watching each year, across 90 countries worldwide (Parsons et al., 2003). The industry provides many small coastal communities with income and employment (Parsons, 2012).

Global populations of many cetaceans are declining (IUCN, 2012, Pace et al., 2015). Of the eighty-nine known cetacean species, the International Union for the Conservation of Nature classifies thirty-seven as least concern, twenty-eight at risk,

including four as 'Critically Endangered'; ten as 'Endangered'; seven as 'Vulnerable' and seven as 'Near Threatened', and finally twenty-four species which are data deficient (IUCN, 2019). This means there is over half of the cetacean species (58%) which are either at risk or that there is little or no data available on their abundance and distribution to state their conservation status.

1.4.1. Threats to cetaceans

Changes in climate, including rise in water temperatures, loss of sea ice and changes in ocean currents, are a noteworthy threat to cetaceans (Yadav and Gjerde, 2020). These changes may threaten cetacean populations directly, for example water temperatures are often a tool of indicating the movements of other cetaceans, changes in temperatures may impact survival and mating successes (Roberts et al., 2017), or indirectly, e.g. through alterations to the distribution and abundance of prey (Learmonth et al., 2006; Simmonds and Isaac, 2007). Species with restricted geographical distributions and limited ability for range shifts are expected to be most at risk (Simmonds and Elliot, 2009). Noteworthy is the vaquita (*Phocoena sinus*), this species is endemic to the Gulf of California, and is currently the most endangered marine mammal in the world (Rodriguez-Perez et al., 2021). This species was thought to only have twenty individuals left in 2018 (Jaramillo-Legorreta et al., 2019) and has the narrowest geographical range of all cetaceans. Any major change in the vaquitas localised habitat would put this species further at risk of extinction. In addition, many river dolphins in both Asia and South America may be vulnerable to changes in water temperature and declining prey availability in their restricted river systems (Simmonds and Elliot, 2009). Range shifts in response to increases in water temperature may result in novel species interactions (Van Bressem et al., 2009) which may lead to exposure to previously unencountered infectious diseases (Weiss et al., 2019). Susceptibility to disease is further increased by other factors, such as depletion of food supplies (Johnson et al. 2009), increased levels of immunosuppressive contaminants (Van Bressem et al., 2009) and increased stress levels due to human disturbance, such as bycatch, ship traffic noise (Rolland et al., 2012) and fish net entanglement (Rolland et al., 2019). Some cetacean species are potentially more vulnerable to the spread of disease due to their social interactions in multi species groups (Guimarães et al., 2007).

Species that occur in estuaries and inshore waters may incur higher risks than pelagic species as they are exposed to greater levels of anthropogenic activities and environmental degradation, such as biological and chemical pollution (Van Bressem et al., 2009; Fernández-Gavela et al., 2019). Chemical pollutants are known to impact cetaceans. Organochloride pollutants (including pesticides and polychlorinated biphenyls) bioaccumulate through the marine food chain and are thought to be contributing to declining populations through reproductive toxicity in species such as bottlenose dolphins and killer whales (*Orcinus orca;* Jepson et al., 2016). Mercury is a known neuro- and immune-toxin, and bioaccumulates in higher trophic organisms (Kershaw and Hall, 2019). There is also an increasing awareness of the threats to marine organisms from discarded plastics (Galloway et al., 2017). The ingestion of plastic debris is the one of the most common interactions reported between plastics and wildlife (Zhu et al., 2019). Ingestion can cause physical harm, but waste plastics may also contain toxic chemical additives, heavy metals, and organic pollutants (Mato et al., 2001; Koelmans et al., 2016; Massos and Turner, 2017). Plastic debris has been reported be contaminated by persistent organic pollutants (Bakir et al., 2012; Caruso, 2019). Indeed, microplastics can be transferred between trophic levels in oceanic food webs (Gutow et al., 2016) potentially culminating as hazard to human health (Caruso, 2019), although there is limited evidence on plastic and pollutant impacts on cetaceans and should be an area which is further researched

Thousands of cetaceans die every year in UK and European waters due to incidental capture or asphyxiation in fishing gear (Orca, 2019). It is estimated that around 1,500 small toothed-whales are caught annually in the UK (Northridge et al., 2018) and a substantial number of baleen whales are entangled in fishing gear and lines from pot-based fishing (Ryan et al., 2016). While many cetaceans die as a result this, others become injured or lose conspecifics (Dolman & Brakes, 2018). Where drowning or death does not occur, subsequent impairments are faced. This can include decreased foraging skills, increased risk of wound infection and severe tissue damage (Moore and van der Hoop, 2012). Strikes from boats and other vessels are another prevalent threat to cetaceans (Peel et al., 2018). Cetaceans are particularly vulnerable to strikes as they surface to breathe. Differences in breathing behaviours and patterns can be seen across the cetaceans, this often varying due to feeding behaviours and diving activities and durations (Miller, and Roos, 2018). Boats are getting larger and faster,

and the number of boats on the water is increasing in order to meet the need for fishing and transport (Erbe et al., 2019). In recent decades, collisions between cetaceans and vessels have increased significantly (Arregui et al., 2019; Ritter & Panigada, 2019); however, the actual number of strikes is unknown and is likely to be under-reported from larger vessels (Williams & O'Hara, 2010; Rockwood et al., 2017). Greater mortality occurs in areas of high density of shipping activity that overlap with high cetacean abundance. Understanding the abundance and distributions of cetacean species which are localised to dense shipping routes, and therefore those more at risk, is important for conservation mitigation (Rockwood et al., 2017).

When a cetacean is hit, they either sink to the ocean floor or float ashore and become stranded (Berman-Kowalewski et al., 2010). The UK's Cetacean Strandings Investigation Programme record approximately 800 strandings a year on UK beaches and shorelines (Orca, 2019). Bycatch and ship strikes cause a large proportion of strandings in UK waters (Deaville et al., 2019). Reports of strandings have increased over the past decade, with boat strikes being the largest cause of mortality (Peel et al., 2018). Stranding data give us important information about cetacean health and threats, which helps researchers to develop mitigation strategies to protect cetaceans from anthropogenic threats (CEFAS, 2019).

Anthropogenic noise has increased in our oceans over the past 100 years (Buckstaff, 2004; Wright et al., 2007; Orca, 2019), due to the increase in motorised marine vehicles, more freight transferred by shipping, oil and gas exploration, military testing underwater explosions and the development of offshore marine renewable energy installations (Erbe et al., 2019). Sound communications enable cetaceans to sense their environment, and to detect prey (Tønnesen et al., 2020) and for some baleen whales who are low frequency specialists to be able to communicate hundreds of kilometres apart (Tyack and Clark, 2000; Torres, 2017; Deecke, 2018). Anthropogenic underwater noise can have different levels of impacts on cetaceans depending on its intensity, nature and location (Weilgart, 2017). Very loud impulsive sounds, such as those resulting from underwater explosions and pile driving, can cause hearing loss, physical damage, and death if the animal is in close proximity (Boyd et al., 2008). Crushing, fracturing, and haemorrhaging of body tissues and organs can occur if exposed to high intensity shock waves from impulsive sounds (von Benda-Beckmann

et al., 2015). The increase in marine traffic has also led to an increase in lower level background noise (Erbe et al., 2018). This background noise is known to interfere with communication, resulting in masking of communication sound signals (Cunningham et al., 2014). Killer whale communication has been noted to be affected by masking. This can interfere with communication, cause changes in behavioural responses and lead to temporary and permanent hearing loss (Erbe, 2002). An increase in marine traffic in the English Channel is one of the possibilities for the observed alterations of whistles produced by common dolphins (*Delphinus delphis)* in this area (Ansmann et al., 2007).

Offshore marine renewable energy installations also increase anthropogenic disturbance. These installations, and specifically the construction of offshore windfarms has increased as a response to climate change (Gill et al., 2012a). The impacts of these installations often present both long and short-term disruptions at different stages of development (Dolman et al., 2007). The pre-development exploration of sites and construction processes increases the amount of boat traffic passing through areas, which can increase the risk of ship strikes on cetaceans (Dolman et al., 2007; Carter et al., 2008). Installation development also includes pile-driving construction noise and disturbance (Boyd et al., 2008). Longer-term impacts can consist of disruption and damage to benthic habitats; but can also lead to the creation of an artificial reef, which can be beneficial in providing habitat for prey species (Langhamer, 2012). The movements of tagged grey (*Halichoerus grypus)* and harbor seals (*Phoca vitulina*) around two active windfarms were associated to increased levels of foraging on the subsea pipelines of the Alpha Ventus and Sheringham Shoal windfarms (Russell et al., 2014). Another potential long-term impact is the presence of electromagnetic fields (EMFs). EMFs are produced from cables transferring electric currents between turbines and also by exporting cables between the windfarm and stations on shore (Tricas and Gill, 2011). The effect of EMFs on cetaceans is relatively unexplored, however the effects of EMFs on other species such as elasmobranchs has been investigated in literature and was discussed in Section 1.3.2 of this review. It is thought that EMFs generated by cables can interfere with navigation (Lohmann and Ernst, 2014) and can have important behavioural and physiological effects (Tricas and Gill, 2011; Gill et al., 2014; Emma, 2016; Nyqvist et al., 2020). The development of marine renewable energy installations

could, therefore, have an effect on cetacean health, physiology and behaviour. Any adverse effect could cause cetaceans to avoid these areas, which has implications for, ecosystem health, trophic structure and local ecotourism in the longer-term.

1.4.2. Cetacean orientation and navigation

Cetaceans are thought to possess a magnetic sense that is used for orientation, navigation, and migration (Torres, 2017; Zapetis and Szesciorka, 2018; Nyqvist et al., 2020). Detection of magnetic fields are likely due to either a magnetite-based system, or through detection of an induced electric field (Wiltschko and Wiltschko,1995). Induction perception assumes that an electric field can be detected via electroreceptors, generated by the naturally occurring magnetic field. The magnetite-based system, which has been proposed in number of cetacean species (Walker et al., 1992) works via the presence of ferromagnetic particles such as magnetite (iron oxide). These particles have been found in the membrane surrounding the brain and spinal cord of both the bottlenose (Bauer et al., 1985) and short-beaked common dolphin (Zoeger et al., 1981) and is hypothesised to be present in other species of cetaceans (Kremers et al., 2016). These particles act like magnets and it is assumed they function by connecting to the central nervous system and align themselves relative to the geomagnetic field (Kremers et al., 2016). This mechanism is believed to be present in other mammalian species who orientate their body in accordance with magnetic field lines such as bats (Chiroptera; Wang et al., 2007), cattle (Bovidae) and deer (Cervidae; Begall et al., 2008). Kremers et al, (2014) suggests that cetaceans may have inherited magnetosensory perception from their artiodactyl ancestors.

It is known from observations of free-ranging cetaceans, that instances of geomagnetic anomalies have resulted in a number of cetacean beach strandings (Walker et al., 2002; Zapetis and Szesciorka, 2018). Because of this, researchers suggested that they must also be able to utilise geomagnetic cues in normal circumstances such as navigation and sensing (Klinowska,1985). The simplest method of geomagnetic navigation is vector navigation, this relies exclusively on cardinal directional information (Wiltschko and Wiltschko, 2005). This type of navigation has been hypothesised in humpback (Allen, 2013), fin (Walker et al., 1992) and sperm whales (Vanselow et al., 2017). In captivity, bottlenose dolphins were

observed to approach a magnetic object faster than an identical non-magnetic object, owing to a sensory modality (Kremers et al., 2014). However, the research into magnetoreception in cetaceans is limited and needs to be studied in further detail.

1.4.3. Cetacean habitats

One of the key concepts in understanding cetacean ecology and biology is a species preferred habitat. Species-habitat relationships can define ecological niches, in turn determining a species' role in that community or ecosystem (Ballance, 2018). The study of cetacean species-habitat relationships can be complex as marine habitats are often defined by oceanographic features which are not static. For example, some species associate with ice edges (e.g., Killer whales, Pitman and Durban, 2012), or prefer shorelines (e.g., minke whales; *Balaenoptera acutorostrata;* Robinson et al., 2009). For some oceanic species, preferences can be defined by the physical and chemical characteristics of water. For instance, blue whales (*Balaenoptera musculus*) are often found in cool upwelling waters (Ballance, 2018). Observations have also been recorded in where pantropical spotted (*Stenella attenuata*) and spinner (*S. longirostris*) dolphins segregate from common dolphins according water surface temperature and salinity (Ballance, 2018). Although, as in most cases, prey type and availability are likely key drivers in cetacean species-habitat relationships and distribution.

1.4.4. Cetacean feeding ecology

Most of the research that has been conducted on feeding behaviour and consumption comes from the data collected from dead animals, be it incidental mortality or strandings. Hence, we understand that cetaceans feed on four types of prey. The first type of cetacean prey can often be characterised as small individuals that occur at relatively shallow depths, primarily small fish (e.g., herring (*Clupea spp*).; Overholtz and Link, 2007, sardines, (*Sardinops spp*); Marcalo et al., 2018) and planktonic crustaceans (uphausiids, copepods, amphipods; Dauby et al., 2003). These prey generally occur at low trophic levels and have small body sizes occurring in dense accumulations. The cetaceans that feed on this type of prey therefore have to capture multiple individuals at once and have evolved filtering mechanisms (baleen) to strain prey from the water. All mysticetes feed on this prey (Ballance, 2018). The second

type of prey are pelagic fish (e.g., hake (*Merluccius spp.*); Santos et al., 2014) and schooling squids (*Loligo spp., Dosidicus spp.*; Young and Cockroft, 1994). These organisms' school at relatively shallow depths, migrate upwards during the night or are located in and above the sediment of the sea floor. These organisms are larger and occupy higher trophic levels and are captured individually. The cetaceans which feed on these are typically small bodied and include the large schooling dolphins, these dolphins tend to have high tooth counts, pointed teeth and snouts in adaptation to catch and forage for individuals (Balance, 2018). The third type comprises of large solitary squid (e.g., *Gonatus spp.*). Cetacean predators of large squid include the deep divers such as the sperm (Whitehead, 2018), dwarf and pygmy sperm (*Kogia sima, K. breviceps;* Wang et al.,2002), beaked (Ziphiidae; MacLeod et al., 2003) and pilot whales (*Globicephala spp.;* Overholtz and Waring, 1991). These species have rounder heads and well developed melons perhaps indicating an importance of echolocation for prey detection in deep dark waters. The final prey type is species at high trophic levels who themselves are top predators, this can include predatory fish, elasmobranchs, marine mammals, and other cetaceans. Only a small number of cetaceans can actually feed on this prey, including killer (e.g., Reeves et al., 2006; Saulitis et al., 2015; Samarra et al., 2018), pilot and melon headed whales (e.g., Shane 1994; Weller et al., 1996).

Cetaceans feed by two main methods, baleen, and teeth. The baleen is used to strain multiple prey organisms from the water, whereas teeth are used for catching individual organisms. Species which have high teeth count can grasp and bite prey where as those with low teeth count have shown to suction feed (Balance, 2018). Mysticetes have baleen plates on the roof of their mouth, the number, length, and density of fibres per plate vary by species and type of prey consumed (Bannister, 2018). As well as prey type, two different feeding methods are used to corollate to the morphology of their baleen plate. Skimming allows balaenids to swim slowly with their mouths open to capture prey items over a period of time. As for gulpers (most rorquals) they can lunge into dense concentrations of prey and consume large amounts at once (Bannister, 2018).

On the other hand, odontocetes feed differently and capture individual prey organisms. They have been recorded to show a range of prey capture behaviours, including prey

herding (Heithaus et al., 2018), prey debilitation (e.g., "fish whacking"; Scott et al., 1990) and benthic foraging (e.g., Bahamian bottlenose dolphins; Rossbach and Herzing, 1997). Prey herding works by actively manipulating the behaviour of prey in order to capture and consume it. For example, dolphins inhabiting saltmarshes and mangroves have been observed to form groups around fish near mudbanks, force a wave to hit the fish which strands them on the mudbank and the dolphins will then slide up the bank in order to pick up the fish (Heithaus et al., 2018). Other methods such as bubble blowing and surface splashing have also been observed (Heithaus et al., 2018). Bottlenose dolphins have also been observed to strike fish with their tails ("fish whacking") in order to stun or knock the fish into the air in order to consume their prey (Scott et al., 1990). Benthic foraging behaviour has been observed in a small number of cetaceans. Guiana dolphins are known to dig and forage in the sediment, indicated through the presence of mud plumes after dives and mud adhering to the rostrum when surfacing (Rossi-Santos and Wedekin, 2006). Humpback whales intentionally disturb the sandy and shell hashed sea floor by scraping their head along to flush out substate burrowing fish and will then feed on these once in the water column (Hain et al., 1995). Killer whales in New Zealand have been observed to engage in benthic digging for stingrays (Visser, 1999). Bottlenose dolphins are known to use benthic foraging techniques such as crater feeding in the Bahamas (Rossbach and Herzing, 1997) and mud plume feeding in Florida (Lewis and Schroeder, 2003). Observations in grey whales *(Eschrichtius robustus)* have recorded individuals digging through sediment to identify prey as well as using suction to pull sediment and prey into their mouths, and then filtering sediment and water away (Hatler and Darling 1974; Nerini,1984; Würsig et al. 1986).

1.4.5. Cetacean vulnerability to EMFs

Due to ecological factors, exposure to artificial EMFs will differ species to species. Offshore windfarms in Europe exist on average, 23km from shore and 17.4m in water depth (Diaz and Soares, 2020). Therefore, we would expect that species which inhabit shallow coastal waters of Europe may be more exposed to EMFs from subsea cables (Dolman and Simmonds, 2010; Wilson et al., 2010). Furthermore, there is evidence to suggest that some cetacean species can detect geomagnetic fields and may use these to orientate themselves or navigate for seasonal migrations (Zapetis and Szesciorka,

2018; Horton et al., 2020; Zellar et al., 2021). Consequently, we may also assume that if migratory routes or seasonal habitat shifts occur in the vicinity of subsea cables, these species too may be at risk from the presence of artificial EMFs.

Elasmobranchs and platypuses (*Ornithorhynchus anatinus)* use their electrosensory systems for the detection benthic prey that release bioelectric fields (e.g. Manger et al., 1998). Electrosensory perception has since been identified in two species of cetacean, both the Guiana (Czech-Damal et al., 2012) and bottlenose dolphins (Huttner et al., 2021). With both species clearly demonstrating benthic foraging strategies. It is suggested that the presence of electroreceptors on the dolphin's rostrum may facilitate prey detection while digging in the sediment and thus at least act as a supplementary modality to echolocation during benthic feeding. Therefore, we may also assume that other species which conduct shallow benthic foraging along the sea floor may also be able to detect electric fields and thus be at risk to exposure of EMFs from sub-sea cables.

In order to evaluate cetacean vulnerability to EMFs in the UK, species which occupy European and Eastern Atlantic waters were sought (Table 1.5). UK species of cetacean were identified via Reid et al. (2003) and Hammond et al. (2013). Ecological characteristics which have been discussed in 1.4.2-1.4.4 were then recorded for each species in table 1.5. Ecological data were obtained from the IUCN Red list (https://www.iucnredlist.org).

Table1.5: **Species of cetaceans that are prevalent in European waters, their conservation status, estimated population and ecological characteristics**. Estimated populations are reported distribution based on sighting records from Hammond et al. (2013), Beck et al. (2014) and Hammond et al.(2017). (LC: Least Concern, VU: Vulnerable, EN: Endangered, DD: Data Deficient). The species which have been highlighted in grey are key species for consideration.

Scientific name	Common name	IUCN Status	Estimated population European/E. Atlantic waters	Migratory species	Feeding behaviours	Habitat
Balaenoptera acutorostrata [1]	Minke whale	LC	12,000	Long distance migrators	Lunge gulp feeding	Coastal and oceanic waters
Balaenoptera borealis [2]	Sei whale	EN	Insufficient data on sightings	Migratory, but specific patterns unknown	Gulping and skimming	Deep oceanic
Balaenoptera physalus [3]	Fin whale	VU	18,000	Seasonal migratory polar to equator	Skimming	Deep oceanic
Balaenoptera musculus [4]	Blue whale	EN	~500	Some evidence of seasonal migrations	Lunge gulp feeding	Neritic and oceanic
Megaptera novaeangliae [5]	Humpback whale	LC	1,400	Seasonal migratory polar to equator	Lunge gulp feeding, bottom feeding, prey herding	Coastal and oceanic waters
Delphinus delphis [6]	Short-beaked common dolphin	LC	65,000	Small local movements with water temperature	Pelagic shoaling fish feeding	Neritic and pelagic
Globicephala melas [7]	Long-finned pilot whale	LC	25,000	Small local movements with water temperature	Echolocation fish hunting	Oceanic, occasionally coastal
Grampus griseus [8]	Risso's dolphin	LC	11,000	Maintain home ranges	Benthic cephalopods, occasional night time feeding	Deep pelagic waters
Lagenorhynchus acutus [9]	Atlantic white-sided dolphin	LC	15,500	Maintain home ranges	Mixed species feeding groups	Coastal and oceanic waters
Lagenorhynchus albirostris [10]	White-beaked dolphin	LC	35,000	Seasonal migratory polar to equator	Surface and benthic feeders	Oceanic, occasionally coastal
Orcinus orca [11]	Killer whale	DD	10±4	Long distance migrators	Multiple style feeders including benthic foraging	Coastal and oceanic waters
Tursiops truncatus [12]	Bottlenose dolphin	LC	30,000	Maintain home ranges	Multiple style feeders including benthic foraging	Coastal and oceanic waters
Phocoena phocoena [13]	Harbour porpoise	LC	450,000	Small local movements with water temperature	Pelagic shoaling fish feeding and benthic foraging	Mainly coastal and bay waters
Physeter macrocephalus [14]	Sperm whale	VU	13,500	Food related migrations – poorly understood	Deep pelagic fish hunting	Deep Oceanic, occasionally coastal
Hyperoodon ampullatus [15]	Northern bottlenose whale	NT	~20,000	Minimal movements observed	Deep feeding on squid (>800m)	Deep Oceanic

Mesoplodon bidens [16]	Sowerby's beaked whale	LC	Insufficient data on sightings	Minimal movements observed	Suction of deep ocean fish	Deep open oceanic
Ziphius cavirostris [17]	Cuvier's beaked whale	LC	Insufficient data on sightings	Minimal movements observed	Suction of deep ocean fish	Deep open oceanic

[1] Cook, 2018a; [2] Cook, 2018b; [3] Cook, 2018d; [4] Cook, 2018c; [5] Cook, 2018e; [6] Braulik et al., 2021; [7] Minton et al., 2018; [8] Kiszka, J. & Braulik, G., 2018a; [9] Braulik, G., 2019; [10] Kiszka, J. & Braulik, G., 2018b; [11] Reeves et al., 2017; [12] Wells et al., 2019; [13] Braulik et al., 2020; [14] Taylor et al., 2019; [15] Taylor et al., 2008a; [16] Taylor et al., 2008b; [17] Taylor et al., 2008c

1. Of the total 17 species which were identified in UK waters regularly, a total of five species has been identified as potentially vulnerable to the presence of artificial EMFs.

2. Minke whale: this species often occupies coastal waters exploiting the variety of prey availability (Perrin et al., 2018). They also regularly make long distance migrations from continental shelfs back to coastal waters (Cook, 2018a). If their migratory paths coincide with subsea cables, this could potentially lead to disorientation and may affect routes.

3. Humpback whale: this species displays a range of feeding behaviours, which include benthic foraging and digging (Hain et al., 1995; Parks et al., 2014). They also occupy coastal waters in summer and visit island and reefs in winter (Clapham, 2018). Foraging in shallow waters may directly expose the whales the physical cables but also the EMFs which may be produced from them. Undertaking seasonal migrations may be facilitated to geomagnetic sensing, therefore magnetic fields produced by subsea cables may also disorientate routes in leaving or returning to coastal waters.

4. Three species of delphinids: Killer whale, Atlantic white-sided dolphin and bottlenose dolphin. As highlighted in 1.4.4, these species have been observed to forage in the sediment along the sea floor. These species also regularly occupy coastal waters. This coastal foraging behaviour may also directly expose these species to subsea cables from windfarms.

1.5. Knowledge gaps to be addressed by this thesis

This review has summarised the literature on three key areas for the conservation of cetaceans. It has highlighted five important points that need to be considered in order to explore the potential effect of EMFs on cetaceans. These are:

1. We are aware of windfarm growth around the UK. This enables us to have spatial understanding of where potential issue may arise.
2. We do not fully understand the characteristics of EMFs from subsea power cables in the ocean.
3. We have limited data on the sighting records of cetaceans around windfarms. We are aware of the problems that come with monitoring cetaceans in the wild and should consider methods of how to combat this.
4. We have identified potential evolutionary and ecological factors that may explain the evolution of electrosensing and magnetosensing in cetaceans.
5. Two species of dolphin have behaviourally displayed electrosensory capabilities and leads to question which other species may also.

Therefore, the aim of this thesis is to:

Evaluate the potential and impact of electrosensing in cetaceans by:

1. Identifying possible electrosensing cetacean species from anatomical structures
2. Identifying possible electrosensing cetacean species from phylogenetic and ecological traits
3. Making future recommendations for the study of electrosensing in cetaceans.

Chapter 2 of this thesis will describe the anatomy of potential electrosensory organs, in three species of cetacean. It will also discuss their possible role as electrosensory or tactile sensors and will compare these to other mammal follicles which have been observed in literature. It will also finally discuss ecological and phylogenetic considerations which may assist in the identification of electrosensing in more species of cetaceans.

Chapter 3 of this thesis will provide a summary of the literature which has been synthesised in this thesis and will conclude by making future recommendations and highlighting the wider implications of electrosensing cetaceans.

2. Chapter Two: Characterisation of follicle anatomy in cetaceans

This chapter is based on the following publication:

Mynett, N., Mossman, H. L., Huttner, T., & Grant, R. A. (2022). Diversity of vibrissal follicle anatomy in cetaceans. The Anatomical Record, 305 (3), pp.609– 621

This chapter addresses the following aims:

1. Identify possible electrosensing cetacean species from anatomical structures
2. Identifying possible electrosensing cetacean species from phylogenetic and ecological traits

2.1. Introduction

Many aquatic environments already present challenging conditions, these challenges can be emphasised with the lack of light which penetrates to deep and turbid waters (Thewissen and Nummela, 2008). Indeed, the reliance on non-visual sensory systems are important, including hearing, echolocation, and touch (Czech-Damal et al., 2012; Torres 2017). Electroreception has evolved in a range of aquatic and terrestrial species, including elasmobranchs, bony fishes, turtles, crustaceans, amphibians, and some mammals, including monotremes and cetaceans (Czech-Damal et al., 2012; Crampton, 2019; Nyqvist et al., 2020). Electrosensing in cetaceans has been confirmed in the Guiana dolphin (*Sotalia guianensis)*, although Czech-Damal et al. (2012) suggest that it may be more common in other mammals, particularly in other cetaceans. Indeed, Huttner et al., 2021 displayed the bottlenose dolphin (*Tursiops truncatus)* could also successfully detect and respond to an electrical stimulus. The detection of prey in cetaceans is often attributed primarily to echolocation (Kelkar et al., 2018); however, many species may rely on a range of multiple sensory channels, including senses such as electrosensing and mechanosensing (Torres and Read 2009). Electroreception is most likely a short-range sense, used to identify nearby objects from within a few centimetres up to several metres away (Czech-Damal et al., 2013). Electroreception may therefore be a useful sense when visual and mechanical cues are masked, such as in deep oceans, turbid water or during substrate digging.

Many species of cetacean are born with vibrissae on their upper jaw, rostrum and even around the blowhole (Ling, 1977; Drake et al., 2015; Bauer et al., 2018). The study into cetacean vibrissae is particularly interesting due to the nature of anatomical differences which have been observed between mysticetes and odontocetes. Unlike most mammals, many odontocetes, lose their whiskers a week or so after birth (Palmer and Weddell, 1964; Ling 1977; Czech-Damal et al., 2012; Czech-Damal et al., 2013). Many researchers thought that the whisker follicles then become vestigial (Yablokov and Klevezal, 1969; Ling, 1977). However, the investigation of vibrissal follicles in a Guiana dolphin shows that they are still functional and that an electrical stimuli is detected by vibrissal crypts which are atrophied vibrissal follicles (Czech-Damal et al., 2012). Interestingly, two species, beluga whale *(Delphinapterus leucas)* and narwhals (*Monodon monoceros*) do not even possess or develop vibrissal hairs whatsoever (Yablokov et al., 1972). Conversely, literature highlights that some mysticetes maintain fully functioning tactile vibrissae into adulthood (Ogawa and Shida, 1950; Berta et al., 2015; Drake et al., 2015). These findings have been documented in the bowhead (*Balaena mysticetus*; Drake et al., 2015), grey (*Eschrichtius robustus*; Berta et al., 2015), and North Atlantic right whales (*Eubalaena glacialis*; Hamilton et al., 2007). Mercado, 2014, also highlights that humpback whales (*Megaptera novaeangliae*) possess hairs that are contained in tubercles, in which these hairs are thought to act as vibrotactile sensors. In addition, intact hair follicles have been reported in several species of river dolphins as stiff hairs along the rostrum (Bauer et al., 2018) and in adult bottlenose dolphins as a vibrissal hair shaft contained within the follicles of the rostrum (Gerussi et al., 2020).

The diversity of whiskers across the cetaceans suggests that vibrissal follicles are likely to be functional in many species. Unlike in other mammals, where whiskers are purely mechanosensory, it is likely that vibrissae play a role in mechanoreception, proprioception and electroreception in some species of cetaceans. Czech-Damal et al. (2012) suggest that electrosensing may be found in more cetacean species, especially those that occupy turbid waters and forage in substrate, such as by digging their rostrum into sediment (e.g. Rossbach & Herzing 1997; Visser, 1999, Bender et al., 2009). Activities such as these, when visual cues may be masked, presents a plausible idea that electrosensing capabilities may function as a supplementary sense aiding in pray localisation during benthic feeding.

Therefore, the aim of this chapter is to describe the vibrissal follicles of three foetal cetacean species, including two odontocetes: Atlantic white-sided dolphin (*Lagenorhynchus acutus*), harbour porpoise (*Phocoena phocoena*), and one mysticete: common minke whale (*Balaenoptera acutorostrata*). The function of the vibrissal follicle as possible mechanoreception, proprioception and electroreception organs, will be discussed. A comparison to other follicles which have been described in literature will also be discussed. A literature review will introduce the key anatomical terms and structures, which will be considered throughout this chapter.

2.2. Literature review

2.2.1. Electrosensory structures in elasmobranchs and monotremes

Electroreception in marine fishes was first described morphologically by Stefano Lorenzini in 1678, giving rise to the name of the anatomical structures (The ampullae of Lorenzini). Early investigations highlighted that these ampullae were able to detect both thermal and a mechanical stimulus (Murry, 1960). Further anatomical (Murray 1962) and behavioural evidence (Dijkgraaf and Kalmijn 1962) then confirmed the ampullae to function as electroreceptive organs. Elasmobranchs can possess thousands of ampullae of Lorenzini (Newton et al., 2019), however, each of the individual ampulla works independently as a detector of external electric fields (Tricas, 2001). This means that the electrosensory field resolution of a particular species can be defined by the distribution and density of the ampullae (Newton et al., 2019). Ampullae found in elasmobranchs are pores located on the skin, head and often on the pectoral fins (Wueringer et al., 2012). These pores are connected to a canal full of conductive jelly, and terminate in ampullary bulbs (Josberger et al., 2016; Figure 2.1.A). The conductive jelly has similar conductive properties to sea water (Waltman, 1966). This allows for the detected electrical stimulus to be relayed through the jelly to the sensory nerve cells and into the central nervous system (Newton et al., 2019).

Among mammals, electroreception is present in the semi-aquatic platypus, (*Ornithorhynchus anatinus*), the Western (*Zaglossus bruijnii*) and the short beaked echidnas (*Tachyglossus aculeatus*; Czech-Damal et al., 2013). The platypus possesses two types of electroreceptors, which are associated with either mucous or serous glands (Manger et al. 1998; Manger and Pettigrew 1996). Both types of electroreceptors show similar morphology. In both types, nerve fibres form a large bulbous cuff around the basal region of the epidermis of the gland duct (Czech-Damal et al., 2013; Figure 2.1.B). These nerve fibres, which extend from the base of the cuff, provide a series of connections between the terminals (Manger et al. 1998). Entering the water triggers several key physiological processes in the platypus bill, assumed to function in preparation for detecting electric fields (Fjällbrant et al., 1998). Wetting of the bill changes its temperature, and results in the secretion of a conductive fluid from the associated electroreceptor gland (Manger et al., 1998). This conductive fluid plays

the same role as the conductive jelly in the elasmobranch ampullae, and conducts the electric field to the nerves, in which the peripheral nervous system transmits the signal into the central nervous system for processing (Pettigrew, 1999).
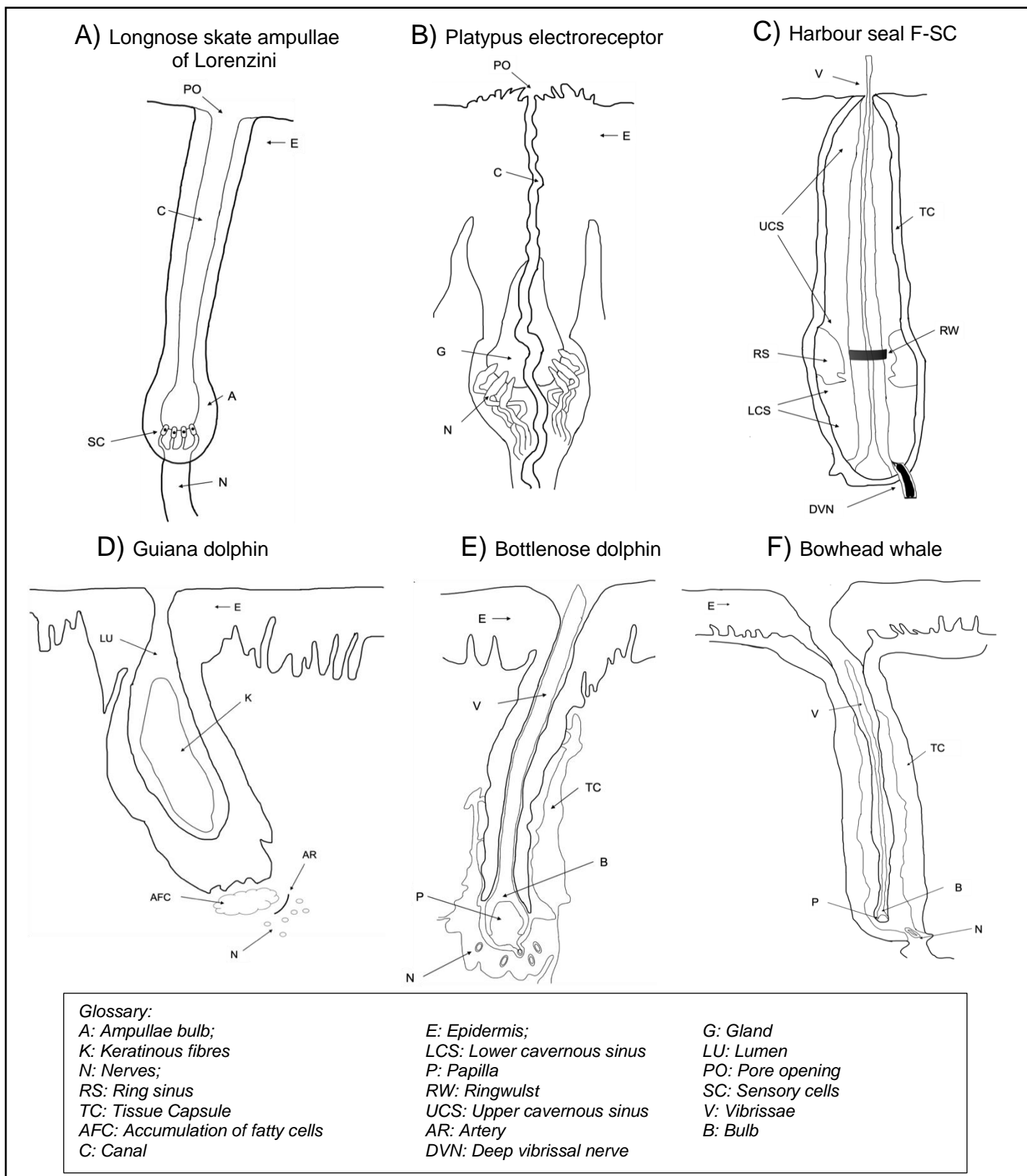
Figure 2.1: **Schematic drawings of sensory *mechanosensory or electrosensory organs discussed in this review*.** A) Ampullae of Lorenzini of a Longnose skate (*Raja binoculata*; adapted from Josberger et al., 2016); B) Mucous/Serous electroreceptor of a Platypus (*Ornithorhynchus anatinus*; adapted from Czech-Damal et al., 2013); C) Follicle Sinus-Complex of a Pinniped (*Phoca vitulina*; adapted from Hanke and Dehnhardt, 2015); D) Vibrissal Crypt of an adult Guiana Dolphin (*Sotalia guianensis*; adapted from Czech-Damal et al., 2012); E) Follicle Sinus-Complex of a neonatal Bottlenose Dolphin (*Tursiops truncatus*; adapted from Gerussi et al., 2020); F) Follicle Sinus-Complex of a neonatal Bowhead whale (*Balaena mysticetus*; adapted from Drake et al., 2015).

2.2.2. Vibrissal follicles in marine mammals

In most mammals, whiskers play a role in mechanosensing (Evans et al., 2019). Of all mammals, whisker follicle anatomy has perhaps been most comprehensively described in pinnipeds (Hanke and Dehnhardt, 2016; Bauer et al., 2018). In pinnipeds, a single vibrissa consists of a hair shaft that is visible protruding from the epidermal layer, and in the dermis sits within a follicle-sinus complex (F-SC). F-SCs consist of a connective tissue capsule supported by dense innervation and a blood sinus complex around the capsule, often denoted as the ringwulst (Rice et al., 1986). In pinnipeds, the follicle is made up of three sections, an upper cavernous sinus (UCS), a ring sinus (RS) and a lower cavernous sinus (LCS). Innervation by the deep vibrissal nerve (DVN) penetrates into the LCS at the bottom of the tissue capsule (Figure 2.1.C). In ringed seals (*Pusa hispida*), the UCS comprises up to 60% of the entire follicle length. One hypothesis for this elongated tripartite follicle is that it allows the mechanoreceptors present around the LCS and RS to be kept at body temperature easier, as they are situated deeper inside the hypodermis (Mauck et al., 2000).

In contrast to pinnipeds, many species of cetaceans lose their facial vibrissae upon maturity (Ling, 1977), potentially indicating cetaceans' lack of dependency on vibrissae due to adaptations in improved hearing and echolocation abilities (Au, 1980,1993). The presence of facial hair, specifically genal and mystacial as well as hair located caudal to the blowhole, is more common in mysticetes than in odontocetes (Drake et al., 2015). Therefore, the sensory hair follicles in some species of mysticetes have previously been investigated and well-described, this includes bowhead, humpback, blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*) and Minke whales Yablokov and Klevesal, 1969).

Ling, (1977), documents that number of vibrissal follicles are variable in mysticetes, however their structure and anatomy are simple and conserved. Mysticetes possess single part capsules containing a hair shaft, but lack intrinsic musculature (Drake et al., 2015). An anatomical investigation of a postnatal bowhead whale identified a thick connective tissue capsule with a hair papilla contained within (Figure 2.1 F; Drake et al., 2015). A single large nerve was identified at the base of the capsule, called the deep vibrissal nerve (DVN), these anatomical features are analogous of pinnipeds.

Mercado (2014) highlighted that humpback whales also possess hairs which are contained in tubercles', in which these protruding hairs are thought to act as vibrotactile sensors (Nakai and Shida, 1948; Yablokov et al., 1974; Ling, 1977). Literature has suggested that the function of the vibrissae of mysticetes act as tactile sensors (e.g. Mercardo, 2014; Drake et al., 2015), due to similarities which have been observed to pinnipeds and other terrestrial mammals. It is assumed that these tactile sensors can be used in the search of food but are more likely to be used as the organ to feel the stream of water (Ogawa and Shida., 1950). To fully understand the vibrissae which are found in mysticetes, further investigation into the gross anatomy of vibrissal follicles in more species of mysticetes would be helpful. In addition, behavioural experimentation would also be beneficial to truly understand their function.

Most odontocetes lose their vibrissae altogether in the first few weeks of life (Bauer et al., 2018; Czech-Damal et al., 2012). Strongly innervated hairless follicle pits have been found in species of adult odontocetes including common (*Delphinus capensis, D. delphis*; Palmer and Weddell, 1964) Guiana (Czech-Damal et al., 2012) and bottlenose (Huttner et al., 2021) dolphins. The fact that the empty follicles remain innervated into adulthood suggests that these follicles, or crypts, are likely to still be functional in adults. Furthermore, Czech-Damal et al. (2012) suggest that they might well serve as electrosensing apparatus, a modality which has been confirmed so far in the Guiana and bottlenose dolphins.

Both histological and behavioural studies were carried out on the Guiana dolphin by Czech-Damal et al. (2012). The structures found consist of elongated lumina and epithelial canals that open to the skin surface (Czech-Damal et al., 2012; Figure 2.1.D). These structures were lacking most of the characteristic features seen in mammalian F-SCs – i.e. vibrissal shaft, hair papilla and ring sinus system and were therefore renamed vibrissal crypts. However, the crypts were surrounded by a dense capillary network. Indeed, silver staining highlighted that dense accumulation of nerve fibres were present at the base and throughout the crypts, features that are also not present in many mammalian F-SCs but can be clearly seen in platypus electroreceptors (Manger et al., 1995). The crypts varied in length of 4.1-7.1 mm deep and 1.2-4.3 mm wide. The lumen of the crypt was filled with a network of

keratinous fibres, and a glycoprotein biogel, potentially acting as an electric signal conduction matrix and aided in the Guiana dolphin detecting the electric stimulus (Czech-Damal et al., 2012, 2013). Noteworthy, a form of biogel is s present on the epidermis of many other odontocetes as well (Baum et al., 2000, 2001). This biogel is rich in glycoproteins and could function as a conductive gel that works in joint with the nerve fibres to detect electric stimuli. This gel may act in a similar function to the gel which can be found in electrosensory follicles in species such as the platypus, and some fish i.e., longnose skate.

As well as a histological investigation, Czech-Damal et al. (2012) also conducted a behavioural test on a 28-year-old male Guiana dolphin to identify the behavioural detection threshold. Under a go/no go protocol the individual was trained to respond to an electrical stimulus in the order of magnitude of that produced by small-medium fish, which consisted of six stimulus strengths. When a stimulus was presented or detected the dolphin was trained to leave the set-up station and was to remain still for when there was no detection of a stimulus. A detection threshold was therefore established upon the 50% success rate in reaction to the stimuli strengths. However, as with all novel experiments, inaccuracies may occur. Such as if the dolphin displayed a negative result, this may not be due to the fact it did not sense the stimuli but instead, learned the incorrect response behaviour as this was the first time experiencing this kind of stimuli. In addition, the dolphin may have been focusing on other sensory input instead and acted in response. The limited experience by both human and dolphin conducting a novel test may also have impacted the outcomes. A control was set up for the experiment, in which adaptations to the set up were conducted. Firstly, a control in which a plastic shell covered the vibrissal crypt, these plastic shells completely covered the openings of the vibrissal crypts. Control trials were triggered at a higher intensity stimulus than the detection threshold of the dolphin that has been identified from the main trial, and the dolphin did not respond as successfully. In an additional control test, there was the presence of the plastic shell cover, but this time sea water was able to come in contact with the vibrissal crypt openings. The results showed that this time the dolphin was not impaired in response to the stimuli when this was the case. These behavioural findings suggest that the source of the detection of the electrical stimuli occurred from the vibrissal crypt, owing their function as electroreceptors.

Gerussi et al. (2020) recently investigated the gross follicle anatomy of common bottlenose dolphins, and instead of hairless follicles as observed by Palmer and Weddell, (1964), they found that adult individuals retain their whisker shafts, albeit contained well within the follicle. Their follicles did however have a dense innervation, similar to the Guiana dolphin, with nerves spreading around the follicle penetrating and terminating at the base and various locations up the sides of the follicle (Gerussi et al., 2020; Figure 2.1.E). They therefore concluded that these follicles may still act as functional sensors and suggested a more proprioceptive role instead but stated that electrosensory ability cannot be ruled out. A proprioceptive role however is reflective of findings by Yablokov et al. (1972) who suggested that small hairs contained within a follicle may act as a sensor to movement of water and head movements.

More recently, Huttner et al. (2021) investigated the anatomical and behavioural evidence for electroreception in the bottlenose dolphin. The anatomical results identified that neonate bottlenose dolphins possess vibrissal follicles with a functional hair papilla and a cavernous sinus, but that adults lack these features. This suggests that there are functional differences of vibrissal follicle structures in neonates and adults in bottlenose dolphins. As in the Guiana dolphin, Huttner et al. (2021) suggests that adult follicles are denoted 'vibrissal crypts' and show a postnatal morphological transformation from a mechanoreceptor to an electroreceptor. The follicles in neonates varied between 4-6mm in length and 0.3-1mm in width, they contained a hair which was curled caudally and protruded 18mm from the skin surface. In adults these follicles lacked a hair shaft and hair papilla but exhibited an expanded lumen of 5.4-7.5mm in length and 0.6-2.4mm in width. Innervation of the follicles was almost equal in both neonates and adults showing functionality in both, even with key mechanosensory features lacking in adults.

In the behavioural experimentation, four bottlenose dolphins were trained on a go/no go paradigm, three different training stimuli were used in stages to teach a generalised behaviour response before exposure to electrical stimuli. These different training modalities were audio, optical and mechanical. In the last stage (electrical) all four dolphins responded correctly with 'go' to the presence of weak DC electric fields with an average of 86.85% success rate in the entire session across all four dolphins ($p < 0.0001$). Unlike in the Guiana dolphin a threshold was unable to be established

however the accurate and reliable actions of the dolphins to stimuli as low as 0.5mV cm^{-1} indicates that these dolphins could detect low field strengths. Control tests were unable to be carried out on the bottlenose dolphins, but Huttner et al. (2021) states that the control tests by Czech-Damal et al. (2012), showed beyond doubt that the crypts were the site of electroreception.

2.2.3. Conclusions

Due to the anatomical diversity and the fact that cetaceans possess both mechanosensory and electrosensory vibrissal follicles, justifies further investigation into this taxon. Therefore, the current study will investigate and qualitatively describe the gross follicle anatomy of three species of cetacean to characterise their follicle anatomy. Comparisons with the findings of other follicle anatomy which have been described in other species of cetaceans such as bottlenose dolphin, Guiana dolphin, and bowhead whale, as well as pinnipeds will be used to examine the anatomical evidence in support of electroreception in cetaceans.

2.3. Methods

Animals Tissue

Samples were obtained from four species of cetacean: harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), minke whale (*Balaenoptera acutorostrata*), and Sowerby's beaked whale (*Mesoplodon bidens*). Sowerby's beaked whale was a stranded adult. Whereas the other three species were foetuses that had died from natural causes and washed up on Scottish beaches. Samples were donated by the National Museum of Scotland in Edinburgh, UK. As is usual for museum store specimens, samples were kept in freezer conditions and occasionally went through freeze-thaw cycles, which affected the quality of samples somewhat and created ice crystals within the sample. This effect can be seen in the minke whale, where repeated freezing and thawing has affected the tissue sample quality and impacted the histological analysis (Figure 2.4.B). Several dimples in the skin of the Sowerby beaked whale were identified under microscope (Figure 2.2); however, no follicles were able to be found. Therefore, this species was removed from the study, leaving three study species.
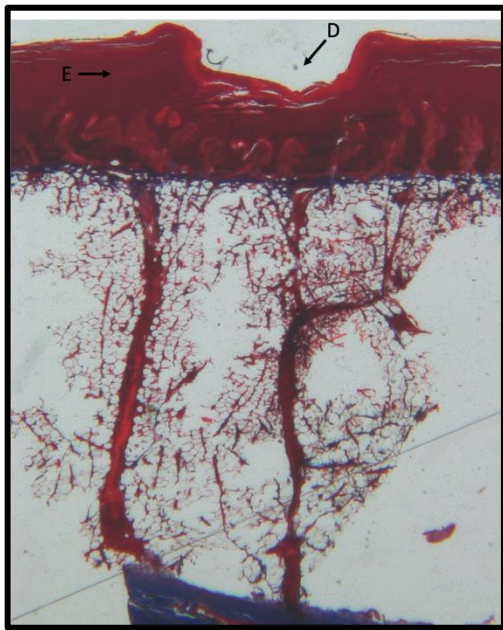
Figure 2.2: **Light micrograph image of a Masson-Trichrome staining of Sowerby's beaked whale upper lip tissue**. Dimple in the skin. Scale bar 1 mm. (Glossary: D: Dimple E: Epidermis).

One individual per species was used in this study, and for each specimen, three to four vibrissal follicles were investigated, (Atlantic white-sided dolphin: 3, harbour porpoise: 4 and minke whale: 4). Dissection of a whole row of vibrissal follicles were collected and an area around each individual follicle was dissected into roughly an 8cm^3 tissue sample cube which had the vibrissal hair intact. Samples were flattened by padding with foam, stored in histology cassettes, and left in 4% paraformaldehyde (PFA) overnight.

Histology

Samples were then subject to dehydration and mounting in paraffin wax for slicing and staining with Masson's Trichrome, based on the protocol described by Grant et al. (2017). Samples were processed through several industrialised methylated spirit (IMS) increasing gradient baths (70%, 80%, 90%, and 100%). They were then immersed in xylene and paraffin wax. Total processing time was approx. 12 hours. Tissue samples were then submerged in hot paraffin wax moulded onto cassettes and set into solid paraffin wax blocks. These were sliced using a Thermos Scientific microtome HM355S into 20 μm thick slices, which fell into a 37-39°C bath and were then mounted onto slides and left to dry. Slides were then moved through a sequence of solutions for the Masson's Trichrome staining protocol. This started with 1 hour in 4% PFA in 0.1 M phosphate buffer, then Bouin's Solution for 3 hours. Slides were then rehydrated using xylene (X_1, X_2) and three IMS solutions (100%, 90% and 70%). Muscle fibres were stained by adding the slides to Biebrich Scarlet acid. Collagen was stained by adding the slides to acid solution (phosphotungstic and phosphomolybdic acids) and aniline blue. Between each stage of staining, the slides were washed multiple times with distilled water. The final stage consisted of dehydrating the slides through reverse IMS gradients (70%, 90%, 100%) and xylene (X_2, X_1). Once completed, slides were dried, and cover slipped with DPX and left to air in the fume hood for 48hrs. Masson's Trichrome is a commonly used stain and allowed for comparison to literature which have investigated cetacean follicle anatomy (Czech-Damal et al., 2012; Drake et al., 2015; Gerussi et al., 2020). As well as Masson's Trichrome staining, three slides per species were selected to be stained with Luxol fast blue solution, this solution stains myelinated fibres blue, which assists in the identification of innervation of the follicle. Slides were then examined, and images captured on a Zeiss Axioimager M1 light microscope (Carl Zeiss Microscopy GmbH,

Jena, Germany) using Zen Pro 3.1 (blue edition; Carl Zeiss Microscopy GmbH, Jena, Germany). Maximum follicle length and width measurements were taken from each follicle, and a mean was presented per species (Table 2.1). Only adjustments in exposure and white balance were made to the images.

2.4.   Results

All three species had an elongated tissue capsule surrounding the vibrissal follicle. All follicles contained a hair, or vibrissal shaft. There was no ringwulst or ring sinus, nor were any muscles or glands associated with the follicles in any of the three species. Results will be discussed species by species below.

Atlantic white-sided dolphin

The specimen which was investigated contained four vibrissae per row on the section dissected from the rostrum. Within each follicle there was a short and dark hair which was curved in shape and protruded out of the follicle approx. 10mm (Figure 2.3.A). These follicles were the longest follicle of all three species (Table 2.1) and displayed a dense accumulation of nerves bundles both surrounding the base of the follicle (Figure 2.3.B-D). Innervation can also be observed running parallel to the follicle and entering at superficial levels up the follicle towards the epidermis (Figure 2.3.D). The follicles were simple in structure and were contained within a tissue capsule (Figure 2.3 A-D).
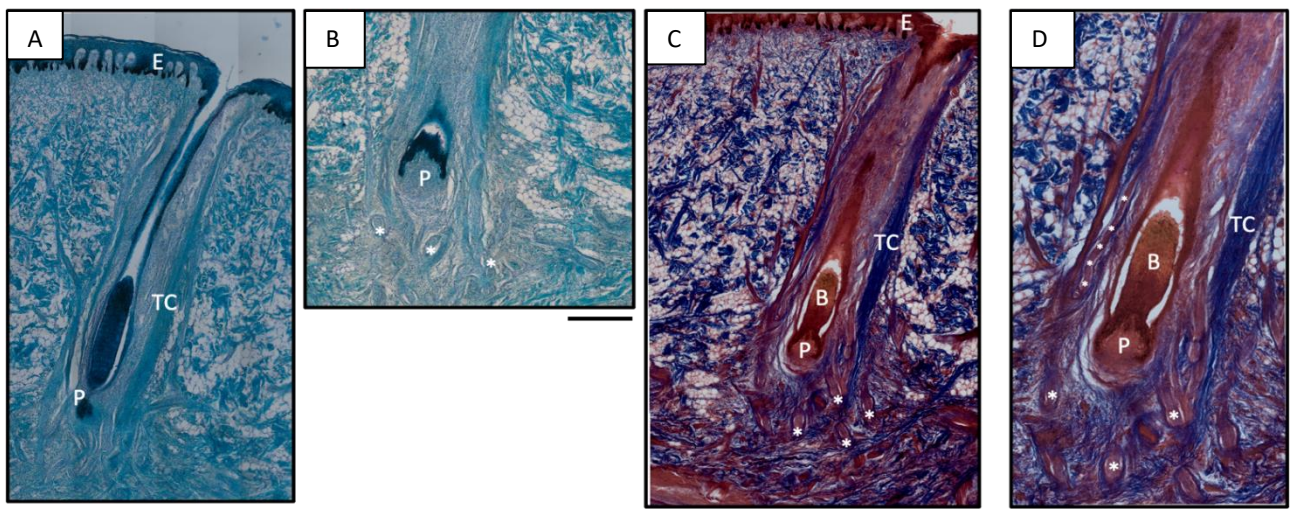
*Figure 2.3: **Light micrographs of cross sections of vibrissal follicle anatomy of Atlantic white-sided dolphin (Lagenorhynchus acutus).** A-B show Luxol fast blue staining. Images C-D show Masson's Trichrome staining. Images A and C show full follicle view, images B and D show close up of follicle base. Image D shows the path of innervation into higher levels of the follicle via path of asterisks (*). B: Hair bulb; E: Epidermis; TC: Tissue capsule; P: Papilla; (*): Nerve bundles. All scale bars are 0.5mm.*

Harbour porpoise

The specimen which was investigated contained two vibrissae per row on the section dissected from the rostrum. Each follicle contained a short and pale hair which protruded out of the follicle approx. 10mm. Large curvature of the vibrissal shafts was observed (Figure 2.4.A). Follicles were thin and were the narrowest out of the three species (Table 2.1). The follicles consisted of both epidermal and dermal parts in which the epidermal layer of the harbour porpoise was thicker than that of the other two species (Figure 2.4.A-B). Nerve bundles and fibres were loose in the surrounding tissue of the follicle, upon closer proximity to the base of the follicle, these fibres appeared to bundle together and entered the follicle mainly in one location (Figure 2.4.C-D). The follicles were simple in structure and were contained within a tissue capsule with a thin follicle wall which was uniform in thickness (Figure 2.4.B).
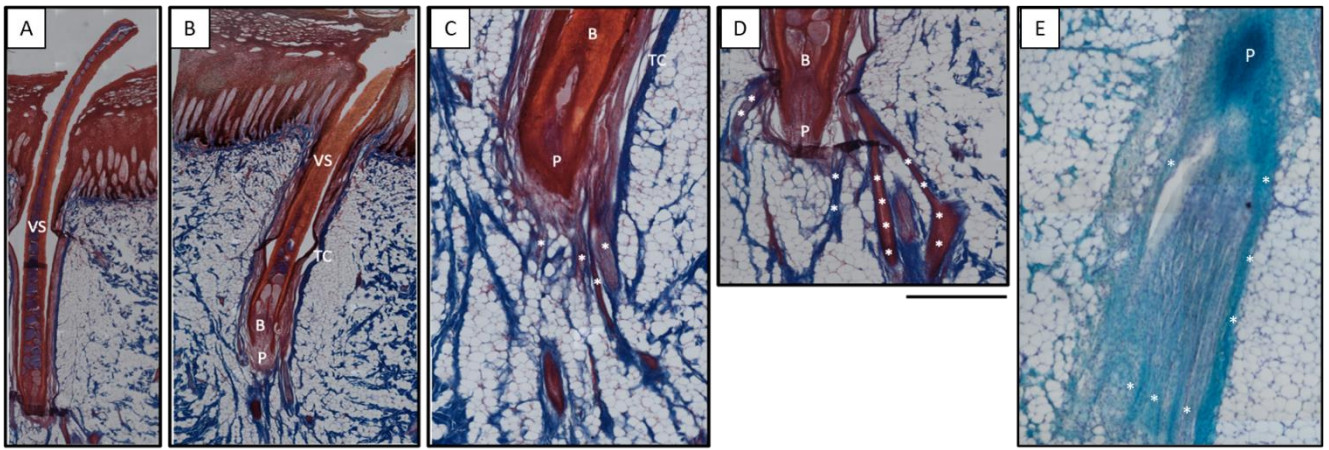
*Figure 2.4: **Light micrographs of cross sections of vibrissal follicle anatomy of Harbour porpoise (Phocoena phocoena).** Images A-D show Masson's Trichrome staining. Image E shows Luxol fast blue staining. Images A and B show full follicle view, images C-E show close up of follicle base. Image D-E shows the paths of innervation into base of the follicle via path of asterisks (*). B: Hair bulb; E: Epidermis; TC: Tissue capsule; P: Papilla. All scale bars are 0.5mm.*

Minke whale (*Balaenoptera acutorostrata*)

The specimen which was investigated contained four vibrissae per row on the section dissected from the rostrum. Each follicle contained a short and pale hair. Follicles were oval and were the widest and shortest out of the three species studied (Table 2.1). The follicle sample contained both epidermal and dermal parts, with a thin epidermis (Figure 2.5.A-B). The follicles were simple in structure and were contained within a tissue capsule with a thin follicle wall which was dissimilar in thickness on either side of the follicle (the wall of the follicle was slightly thicker on the right hand-side of the sliced tissue sample than the left (Figure 2.5.A-B)). Ice crystallisation can potentially be observed in sections of the tissue (Figure 2.5.B). This may have impacted the size of the follicle sinus and tissue capsule through the enlarging of tissue. The innervation was a compact accumulation of nerve fibres which appeared to enter the follicle capsule at a singular insertion point from directly below the follicle (Figure 2.5.C)
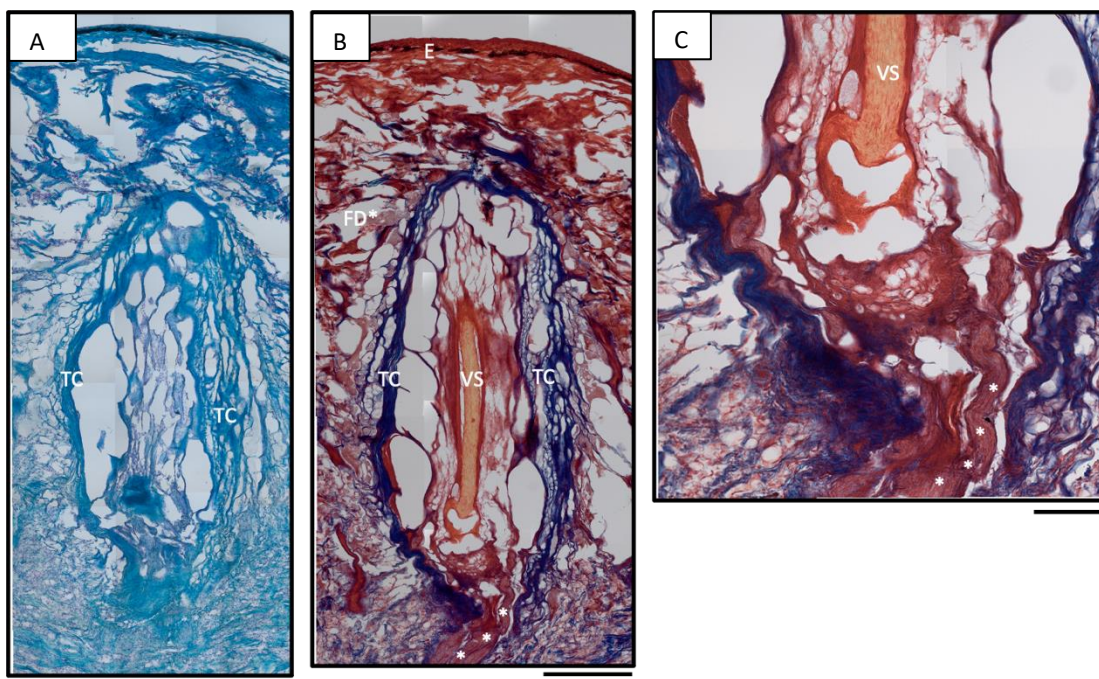
*Figure 2.5: **Light Micrographs of cross sections of vibrissal follicle anatomy of Minke whale (Balaenoptera acutorostrata).** Image A shows Luxol fast blue staining. Images B-C show Masson's Trichrome staining. A and B show full follicle view, C shows close up of follicle base. Images B and C shows the single insertion site path of innervation of the follicle via path of asterisks (*). B: Hair bulb; E: Epidermis; TC: Tissue capsule; P: Papilla; FD*: potential freezer damage. All scale bars are 0.5mm.*

Table 2.1 **Structural characteristics of size of follicles**. *Length and width measurements taken from top of epidermis to the base of tissue capsule. Measurements recorded through microscope imaging and averages calculated from total of number of follicles in a single row for comparison.*

Species	Length (mm)	Average length (mm)	Width (mm)	Average width (mm)
Atlantic white-sided dolphin	3.79 3.64 3.63 3.74	3.70	0.91 0.83 0.81 0.85	0.85
Harbour porpoise	3.33 3.37	3.35	0.58 0.64	0.61
Minke whale	2.94 2.91 2.98 3.01	2.96	1.20 1.16 1.24 1.28	1.22

2.5. Discussion

The data presented in this study characterised the whisker follicle anatomy of three foetal cetacean species. All three species present few (2-4) and short vibrissae, which protrude approx. 10mm from the surface. All the vibrissal follicles were also elongated structures which were all contained within a tissue capsule and had some form of innervation, although they lacked muscles, ringwulst and a ring sinus (Figures 2.3-2.5.). The Atlantic white-sided dolphin possessed a dense accumulation of innervation at the base and side of the follicle, similar to bottlenose and Guiana dolphins.

Delphinid follicles

The densely innervated follicles in the Atlantic white-sided dolphin are comparable to those that have been previously described in the bottlenose dolphin (Gerussi et al., 2020) and display similar anatomical characteristics to the Guiana dolphins innervated vibrissal crypts (Czech-Damal et al., 2012). In Atlantic white sided dolphin, the deep vibrissal nerve (DVN) branched around the follicle and even travelled up parallel to the follicle and inserted in more superficial heights (Figure 2.3.D). Both the bottlenose and Atlantic white sided dolphins have large follicles that are innervated by nerve fibres around the base and the sides of the follicle. The presence of a densely innervated follicle is also observed in platypuses and is believed to play a crucial role in the transduction of electrical stimuli (Manger et al., 1995; Czech-Damal et al., 2013). The nature of this innervation makes it plausible that the Atlantic white-sided dolphins may also be able to operate as electrosensory organs. The similarities which have been observed in these three dolphin species indicate that investigation into more species of the delphinids should be conducted.

Whisker follicles in porpoises and baleen whales

Unlike the delphinids, the harbour porpoise and minke whale displayed a singular innervation site at the base of the follicle. This was similar to the structures seen in sensory hairs of other cetaceans that are thought to serve as tactile sensors, specifically in mysticetes such as the bowhead whale (Berta et al., 2015). This may suggest that the minke whale and harbour porpoise vibrissae are primarily for mechanoreception too. It was originally hypothesised that many of the mysticetes use facial sensory hairs to detect food when surface feeding (Nakai and Shida, 1948),

which has been reported in the bowhead whale (Drake et al., 2015). Thus, it is presumed that the sensory hairs in the bowhead whale act as sensors changes in the environment, such as during breaching and detecting the change between water and air or water flow when feeding (Drake et al., 2015). Indeed, many mysticetes may use sensory hairs in the tactile sensing of prey and water and this may explain the simpler innervation and sensory hair type observed in the minke whale and harbour porpoise.

Echolocation in cetaceans

Sensory adaptations in species of cetacean are associated with improved hearing abilities. Utilising echolocation as their main source of information for finding, tracking, and catching prey items (Wisniewska et al., 2016). Echolocation capabilities in dolphins in the past have been studied in detail (Au et al., 2000; Kremers et al., 2016). The maximum detection range of a 30 cm fish by a bottlenose dolphin was ~173m (Au et al., 2007). Additionally, Au and Snyder (1980) demonstrated that bottlenose dolphins can detect small objects (~8cm) at distances over 100 m. In comparison to odontocetes, less research has been conducted on the acoustic abilities of baleen whales due to their size and limited ability to keep them in captivity (Torres, 2017). In the wild, baleen whales produce low frequency calls enabling long range vocalisations of distances of 9-45km, varying by species (Stafford et al.2007, Clark et al.2010). In addition to being able to locate prey over distances, the distinction of prey type and quality is critical to foraging success. Dolphins such as bottlenose dolphins may be capable to discriminate different types of species of fish (Auet al.2009), through echolocation capabilities by using the echo spectrum shape and changes in target strength (DeLong et al., 2006). However, many oceans' environments present variable sea floor structure and conditions ranging from sandy to silty sediment or even rock beds. These locations therefore possess different reflectivity and conditions to navigate (Dähne et al., 2020). These variable conditions can affect reverberation of sound and therefore the speed of sound in the water (Dähne et al., 2020). Certain foraging behaviours are known to create turbid waters and mud plumes, making the conditions of the water unclear and dense with sediment. When this occurs, it can become challenging to detect sound accurately (Wisniewska et al., 2016). Electroreception may therefore function as a supplementary sensory modality to echolocation to aid in close range prey localization during benthic feeding.

Feeding behaviours

Certain ecological factors may be associated with the presence of electrosensing modalities. Specifically, we might associate electrosensing with certain feeding behaviours, including benthic foraging. The fact that Guiana dolphins forage in murky turbid water was proposed as a need for the evolution of the electrosensory organ (Czech-Damal et al., 2012). They are known to dig and forage in the sediment. This is indicated through the presence of mud plumes after dives and mud adhering to the rostrum when surfacing (Rossi-Santos and Wedekin, 2006). Czech-Damal et al. (2012) suggest that other cetacean species that forage in a similar way may also electrosense. Many other toothed whales report displaying benthic foraging behaviours, for example common bottlenose dolphins display a range of these behaviours when feeding, such as crater feeding (Rossbach and Herzing, 1997) and mud plume feeding (Lewis and Schroeder, 2003). Atlantic white sided dolphins have been observed to feed at the surface, although there is research documenting their benthic foraging behaviours (Craddock et al., 2009). A study on Atlantic spotted dolphins (*Stenella frontalis)* observed feeding behaviours both during the day and at night-time periods in the deeper waters of the Bahamas (Herzing and Elliser, 2014). In addition, a study into the diving and deep foraging behaviours of Risso's dolphins (*Grampus griseus*) identified that their foraging behaviours adjusted in accordance with longer winter nights in the Mediterranean sea, displaying longer periods of foraging during the night (Giorli et al.,2016). These behaviours suggest that the Atlantic spotted and Risso's dolphins exhibit nocturnal feeding patterns, which are limited by the availability of daylight. Therefore, whilst vision, echolocation or both may first be used in localisation and tracking of potential pray, electroreception may provide important sensory information when the cetacean is near prey, when visual or audio cues may no longer be of use.

Phylogenetic considerations

A phylogenetic tree was produced to identify the species that may electrosense. Datasets were downloaded from '10K trees' (https://10ktrees.nunn-lab.org), and a consensus tree (from 100 trees) with posterior probabilities were plotted using FigTree v1.4.4 (Figure 2.6).
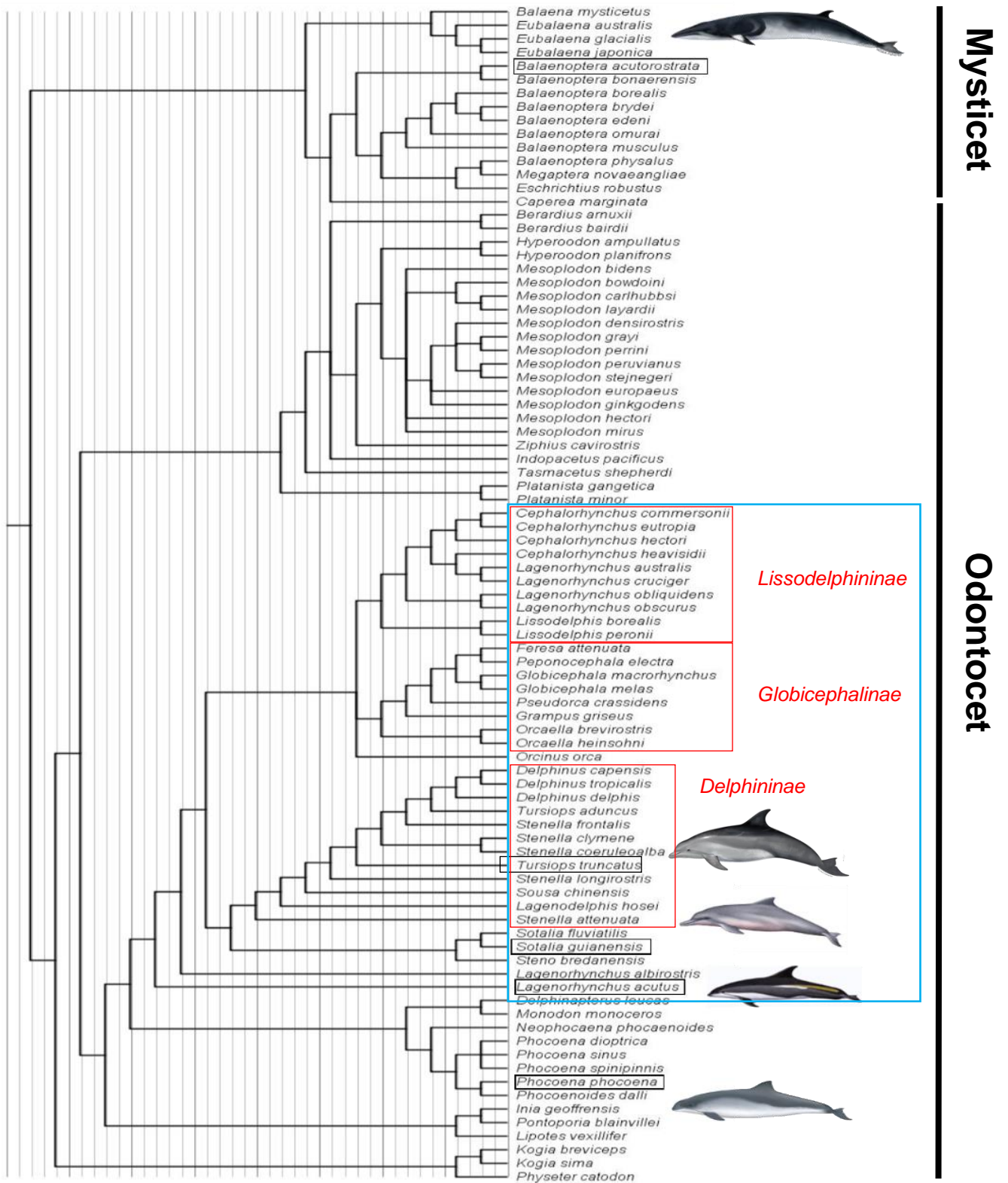
Figure 2.6: **Cetacean phylogenetic tree**. *Constructed using data from 10k trees (https://10ktrees.nunn-lab.org). The family Delphinidae is identified by the blue box and subfamilies identified by red boxes. Relevant species include: Balaenoptera acutorostrata – minke whale; Tursiops truncatus – bottlenose dolphin; Sotalia guianensis – Guiana dolphin; Lagenorhynchus acutus – Atlantic white-sided dolphin; Phocoena phocoena – harbour porpoise*

The Delphinidae are the largest family of odontocetes with three main subfamilies: Delphininae, Globicephalinae and Lissodelphininae (Figure 3.1). The divergence of the Atlantic white-sided dolphin occurred prior to the divergence of the subfamily lineages (LeDuc et al., 1999; May-Collado and Agnarsson, 2006; Agnarsson and May-Collado, 2008; Caballero et al., 2008; McGowen et al., 2009) however the species is still considered part of the family Delphinidae. Additionally, the genera Sotalia and Steno have been described as a sister taxon to the subfamily Delphininae (Caballero et al. 2008; Figure 3.1).The placement of the bottlenose dolphin within the Delphininae subfamily is well supported (Caballero et al., 2008; McGowen et al., 2009). Anatomical similarities observed between the Atlantic white sided, bottlenose and Guiana dolphins, who are members of the Delphinidae, could suggest the possibility that other Delphinids may possess similar anatomical features. This therefore presents an interesting taxon to investigate in relation electrosensory perception

The harbour porpoise is part of the family Phocoenidae. This could explain the differences between the follicle structure and lack of dense innervation. The minke and bowhead whales underwent divergence separately to dolphin species (McGowen et al., 2009). This has resulted in different adaptations, the most striking being the presence of the baleen plate and the resulting differences in feeding, which may mean they do not need electrosensory organs.

Comparing to other mammalian species

Throughout the transition from terrestrial into aquatic environments, marine mammals have undergone sensory specialisation (Bauer et al., 2018). This is especially true in pinnipeds, who have the most diverse whisker morphology, in terms of shape, surface texture, organisation and number, of all mammals (Mattson and Marshall, 2016; Dougill et al., 2020). Conversely, very little is currently known about the hair shape and surface texture of cetacean vibrissae (Bauer et al., 2018). This is likely, in part, due to the loss of the hairs in many species of odontocetes. However, I suggest that as in pinnipeds, adaptation to the aquatic environment has also led to vibrissal diversity in cetaceans. Indeed, cetacean vibrissae vary in number, position and in function, possibly serving as electrosensors in some delphinid species.

Overall, cetacean vibrissal follicles lack key features that are observed in other mammals, including muscles, ringwulst and ring sinus. However, these features are also absent in other species, especially in terrestrial, diurnal mammals such as such as primates (Primatomorpha), horses (Equidae) and deer (Cervidae); which also present thin and reduced whiskers and follicles (Muchlinski et al., 2013; Muchlinski et al., 2020), similar to those I observed in cetaceans. Whiskers in these diurnal species may be reduced due to a greater reliance on vision, as well as an increase in fingertip tactile sensing in primates (Dahiya et al., 2009). This may also be true in cetaceans who have evolved a greater reliance on other senses, such as echolocation. However, the function of the whisker follicle evolving to serve an electrosensory purpose may also reduce the mechanosensory needs of the tactile whisker follicle use in cetaceans.

Histological sample material

Only foetal specimens were used in this study. This made locating the vibrissae easier for histology. Gerussi et al. (2020) documented that there was not much variation of structural change when bottlenose dolphins reached maturity. Therefore, the samples in this study are to be representative of the adult samples too. However, while the gross anatomy of the follicles is unlikely to differ from birth to mature adult, some species of odontocetes appear to have a reduction in or lose their vibrissal hair shafts. Whilst at least two species of river dolphin retain their vibrissae as stiff hairs into maturity (Bauer et al., 2018). Therefore, the size of the hair shaft in an adult specimen is therefore more likely to give a clue of the function of the follicle and should be further explored. Though the presence of vibrissae in foetal animals may suggest a function associated with basic tactile sensing in the initial stage of life. This could include creating a close contact with the mother, recognition and locating the nipple for nursing (Gerussi et al. 2020).

Conclusions

This study has shown that the anatomy of vibrissal follicles in cetaceans is diverse and that evolutionary, phylogenetic, and ecological factors may be key drivers for this diversity. The differences in follicle anatomy are likely to be associated with function, and that it is plausible that benthic and nocturnal foraging behaviours are key for the evolution of an electrosensory modality. The similarity between the follicles of different delphinids may also suggest that follicle anatomy is phylogenetically associated, and

that delphinid species are more likely to have electrosensory follicles than mysticetes or other odontocetes. In addition, a key commonality of electrosensing in elasmobranchs, platypuses and the Guiana dolphin is the presence of an electroconductive gel (Czech-Damal et al., 2012; Czech-Damal et al., 2013; Josberger et al., 2016). The presence of a conductive gel in vibrissae follicles of cetaceans may also indicate electrosensory abilities. Therefore, cetacean vibrissal follicle contents should be investigated further for conductivity and material properties.

3. Chapter Three: Studying the implications of EMFs on cetaceans and future recommendations

This chapter addresses the following aims:

1. Making future recommendations for the study of electrosensing in cetaceans

3.1. Introduction

Growth of the offshore windfarm industry in Europe has increased in the past two decades (Hutchison et al., 2020). A large majority of this growth has occurred on the English East coast in the North Sea (Díaz and Soares, 2020), with the United kingdom (UK) having more offshore windfarms than any other European country (Díaz and Soares, 2020). This thesis was able to accumulate the spatial data of offshore windfarms to identify the scale of their growth and the potential issues that they may cause. It has also highlighted that the available data on cetacean sightings around the UK have significant drawbacks. Therefore, limiting the ability to compare historical sighting data between time periods of specific cetacean abundance and distribution.

The characteristics of EMFs which are produced from subsea power cables from windfarms depend on a range of factors, which include: their location, the type of cable, the type of power supply (HVDC vs HVAC; CMAS, 2003; Öhman et al., 2007; Copping et al., 2013). However, the number of scientific publications on the specific characteristics of in situ subsea power cables is scarce (Taormina et al., 2018). This prevents researchers from precisely assessing the potential impacts of EMF emissions on marine organisms *in situ* (CMAS, 2003). Although, some studies have investigated the effect of a range of EMFs *ex situ*, observing behavioural and physiological effects on marine organisms (Gill et al., 2009; Tricas and Gill, 2011; Hutchison et al., 2018; Gill and Desender, 2020). This thesis has synthesised some of the literature that is available from these studies.

Chapter one also reviewed the threats cetaceans face and ecological factors which are key for their survival. Factors such as feeding habits, habitats and migration

patterns may affect the level of exposure to artificial EMFs from subsea cables, certain species may face. Five species were identified as vulnerable to artificial EMFs in UK waters.

Vibrissae are present on the faces of most mammals (Ahl, 1986; Grant & Goss, 2021). Unlike in other mammals, where vibrissae are purely mechanosensory, it is likely that they play a role in mechanoreception, proprioception and electroreception in cetaceans. Chapter two qualitatively described the gross vibrissal anatomy of foetuses of three species of cetacean and compared the findings to previous anatomical descriptions. Two members of the family Delphinidae, the Atlantic white-sided and bottlenose dolphins have vibrissal follicles that are densely innervated by nerve fibres around the base and the sides of the follicle. The nature of this innervation makes it plausible that the follicles of Atlantic white-sided and bottlenose dolphins may also be able to operate as electrosensory organs. Indeed, recent evidence from Huttner et al., (2021) demonstrated electroreceptive behaviours in four bottlenose dolphins. Chapter two also reviewed ecological and phylogenetic considerations for the evolution of electrosensing in cetaceans. Differences in follicle anatomy in Cetacea are likely to be associated with function, and it is plausible that benthic foraging in sea floor sediment is one of the key drivers in the evolution of electroreception. Also, the anatomical similarities which have been observed across the delphinids also suggests phylogenetic relationships may also play a role in the presence of electrosensory perception. This certainly provides an interesting group to further study this sensory modality in.

3.2.   Future recommendations

Data

Data on the locations of offshore windfarm locations and their cables are freely available, however the available data on cetacean sightings are problematic. Traditional boat and aerial transect surveys of cetaceans have major drawbacks including systematic bias in the species that are recorded, incorrect identification of species, temporal and spatial heterogeneity in survey efforts or safety concerns if travelling near to windfarms (Clough et al., 2012).

Not enough data are available to confidently determine whether windfarms are affecting cetaceans due to EMFs. Further efforts need to be invested in the cetacean surveys in European waters, especially around UK windfarms and cable sites. Since we know the current locations of UK windfarms and cables (figure 1.1), this allows special locational survey efforts. Behavioural data also need to be collected. However, baseline data are also lacking, and we are therefore unable to reliably examine cetacean distribution and behaviour in the absence of windfarms and cables in situ. We are currently limited to measuring changes over time as more windfarms are developed, rather than measuring the effect of their presence.

Furthermore, due to the variability and uncertainty of EMF production from subsea cables; we are not able to reliably state the strengths of artificial EMFs present in our oceans. Legislation regarding the commissioning of windfarms could call for compulsory reports of annual EMF production and surveying in the long term. This could then be usefully complimented by cetacean sighting and behavioural data.

Cetacean species

In chapter two, differences in vibrissal number, follicle size and shape, and innervation distribution were observed in the three species which were examined. Systematically examining vibrissal shafts and follicles across more species of cetaceans would be beneficial, especially focusing on delphinids. Modern technology now allows detailed quantitative anatomical analysis to be conducted and it is even possible to measure the conductivity of the material that is found within the follicle, to judge electroreceptive capabilities. The amount of innervation which surround the follicle should also be

considered for investigations to aid in estimating vibrissal sensitivity. However, this can be time consuming, difficult to measure and requires good anatomical samples (Marshall et al., 2006). Unfortunately, many cetacean specimens often come from beach strandings or museum freezer specimens which often can degrade the tissue quality, as we have seen in the sample of minke whale. Therefore, to further review vibrissal function and sensitivity in cetaceans, we need additional behavioural studies in more species of cetaceans. The easiest way to conduct behavioural experimentations is to do so in captivity, but this faces both practical and ethical challenges, with a recent increase in opposition to cetaceans in captivity (Muka and Zarpentine, 2021). However, I do suggest that investigating the anatomy of follicles and behavioural responses of delphinids would be a good starting point to understand the associations between vibrissal form and function in cetaceans. Huttner et al., 2021, demonstrated methods in which cross sensory modality learning can be taught in bottlenose dolphins and thus may be a reference point for further studies.

3.3. Wider implications

Some subsea cables may release magnetic field greater than those of the Earth's geomagnetic field (see Dhanak et al., 2016). If migratory paths of cetaceans pass over these subsea cables this may distort their navigation and may lead to increased strandings (Zapetis and Szesciorka, 2018), however this has not yet been confirmed. Although, incidences of sperm whales becoming entangled in newly developed submarine tele communication cables were reported. This then rarely occurred once the cables were redesigned and as a result no longer emitted electric fields (Wood & Carter, 2008).

While electrosensing has been found in the Guiana dolphin (Czech-Damal et al., 2012), the threshold was around 460µV/m, which is higher than the reported values which are produced from subsea cables (Öhman et al., 2007; Taormina et al., 2018). This suggests that the levels of EMFs produced from subsea cables may not be high enough to trigger the detection in Guiana dolphins. However, as the detection thresholds may differ between the lab and field, and we do not have a good understanding of the EMFs stimuli around subsea cables *in situ*, artificial EMFs produced from subsea cables may yet be detectible by the Guiana dolphin. Electrosensory perception has now also been identified in the bottlenose dolphin (Huttner et al., 2021), although the detection threshold is still under investigation. As these are a species are prevalent in UK waters, they may be at risk of exposure to electric fields from subsea cables from the increased growth of offshore windfarms in UK waters. Exposure is likely to have behavioural and physiological effects, similar to those we have observed in other marine species. These can include impacted migration, foraging, reproduction and general health and welfare. It is crucial that we further explore this sensory modality in bottlenose dolphins to establish a threshold detection value to assess if artificial EMFs from subsea cables are a hazard to this species. If electrosensory perception is also present in other species of delphinids this may increase the number of species which will be vulnerable to artificial EMFs from subsea windfarm cables.

3.4. Conclusions

This thesis **evaluated the potential and impact of electrosensing in cetaceans.** This was achieved by addressing four objectives:

1. *Identifying possible electrosensing cetacean species from anatomical structures*

I suggest that innervation patterns around the base and sides of the vibrissal follicle, and a large follicle size, may be indicative of an electrosensory follicle. This appears to be the case in the Guiana dolphin, as well as in other members of the family Delphinidae, including the bottlenose dolphin and the Atlantic white-sided dolphin.

2. *Identifying candidate cetacean species for electrosensing capabilities from phylogenetic and ecological traits*

I suggest that delphinids are an interesting group to study, due to the innervation patterns and anatomical similarities of their vibrissal follicles. Moreover, species which forage benthically may benefit from another sensory modality which would aid in successful prey capture. Species which migrate, exhibit preference for coastal habitats and forage benthically may be more affected by artificial EMFs. In the UK, the minke whale, humpback whale, Atlantic white sided dolphin, white beaked dolphin and bottlenose dolphin are such species.

3. *Identifying the distribution of current wind farm, cable and cetacean data*

Current windfarm and cable data are freely available, however, the temporal and spatial resolution of the cetacean data is problematic. Sighting data are not available around wind farms and very limited behavioural recordings exist. Reliable baseline sighting or behaviour data are also not available.

4. *Making future recommendations for the study of electrosensing in cetaceans.*

I recommend that the specifically delphinids are a species to focus on in further studies, since they are prevalent in European waters. They are also available in captive collections for ex-situ research. For future work in situ, this could consist of improving sightings data collection, especially developing long-term consistent datasets around windfarms, including both sighting and behavioural data. Although no evidence exists to ascertain whether EMFs are directly affecting cetaceans, many of

their prey items, including fish and crustaceans can, which is likely to affect cetacean foraging and distribution. Therefore, I recommend that the effect of EMFs on cetaceans needs to be studied further as both a primary and secondary impact.

This thesis has highlighted the diversity in cetacean vibrissal anatomy and reviewed the literature on cetacean ecology that may result in the evolution of electromagnetic sensing in cetaceans. The fact two species of dolphin have displayed experimental evidence for electroreception also suggests that this sensory modality may be prevalent in more species. This is something which should be further investigated across the taxa. The links between the discovery of this sensory modality in cetaceans and their ecology is crucial in the conservation of cetaceans. This is especially apparent considering anthropogenic actions in response to climate change with offshore marine renewable energy.

4. References:

Agnarsson, I. and May-Collado, L.J. (2008). The phylogeny of Cetartiodactyla: the importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome b to provide reliable species-level phylogenies. *Molecular Phylogenetics and Evolution*, 48(3), pp.964-985.

Ahl, A. S. (1986). The role of vibrissae in behavior: A status review. *Veterinary Research Communications*, 10, pp.245–268.

Aldersey-Williams, J., Broadbent, I.D. and Strachan, P.A. (2020). Analysis of United Kingdom offshore wind farm performance using public data: Improving the evidence base for policymaking. *Utilities Policy*, *62*, pp.100985.

Allan, L. 2011. Marine mammal monitoring from coastal sites in Cardigan Bay, UK, 2004-2009. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/716) on 2022-01-11.

Ansmann, I.C., Goold, J.C., Evans, P.G. and Keith, S.G. (2007). Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles. *Marine Biological Association of the United Kingdom. Journal of the Marine Biological Association of the United Kingdom*, *87*(1), pp.19.

Ardelean, M., Minnebo, P. (2015) HVDC Submarine Power Cables in the World; EUR 27527 EN; doi: 10.2790/95735

Arnold, C., L. J. Matthews, and C. L. Nunn. (2010). The 10kTrees Website: A new online resource for primate phylogeny. *Evolutionary Anthropology* 19, pp.114-118

Arregui, M., Bernaldo de Quirós, Y., Saavedra, P., Sierra, E., Suárez-Santana, C.M., Arbelo, M., Díaz-Delgado, J., Puig-Lozano, R., Andrada, M. and Fernández, A. (2019). Fat embolism and sperm whale ship strikes. *Frontiers in Marine Science*, *6*, pp.379.

Au, W.W.L. (1980). Echolocation signals of the Atlantic bottlenose dolphin (*Tursiops truncatus*) in open waters. *Animal sonar systems*, 28, pp. 251-282. Boston, Springer.

Au W.W.L. (1993). Characteristics of Dolphin Sonar Signals. In *The Sonar of Dolphins.* New York, Springer

Bailey, H., Senior, B., Simmons, D., Rusin, J., Picken, G. and Thompson, P.M. (2010). Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals. *Marine Pollution Bulletin*, *60*(6), pp.888-897.

Ballance, L.T. (2018). Cetacean ecology. *In* Würsig,B., Thewissen J.G.M *Encyclopedia of marine mammals*. 3rd ed. Academic Press, pp. 172-180.

Bannister, J.L., (2018). Baleen whales (mysticeti). *In* Würsig,B., Thewissen J.G.M *Encyclopedia of marine mammals*. 3rd ed. Academic Press, pp. 62-69.

Barros, N.B. and Wells, R.S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy,* 79(3), pp.1045-1059.

Bauer, G.B., Fuller, M., Perry, A., Dunn, J.R. and Zoeger, J. (1985). Magnetoreception and biomineralization of magnetite in cetaceans. *In* Kirschvink, J., Jones, D., MacFadden, B., (eds): *Magnetite Biomineralization and Magnetoreception in Rrganisms* (pp. 489-507). Springer, Boston, MA.

Bauer, G.B., Reep, R.L. and Marshall, C.D. (2018). The tactile senses of marine mammals. *International Journal of Comparative Psychology*, *31*. Retrieved online from: https://escholarship.org/uc/item/1vk1c9z1

Baum, C., Stelzer, R., Meyer, W., Fleischer, L.G. and Siebers, D. (2000). A cryo-scanning electron microscopic study of the skin surface of the pilot whale Globicephala melas. *Aquatic Mammals 26 (1)*, pp.7-16.

Baum, J.K. and Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78(4), pp.699-714.

Beck, S., Foote, A.D., Koetter, S., Harries, O., Mandleberg, L., Stevick, P.T., Whooley, P. and Durban, J.W. (2014). Using opportunistic photo-identifications to detect a population decline of killer whales (*Orcinus orca*) in British and Irish waters. *Journal of the Marine Biological Association of the United Kingdom*, *94*(6), pp.1327.

Bedore, C. B., Harris, L. L., & Kajiura, S. M. (2014). Behavioural responses of batoid elasmobranchs to prey-simulating electric fields are correlated to peripheral sensory morphology and ecology. *Zoology*, 117, pp.95–103.

Begall S, Cerveny J, Neef J, Vojtech O and Burda H. (2008) Magnetic alignment in grazing and resting cattle and deer. *Proceedings of the National Acadamy of Science* 105, pp.13451–13455

Bejder, L., Videsen, S., Hermannsen, L., Simon, M., Hanf, D. and Madsen, P.T. (2019). Low energy expenditure and resting behaviour of humpback whale mother-calf pairs highlights conservation importance of sheltered breeding areas. *Scientific Reports*, *9*(1), pp.1-11.

Bender, C.E., Herzing, D.L. and Bjorklund, D.F. (2009). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition*, 12(1), pp.43-53.

Berman-Kowalewski, M., Gulland, F.M., Wilkin, S., Calambokidis, J., Mate, B., Cordaro, J., Rotstein, D., St Leger, J., Collins, P., Fahy, K. and Dover, S. (2010). Association between blue whale (*Balaenoptera musculus*) mortality and ship strikes along the California coast. *Aquatic Mammals*, 36(1), pp.59-66.

Berta, A., Ekdale, E. G., Zellmer, N. T., Deméré, T. A., Kienle, S. S., & Smallcomb, M. (2015). Eye, nose, hair, and throat: External anatomy of the head of a neonate gray whale (Cetacea, Mysticeti, Eschrichtiidae). *The Anatomical Record*, 298, pp.648–659

Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, C., Carlotti, F. and Christaki, U. (2007). Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. *Nature*, 446(7139), pp.1070-1074.

Bochert, R. and Zettler, M.L. (2006). Effect of electromagnetic fields on marine organisms. *In* Koller, j., Koppel, J., Peters, W., (eds): Offshore Wind Energy, pp. 223-234. Springer, Berlin, Heidelberg.

Bodznick, D. and Montgomery, J.C., 2005. The physiology of low-frequency electrosensory systems. In Bullock, T., Hopkins, C., Popper., A., Fay, R., (eds): *Electroreception* (pp. 132-153). Springer, New York, NY.

Boehlert, G.W. and Gill, A.B. (2010). Environmental and ecological effects of ocean renewable energy development: a current synthesis. *Oceanography*, *23*(2), pp.68-81.

Boisseau O, OBIS-SEAMAP, ACCOBAMS and WDCS (2021). Visual sightings from Song of the Whale 1993-2013. OBIS-SEAMAP. Occurrence dataset https://doi.org/10.15468/5c69jn accessed via GBIF.org on 2022-01-11.

Bowen W.D. (1997) Role of marine mammals in aquatic ecosystems. M*arine Ecology Progress Series,* 158, pp.267-274.

Boyd, I.L., Brownell, B., Cato, D.H., Clarke, C., Costa, D., Evans, P., Gedamke, J., Gentry, R. and Gisiner, B. (2008). The effects of anthropogenic sound on marine mammals: a draft research strategy. ESF Marine Board Position Paper 13. European Science Foundation, Marine Board. Oostende, Belgium.

Braulik, G. (2019). *Lagenorhynchus acutus*. The IUCN Red List of Threatened Species 2019: e.T11141A50361160. https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T11141A50361160.en. Downloaded on 24 September 2020.

Braulik, G., Jefferson, T.A. & Bearzi, G. (2021). *Delphinus delphis* (amended version of 2021 assessment). The IUCN Red List of Threatened Species 2021: e.T134817215A199893039. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T134817215A199893039.en. Downloaded on 24 September 2020

Braulik, G., Minton , G., Amano, M. & Bjørge, A. (2020). *Phocoena phocoena*. The IUCN Red List of Threatened Species 2020: e.T17027A50369903. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T17027A50369903.en. Downloaded on 24 September 2020.

Brown, V.C. and Simmonds, M.P. (2009). A further update on the distributions of marine renewable energy plants in Europe. Paper submitted to the Scientific Committee of the International Whaling Commission IWC. *IWC/SC/61 E*, *7*, pp.2009.

Buckstaff, K.C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, *20*(4), pp.709-725.

Buesseler, K.O. and Boyd, P.W. (2003). Will ocean fertilization work? *Science*, 300(5616), pp.67-68.

Burek, K.A., Gulland, F.M. and O'Hara, T.M. (2008). Effects of climate change on Arctic marine mammal health. *Ecological Applications*, *18*(sp2), pp.S126-S134.

Caballero, S., Jackson, J., Mignucci-Giannoni, A.A., Barrios-Garrido, H., Beltrán-Pedreros, S., Robertson, K.M. and Baker, C.S. (2008). Molecular systematics of South American dolphins Sotalia: Sister taxa determination and phylogenetic relationships, with insights into a multi-locus phylogeny of the Delphinidae. *Molecular Phylogenetics and Evolution*, 46(1), pp.252-268.

Camphuysen, C.J. and Leopold, M.F. (1993). The harbour porpoise (*Phocoena phocoena*) in the southern North Sea, particularly the Dutch sector. *Lutra*, 36, pp.1-24.

Camphuysen, K.J., Fox, A.D., Leopold, M.F. & Petersen, I.K. (2004). Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K.: a comparison of ship and aerial sampling methods for marine birds, and their applicability to offshore wind farm assessments (PDF, 2.7 mb), NIOZ report to COWRIE (BAM – 02-2002), Texel, 37pp. https://tethys.pnnl.gov/sites/default/files/publications/Camphuysen-et-al-2004-COWRIE.pdf

Carstensen, J., Henriksen, O.D. and Teilmann, J. (2006). Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series*, 321, pp.295-308.

Carter, C.J., Wilson, B. and Black, K. (2008). Marine Renewable Energy Devices: A Collision Risk for Marine Mammals? *In* ASCOBANS/ECS*. Proceedings of the 21st ASCOBANS/ECS workshop on offshore wind farms and marine mammals: Impacts and methodologies for assessing impacts.* The Aquarium, San Sebastian, Spain, 21st April 2007. Evans, P., (eds). Pp.60-62

CEFAS. (2019) *Cetacean bycatch workshop: Hauling up solutions.* [Online] Available at: https://www.cefas.co.uk/cetacean-bycatch-workshop/ [Accessed on 11th August 2020]

Clapham, P.J. (2018). Humpback whale: *Megaptera novaeangliae. In* Würsig,B., Thewissen J.G.M *Encyclopedia of Marine Mammals.* 3rd ed. pp. 489-492, Academic Press.

Clough, S.C., McGovern, S., Campbell, D. and Rehfisch, M.M. (2012). Aerial survey techniques for assessing offshore wind farms. *Unknown place of publication*:

International Council for the Exploration of the Sea. *[Online]* Date accessed: 2022-01-19 https://www.ices.dk/sites/pub/CM%20Doccuments/CM-2012/O/O1812.pdf

CMACS, A. (2003). Baseline Assessment of Electromagnetic Fields Generated by Offshore Windfarm Cables.

Constantine, R., Johnson, M., Riekkola, L., Jervis, S., Kozmian-Ledward, L., Dennis, T., Torres, L.G. and de Soto, N.A. (2015). Mitigation of vessel-strike mortality of endangered Bryde's whales in the Hauraki Gulf, New Zealand. *Biological Conservation*, *186*, pp.149-157.

Cooke, J.G. (2018a). *Balaenoptera acutorostrata*. The IUCN Red List of Threatened Species 2018: e.T2474A50348265. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2474A50348265.en. Downloaded on 24 September 2020

Cooke, J.G. (2018b). *Balaenoptera borealis*. The IUCN Red List of Threatened Species 2018: e.T2475A130482064. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2475A130482064.en. Downloaded on 24 September 2020.

Cooke, J.G. (2018c). *Balaenoptera musculus* (errata version published in 2019). The IUCN Red List of Threatened Species 2018: e.T2477A156923585. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2477A156923585.en. Downloaded on 24 September 2020

Cooke, J.G. (2018d). *Balaenoptera physalus*. The IUCN Red List of Threatened Species 2018: e.T2478A50349982. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2478A50349982.en. Downloaded on 24 September 2020.

Cooke, J.G. (2018e). *Megaptera novaeangliae*. The IUCN Red List of Threatened Species 2018: e.T13006A50362794. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T13006A50362794.en. Downloaded on 24 September 2020.

Coombs, E.J., Deaville, R., Sabin, R.C., Allan, L., O'Connell, M., Berrow, S., Smith, B., Brownlow, A., Doeschate, M.T., Penrose, R. and Williams, R. (2019). What can cetacean stranding records tell us? A study of UK and Irish cetacean diversity over the past 100 years. *Marine Mammal Science*, *35*(4), pp.1527-1555.

Copping, A., Hanna, L., Whiting, J., Geerlofs, S., Grear, M., Blake, K., Coffey, A., Massaua, M., Brown-Saracino, J. and Battey, H. (2013). Environmental effects of marine energy development around the world. Annex IV Final Report (No. PNNL-22176). IEA Ocean Energy Systems Initiative, Annex IV, Richland, WA (United States); Pacific Northwest National Laboratory, Richland, WA (United States).

Craddock, J.E., Polloni, P.T., Hayward, B. and Wenzel, F. (2009). Food habits of Atlantic white-sided dolphins (*Lagenorhynchus acutus*) off the coast of New England. *Fishery Bulletin*, *107*(3), pp.384-394.

Crampton, W.G. (2019). Electroreception, electrogenesis and electric signal evolution. *Journal of Fish Biology*, *95*(1), pp.92-134.

Cunningham, K.A. and Mountain, D.C. (2014). Simulated masking of right whale sounds by shipping noise: Incorporating a model of the auditory periphery. *The Journal of the Acoustical Society of America*, *135*(3), pp.1632-1640.

Czech-Damal, N.U., Liebschner, A., Miersch, L., Klauer, G., Hanke, F.D., Marshall, C., Dehnhardt, G. and Hanke, W. (2012). Electroreception in the Guiana dolphin (*Sotalia guianensis*). *Proceedings of the Royal Society B: Biological Sciences*, *279*(1729), pp.663-668.

Czech-Damal, N.U., Dehnhardt, G., Manger, P. and Hanke, W. (2013). Passive electroreception in aquatic mammals. Journal of Comparative Physiology A, 199(6), pp.555-563.

Dahiya, R.S., Metta, G., Valle, M. and Sandini, G. (2009). Tactile sensing—from humans to humanoids. *IEEE Transactions on Robotics*, *26*(1), pp.1-20.

Dauby, P., Nyssen, F. and De Broyer, C. (2003). Amphipods as food sources for higher trophic levels in the Southern Ocean: a synthesis. *Antarctic Biology in a Global Context*, pp.129-134.

Deaville, R. Jepson, P. Perkins, M. Brownlow, A. Davison, N. ten Doeschate, M. Smith, B. Allan, L. Clery, M. Swindells, K. Wilson, S. Sabin, R. Penrose, R. Barnett, J. Astley, K. Clear, N. Crosby, A. Williams, R. (2019). *UK Cetacean Strandings Investigation Programme final contract report to Defra.* London*, DEFRA (MB0111 2011-2017).*

Deecke, V.B. (2018). 7 Dolphins and Whales–Taking cognitive research out of the tanks and into the wild. *In* Bueno-Guerra, N., Amici, F., (eds) *Field and Laboratory Methods in Animal Cognition: A Comparative Guide*. Cambridge, Cambridge University Press. pp.146-174.

Del Mar Otero, M. and Conigliaro, M. (2012). Marine Mammals and Sea Turtles of the Mediterranean and Black Seas. *IUCN: Gland*, *32*.

Denman, K.L. (2008). Climate change, ocean processes and ocean iron fertilization. *Marine Ecology Progress Series*, *364*, pp.219-225.

de Vries H, Lemmens M (2021). Observation.org, Nature data from around the World. Observation.org. Occurrence dataset https://doi.org/10.15468/5nilie accessed via GBIF.org on 2022-01-11.

Dhanak, M., Spieler, R., Kilfoyle, K., Jermain, R.F., Frankenfield, J., Ravenna, S., Dibiasio, C., Coulson, R., Henderson, E. and Venezia, W. (2016). *Effects of EMF Emissions from Cables and Junction Boxes on Marine Species* (No. DOEFAU-0006386)., Boca Raton, FL (United States). Florida Atlantic University.

Díaz, H. and Soares, C.G. (2020). Review of the current status, technology and future trends of offshore wind farms. *Ocean Engineering, 209*.

Diederichs, A., Nehls, G., Dähne, M., Adler, S., Koschinski, S. and Verfuß, U. (2008). Methodologies for measuring and assessing potential changes in marine mammal behaviour, abundance or distribution arising from the construction, operation and decommissioning of offshore windfarms. Germany, *BioConsult SH.*

Dijkgraaf, S. and Kalmijn, A.J. (1962). Behavioral experiments of the function of the ampullae of Lorenzini. *Natural Sciences*, *49*(17), pp.400-400.

Dolman, S.J., Green, M. and Simmonds, M.P. (2007). Marine renewable energy and cetaceans. *Report for the Scientific Committee. Whale and Dolphin Conservation Society, Chippenham, United Kingdom, SN15 1LJ UK.*

Dolman, S. and Simmonds, M. (2010) Towards best environmental practice for cetacean conservation in developing Scotland's marine renewable energy. *Marine Policy*, *34*(5), pp.1021-1027

Dolman, S.J. and Brakes, P. (2018). Sustainable fisheries management and the welfare of bycaught and entangled cetaceans. *Frontiers in Veterinary Science*, *5*, pp.287.

Dougill, G., Starostin, E.L., Milne, A.O., van der Heijden, G.H., Goss, V.G. and Grant, R.A. (2020). Ecomorphology reveals Euler spiral of mammalian whiskers. *Journal of Morphology*, *281*(10), pp.1271-1279.

Drake, S.E., Crish, S.D., George, J.C., Stimmelmayr, R. and Thewissen, J.G.M., (2015). Sensory Hairs in the Bowhead Whale, *Balaena mysticetus* (Cetacea, Mammalia). *The Anatomical Record*, *298*(7), pp.1327-1335.

Dudzinski, K.M., Thomas, J.A. and Gregg, J.D. (2009). Communication in marine mammals. *In* Perrin, W., Wursig, B., Thewissen, J, G.M. (eds) *Encyclopedia of marine mammals,* 2nd edition, pp. 260-269. USA, Academic Press.

Emma, B. (2016). A Review of the evidence of electromagnetic field (EMF) effects on marine organisms. *Research and Reviews: Journal of Ecology and Environmental Science 4*(4).

Erbe C., Dunlop R., Dolman S. (2018) Effects of Noise on Marine Mammals. In: Slabbekoorn H., Dooling R., Popper A., Fay R. (eds) Effects of Anthropogenic Noise on Animals. Springer Handbook of Auditory Research, vol 66. Springer, New York, NY.

Erbe, C. (2002). Underwater noise of whale-watching boats and potential effects on killer whales (Orcinus orca), based on an acoustic impact model. *Marine mammal science*, 18(2), pp.394-418.

Erbe, C., Marley, S.A., Schoeman, R.P., Smith, J.N., Trigg, L.E. and Embling, C.B. (2019). The effects of ship noise on marine mammals—A review. *Frontiers in Marine Science*, *6*, pp.606.

Estes, J.A., Tinker, M.T., Williams, T.M. and Doak, D.F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, *282*(5388), pp.473-476.

European Council conclusions. EUCO 169/14 of 24th of October 2014 on the 2030 Climate and energy policy framework. 24/10/14, pp.5. [Online] Available at: https://www.consilium.europa.eu/media/24561/145397.pdf [Accessed 23rd October 2020]

Evans, P.G. and Hammond, P.S. (2004). Monitoring cetaceans in European waters. *Mammal Review*, 34(1-2), pp.131-156.

Evans, M.H., Loft, M.S., Campagner, D. and Petersen, R.S. (2019). Sensing the environment with whiskers. *Oxford Research Encyclopedia of Neuroscience*. [Online] 'Published online' 23rd May 2019 [Accessed 11th September 2021] DOI: 10.1093/acrefore/9780190264086.013.226

Fernández-Gavela, A., Herranz, S., Chocarro, B., Falke, F., Schreuder, E., Leeuwis, H., Heideman, R.G. and Lechuga, L.M. (2019). Full integration of photonic nanoimmunosensors in portable platforms for on-line monitoring of ocean pollutants. *Sensors and Actuators B: Chemical*, *297*, pp.126758.

Ferrari, T. (2017). Cetacean beachings correlate with geomagnetic disturbances in Earth's magnetosphere: An example of how astronomical changes impact the future of life. *International Journal of Astrobiology*, 16(2), pp.163-175

Fjällbrant, T.T., Manger, P.R. and Pettigrew, J.D. (1998). Some related aspects of platypus electroreception: temporal integration behaviour, electroreceptive thresholds and directionality of the bill acting as an antenna. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1372), pp.1211-1219.

Foote, A.D., Osborne, R.W. and Hoelzel, A.R. (2004). Whale-call response to masking boat noise. *Nature*, *428*(6986), pp.910-910.

Formicki, K. and Winnicki, A. (1998). Reactions of fish embryos and larvae to constant magnetic fields. *Italian Journal of Zoology*, *65*(S1), pp.479-482.

Fuxjager, M.J., Davidoff, K.R., Mangiamele, L.A. and Lohmann, K.J. (2014). The geomagnetic environment in which sea turtle eggs incubate affects subsequent magnetic navigation behaviour of hatchlings*. Proceedings of the Royal Society B: Biological Sciences*, 281(1791), 20141218.

Galloway, T.S., Cole, M. and Lewis, C. (2017). Interactions of microplastic debris throughout the marine ecosystem. *Nature Ecology and Evolution*, *1*(5), pp.1-8.

Gatesy, J., Geisler, J.H., Chang, J., Buell, C., Berta, A., Meredith, R.W., Springer, M.S. and McGowen, M.R. (2013). A phylogenetic blueprint for a modern whale. *Molecular Phylogenetics and Evolution*, *66*(2), pp.479-506

Geraci, J.R. and Lounsbury, V.J. (2005). *Marine Mammals Ashore: A Field Guide For Strandings*. National Aquarium in Baltimore.

Gerussi, T., Graïc, J. M., de Vreese, S., Grandis, A., Tagliavia, C., De Silva, M., … Cozzi, B. (2020). The follicle-sinus complex of the bottlenose dolphin (*Tursiops truncatus*). Functional anatomy and possible evolutional significance of its somato-sensory innervation. *Journal of Anatomy*, 238, pp.942–955

Gill, A.B. (2005). Offshore renewable energy: ecological implications of generating electricity in the coastal zone. *Journal of Applied Ecology*, 42, pp.605–615.

Gill, A.B. & Kimber, J. (2005). The potential for cooperative management of elasmobranchs and offshore renewable energy developments in UK waters. *Journal of the Marine Biological Association of the United Kingdom*, 85, pp.1075–1081.

Gill, A.B. and Desender, M., (2020). *2020 State of the Science Report-Chapter 5: Risk to Animals from Electromagnetic Fields Emitted by Electric Cables and Marine Renewable Energy Devices* (No. PNNL-29976CHPT5). Pacific Northwest National Lab.(PNNL), Richland, WA (United States).

Gill, A.B. and Taylor, H. (2001). *The potential effects of electromagnetic fields generated by cabling between offshore wind turbines upon elasmobranch fishes*. Liverpool, The University of Liverpool.

Gill, A.B., Gloyne-Phillips, I., Neal, K.J. & Kimber, J.A. (2005*). The Potential Effects of Electromagnetic Fields Generated by Sub-Sea Power Cables Associated with Offshore Wind Farm Developments on Electrically and Magnetically Sensitive Marine Organisms – A Review*. Cranfield, COWRIE

Gill, A.B., Huang, Y., Gloyne-Philips, I., Metcalfe, J., Quayle, V., Spencer, J. & Wearmouth, V. (2009). COWRIE 2.0 Electromagnetic Fields (EMF) Phase 2: EMF-sensitive fish response to EM emissions from sub-sea electricity cables of the type used by the offshore renewable energy industry. Cranfield, COWRIE.

Gill, A.B., Huang, Y., Spencer, J. and Gloyne-Philips, I. (2012a). *Electromagnetic fields emitted by high voltage alternating current offshore wind power cables and interactions with marine organisms*. COWRIE. *Electromagnetics in Current and Emerging Energy and power systems seminar*. Institution of Engineering and Technology, London, 23rd June 2012. TETHYS, pp.1-5

Gill, A.B., Bartlett, M. and Thomsen, F. (2012b). Potential interactions between diadromous fishes of UK conservation importance and the electromagnetic fields and subsea noise from marine renewable energy developments. *Journal of Fish Biology, 81*(2), pp.664-695.

Gill A., Gloyne-Philips I., Kimber J., Sigray P. (2014) Marine Renewable Energy, Electromagnetic (EM) Fields and EM-Sensitive Animals. *In*: Shields M., Payne A. (eds) Marine Renewable Energy Technology and Environmental Interactions. Humanity and the Sea. Springer, Dordrecht

Gilles, A., Scheidat, M. and Siebert, U. (2009). Seasonal distribution of harbour porpoises and possible interference of offshore wind farms in the German North Sea. *Marine Ecology Progress Series*, *383*, pp.295-307.

Gillis, J.A., Modrell, M.S., Northcutt, R.G., Catania, K.C., Luer, C.A. and Baker, C.V. (2012). Electrosensory ampullary organs are derived from lateral line placodes in cartilaginous fishes. *Development*, *139*(17), pp.3142-3146.

Gould, J.L. (2008). Animal navigation: the evolution of magnetic orientation. *Current Biology*, *18*(11), pp.482-484.

Gov.uk. (2020). *New plans to make UK world leader in green energy.* 6th October. [Online] Available at: https://www.gov.uk/government/news/new-plans-to-make-uk-world-leader-in-green-energy [Accessed 14th December 2020]

Grant, R.A. and Goss, V.G. (2022). What can whiskers tell us about mammalian evolution, behaviour, and ecology? *Mammal Review*, 52(1), pp.148-163.

Grant, R.A., Haidarliu, S., Kennerley, N.J. and Prescott, T.J. (2013). The evolution of active vibrissal sensing in mammals: evidence from vibrissal musculature and function in the marsupial opossum *Monodelphis domestica*. *Journal of Experimental Biology*, *216*(18), pp.3483-3494.

Guimarães Jr, P.R., de Menezes, M.A., Baird, R.W., Lusseau, D., Guimaraes, P. and Dos Reis, S.F., (2007). Vulnerability of a killer whale social network to disease outbreaks. *Physical Review E*, 76(4), p.042901.

Gutow, L., Eckerlebe, A., Giménez, L. and Saborowski, R. (2016). Experimental evaluation of seaweeds as a vector for microplastics into marine food webs. *Environmental Science & Technology*, *50*(2), pp.915-923.

Häder, D.P., Banaszak, A.T., Villafañe, V.E., Narvarte, M.A., González, R.A. and Helbling, E.W. (2020). Anthropogenic pollution of aquatic ecosystems: Emerging problems with global implications. *Science of the Total Environment*, *713*, pp.136586.

Haelters J, Vandenberghe T (2019). Belgian Marine Mammals database. Royal Belgian Institute of Natural Sciences. Occurrence dataset https://doi.org/10.15468/m9j4d4 accessed via GBIF.org on 2022-01-11.

Hain, J.H.W., Ellis, S.L., Kenney, R.D., Clapham, P.J., Gray, B.K., Weinrich, M.T. and Babb, I.G. (1995), Apparent bottom feeding by humpback whales on stellwagen bank. *Marine Mammal Science*, 11, pp.464-479

Haine, O. S., Ridd, P. V., & Rowe, R. J. (2001). Range of electrosensory detection of prey by *Carcharhinus melanopterus* and *Himantura granulata*. *Marine and Freshwater Research*, 51, pp.291–296

Halvorsen-Weare, E.E., Gundegjerde, C., Halvorsen, I.B., Hvattum, L.M. and Nonås, L.M. (2013). Vessel fleet analysis for maintenance operations at offshore wind farms. *Energy Procedia*, *35*, pp.167-176.

Hamilton, P. K., Knowlton, A. R., & Marx, M. K. (2007). Right whales tell their own stories: The photo-identification catalog. In S. D. Kraus & R. M. Rolland (Eds.), *The Urban Whale: North Atlantic Right Whales at the Crossroads*. pp. 75–104. Harvard University Press.

Hammond, P.S., Benke, H., Breggren, P., Collet, A., Heide-Jørgensen, M.P., Heimlich-Boran, S., Leopold, M. and Øien, N. (1995). The distribution and abundance of harbour porpoises and other small cetaceans in the North Sea and adjacent waters. Cambridge, ICES.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K., Karczmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y., Wells, R.S. & Wilson, B. (2008). *Delphinus delphis*. The IUCN Red List of Threatened Species 2008: e.T6336A12649851. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T6336A12649851.en. Downloaded on 24 September 2020.

Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, L., Cañadas, A., Desportes, G., Donovan, G.P., Gilles, A., Gillespie, D. and Gordon, J. (2013). Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation*, *164*, pp.107-122.

Hanke, W. and Dehnhardt, G. (2016). Vibrissal touch in pinnipeds. In *Scholarpedia of Touch*, pp. 125-139. Paris, Atlantis Press.

Hansson, B.O.N., (1954). Submarine cable for 100-kv DC power transmission. *Electrical Engineering*, 73(7), pp.602-602.

Harada, Y., Taniguchi, M., Namatame, H., and Iida, A. (2001). Magnetic materials in otohths of bird and fish lagena and their function. *Acto Oto-Laryngologica* (121), pp.590-595

Harder, J.H., Hill, H.M., Dudzinski, K.M., Sanabria, K.T., Guarino, S., Kuczaj, I.I. and Stan, A. (2016). The development of echolocation in bottlenose dolphins. *International Journal of Comparative Psychology*, *29*(1).

Harris, L. L., Bedore, C. B., & Kajiura, S. M. (2015). Electroreception in the obligate freshwater stingray, *Potamotrygon motoro. Marine and Freshwater Research*, 66, pp.1027–1036

Hartvedt, S. 2020. Incidental sightings of marine mammals. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/103152572) on 2022-01-11 and originated from OBIS (https://obis.org/dataset/dd335e79-f580-44a1-bedc-1476437eb73e)

Hassel, M., Utne, I.B. and Vinnem, J.E. (2017). Allision risk analysis of offshore petroleum installations on the Norwegian Continental Shelf—an empirical study of vessel traffic patterns. *WMU Journal of Maritime Affairs*, 16(2), pp.175-195.

Hatler, D. F., and J. D. Darling. (1974). Recent observations of the gray whale in British Columbia. Canadian Field-Naturalist, 88, pp.449-459.

Herbert, G.J., Iniyan, S., Sreevalsan, E. and Rajapandian, S. (2007). A review of wind energy technologies. *Renewable and Sustainable Energy Reviews*, *11*(6), pp.1117-1145.

Horton, T. W., Zerbini, A. N., Andriolo, A., Danilewicz, D., & Sucunza, F. (2020). Multi-decadal humpback whale migratory route fidelity despite oceanographic and geomagnetic change. *Frontiers in Marine Science*, *7*, 414.

Hoyt, E. (2001). *Whale watching 2001: Worldwide tourism numbers, expenditures, and expanding socioeconomic benefits*. Yarmouth, Massachusetts, International Fund for Animal Welfare.

Hutchison, Z., Sigray, P., He, H., Gill, A.B., King, J. and Gibson, C. (2018). *Electromagnetic Field (EMF) impacts on elasmobranch (shark, rays, and skates) and American lobster movement and migration from direct current cables*. Sterling Virginia, US Department of the Interior, Bureau of Ocean Energy Management.

Hutchison, Z.L., Gill, A.B., Sigray, P., He, H. and King, J.W. (2020). Anthropogenic electromagnetic fields (EMF) influence the behaviour of bottom-dwelling marine species. *Scientific Reports*, *10*(1), pp.1-15.

Hüttner, T., von Fersen, L., Miersch, L., Czech, N.U. and Dehnhardt, G. (2021). Behavioral and anatomical evidence for electroreception in the bottlenose dolphin (*Tursiops truncatus*). *The Anatomical Record*. 305(3), pp.592-608

Hyvärinen, H., Palviainen, A., Strandberg, U. and Holopainen, I.J. (2009). Aquatic environment and differentiation of vibrissae: comparison of sinus hair systems of ringed seal, otter and pole cat. *Brain, Behavior and Evolution*, *74*(4), pp.268-279.

iNaturalist contributors, iNaturalist (2022). iNaturalist Research-grade Observations. iNaturalist.org. Occurrence dataset https://doi.org/10.15468/ab3s5x accessed via GBIF.org on 2022-01-11.

Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., James Grecian, W., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J. and Godley, B.J. (2009). Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*, *46*(6), pp.1145-1153.

Inventaire National du Patrimoine Naturel N (2022). Données du Réseau d'observateurs des mammifères marins en mer de la Manche. Version 1.1. UMS PatriNat (OFB-CNRS-MNHN), Paris. Occurrence dataset https://doi.org/10.15468/66t8r0 accessed via GBIF.org on 2022-01-11

Inventaire National du Patrimoine Naturel N (2022). Données du Réseau d'observateurs des mammifères marins en mer de la Manche - Observations du Grand dauphin du Golfe normand-breton. Version 1.1. UMS PatriNat (OFB-CNRS-MNHN), Paris. Occurrence dataset https://doi.org/10.15468/lvuc98 accessed via GBIF.org on 2022-01-11.

Inventaire National du Patrimoine Naturel N (2022). Inventaire des Mammifères de France - Inventaire des Mammifères marins de France (métropole et outre-mer). Version 1.1. UMS PatriNat (OFB-CNRS-MNHN), Paris. Occurrence dataset https://doi.org/10.15468/qsofh6 accessed via GBIF.org on 2022-01-11.

Islam, M.S. and Tanaka, M. (2004). Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. *Marine Pollution Bulletin*, *48*(7-8), pp.624-649.

Jaramillo-Legorreta, A.M., Cardenas-Hinojosa, G., Nieto-Garcia, E., Rojas-Bracho, L., Thomas, L., Ver Hoef, J.M., Moore, J., Taylor, B., Barlow, J. and Tregenza, N., (2019). Decline towards extinction of Mexico's vaquita porpoise (Phocoena sinus). Royal Society open science, 6(7), p.190598.

Jepson, P.D., Arbelo, M., Deaville, R., Patterson, I.A.P., Castro, P., Baker, J.R., Degollada, E., Ross, H.M., Herráez, P., Pocknell, A.M. and Rodriguez, F. (2003). Gas-bubble lesions in stranded cetaceans. *Nature*, *425*(6958), pp.575-576.

Jepson, P.D., Deaville, R., Barber, J.L., Aguilar, À., Borrell, A., Murphy, S., Barry, J., Brownlow, A., Barnett, J., Berrow, S. and Cunningham, A.A. (2016). PCB pollution continues to impact populations of orcas and other dolphins in European waters. *Scientific Reports*, *6*, p.18573.

Johnson, C.K., Tinker, M.T., Estes, J.A., Conrad, P.A., Staedler, M., Miller, M.A., Jessup, D.A. and Mazet, J.A. (2009). Prey choice and habitat use drive sea otter pathogen exposure in a resource-limited coastal system. *Proceedings of the National Academy of Sciences*, *106*(7), pp.2242-2247.

Josberger, E.E., Hassanzadeh, P., Deng, Y., Sohn, J., Rego, M.J., Amemiya, C.T. and Rolandi, M. (2016). Proton conductivity in ampullae of Lorenzini jelly. *Science Advances*, *2*(5). p.e1600112

Kaiser, M.J., Galanidi, M., Showler, D.A., Elliott, A.J., Caldow, R.W., Rees, E.I.S., Stillman, R.A. and Sutherland, W.J. (2006). Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. *Ibis*, *148*, pp.110-128.

Kajiura, S. M., & Holland, K. N. (2002). Electroreception in juvenile scalloped hammerhead and sandbar sharks. *Journal of Experimental Biology*, 205, pp.3609–3621

Kajiura, S. M. (2003). Electroreception in neonatal bonnethead sharks, *Sphyrna tiburo*. *Marine Biology*, 143, pp.603–611

Kajiura, S. M., & Fitzgerald, T. P. (2009). Response of juvenile hammerhead sharks to electric stimuli. *Zoology*, 112, pp.241–250.

Kalmijn, A.J., 1982. Electric and magnetic field detection in elasmobranch fishes. *Science*, *218*(4575), pp.916-918.

Katona, S. and Whitehead, H. (1988). Are cetacea ecologically important. Oceanography and Marine Biology Annual Review, 26, pp.553-568

Keijl G, Creuwels J (2022). walvisstrandingen_nl. Version 1.9. Naturalis Biodiversity Center. Occurrence dataset https://doi.org/10.15468/6363ua accessed via GBIF.org on 2022-01-11.

Kelkar, N., Dey, S., Deshpande, K., Choudhary, S.K., Dey, S. and Morisaka, T. (2018). Foraging and feeding ecology of *Platanista*: An integrative review. *Mammal Review*, *48*(3), pp.194-208.

Kempster, R. M., Egeberg, C. A., Hart, N. S., & Collin, S. P. (2016). Electrosensory-driven feeding behaviours of the port Jackson shark (*Heterodontus portusjacksoni*) and western shovelnose ray (*Aptychotrema vincentiana*). Mar*ine and Freshwater Research*, 67, pp.187–194

Kershaw, J.L. and Hall, A.J. (2019). Mercury in cetaceans: exposure, bioaccumulation and toxicity. *Science of The Total Environment*, *694*, p.133683.

King, D.A. (2004). Climate change science: adapt, mitigate, or ignore? *Science, 303(5655),* pp.176-177

Kirschvink, J.L. (1990). Geomagnetic sensitivity in cetaceans: an update with live strandings records in the United States*. In* Thomas, J., Kastelein, R. (eds). Sensory Abilities of Cetaceans, pp. 639–649. New York, NY, Plenum Press,

Kirschvink, J.L. (1997). Homing in on vertebrates. *Nature*, 390(6658), pp.339-340.

Kiszka, J. & Braulik, G. (2018). *Grampus griseus*. The IUCN Red List of Threatened Species 2018: e.T9461A50356660. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T9461A50356660.en. Downloaded on 24 September 2020.

Kiszka, J. & Braulik, G. (2018). *Lagenorhynchus albirostris*. The IUCN Red List of Threatened Species 2018: e.T11142A50361346. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T11142A50361346.en. Downloaded on 24 September 2020.

Klinowska, M., (1985). Cetacean live stranding sites relate to geomagnetic topography. Aquatic Mammals, 1(1), pp.27-32.

Kock, K. and Benke, H. (1995). On the by-catch of harbour porpoise (*Phocoena phocoena*) in German fisheries in the Baltic and the North Sea. *Archive of Fishery and Marine Research*, 44, pp.114.

Koelmans, A.A., Bakir, A., Burton, G.A. and Janssen, C.R. (2016). Microplastic as a vector for chemicals in the aquatic environment: Critical review and model-supported reinterpretation of empirical studies. *Environmental Science and Technology*, *50*(7), pp.3315-3326.

Kooyman, G.L., Castellini, M.A. and Davis, R.W. (1981). Physiology of diving in marine mammals. *Annual Review of Physiology*, 43(1), pp.343-356.

Kremers, D., Célérier, A., Schaal, B., Campagna, S., Trabalon, M., Böye, M., Hausberger, M. and Lemasson, A. (2016). Sensory perception in cetaceans: Part I— Current knowledge about dolphin senses as a representative species. *Frontiers in Ecology and Evolution*, *4*, pp.49.

Krylov, V.V., Izyumov, Y.G., Izvekov, E.I. and Nepomnyashchikh, V.A. (2014). Magnetic fields and fish behavior. *Biology Bulletin Reviews*, *4*(3), pp.222-231.

Krzemieniewski, M., Teodorowicz, M., Debowski, M. and Pesta, J. (2004). Effect of a constant magnetic field on water quality and rearing of European sheatfish *Silurus glanis* L. larvae. *Aquaculture Research*, *35*(6), pp.568-573.

Lacey, C. (2014). SCANS II cetacean sightings from aerial surveys 2005. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1153) on 2022-01-11.

Lacey, C. (2014). SCANS II cetacean sightings on primary platform of vessel surveys 2005. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1150) on 2022-01-11.

Lacey, C. (2014). SCANS II cetacean sightings on tracker platform of vessel surveys 2005. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1152) on 2022-01-11.

Lacey, C. (2015). SCANS I cetacean sightings 1994. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1183) on 2022-01-11. https://doi.org/10.15468/wr2p82 accessed via GBIF.org on 2022-01-11

Langhamer, O., (2012). Artificial reef effect in relation to offshore renewable energy conversion: state of the art. *The Scientific World Journal*, *2012*.

Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J.G. and Smetacek, V. (2010). Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proceedings of the Royal Society B: Biological Sciences*, 277(1699), pp.3527-3531.

LeDuc, R.G., Perrin, W.F. and Dizon, A.E. (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Marine Mammal Science*, 15(3), pp.619-648.

Lewis, J.S. and Schroeder, W.W., (2003). Mud plume feeding, a unique foraging behavior of the bottlenose dolphin in the Florida Keys. *Gulf of Mexico Science, 21*(1), pp.9.

Ling, J. K. (1977). Vibrissae of marine mammals. In R. J. Harrison (Ed.), Functional anatomy of marine mammals (pp. 387– 415). Cambridge, MA: Academic Press

Lohmann, K., Pentcheff, N., Nevitt, G., Stetten, G., Zimmer-Faust, R., Jarrard, H. and Boles, L.C., (1995). Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *Journal of Experimental Biology, 198*(10), pp.2041-2048.

Lohmann, K.J. and Johnsen, S. (2000). The neurobiology of magnetoreception in vertebrate animals. *Trends in Neurosciences, 23*(4), pp.153-159

Lohmann, K.J., Putman, N.F. and Lohmann, C.M. (2008). Geomagnetic imprinting: A unifying hypothesis of long-distance natal homing in salmon and sea turtles. *Proceedings of the National Academy of Sciences*, 105(49), pp.19096-19101.

Lohmann, K.J. and Ernst, D.A. (2014). The geomagnetic sense of crustaceans and its use in orientation and navigation. *In* Derby, C.D., Thiel, M., (eds). *Nervous Systems and Control of Behavior*, Oxford, Oxford University Press, pp.321-336.

Love, M.S., Nishimoto, M.M., Clark, S. and Bull, A.S. (2015). Identical response of caged rock crabs (Genera *Metacarcinus* and *Cancer*) to energized and unenergized undersea power cables in Southern California, USA. *Bulletin, Southern California Academy of Sciences, 114*(1), pp.33-41.

Love, M.S., Nishimoto, M.M., Clark, S., McCrea, M. and Bull, A.S. (2017). Assessing potential impacts of energized submarine power cables on crab harvests. *Continental Shelf Research, 151*, pp.23-29

Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J. and Benvenuti, S. (2007). Marine turtles use geomagnetic cues during open-sea homing. *Current Biology*, 17(2), pp.126-133.

MacLeod, C.D., Santos, M.B. and Pierce, G.J. (2003). Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association of the United Kingdom*, 83(3), pp.651-665.

Madsen, P.T., Wahlberg, M., Tougaard, J., Lucke, K. and Tyack, A.P. (2006). Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Marine Ecology Progress Series, 309*, pp.279-295.

Manger, P.R., Keast, J.R., Pettigrew, J.D. and Troutt, L. (1998). Distribution and putative function of autonomic nerve fibres in the bill skin of the platypus (Ornithorhynchus anatinus). *Philosophical Transactions of the Royal Society B: Biological Sciences, 353*(1372), pp.1159-1170.

Manger, P.R. and Pettigrew, J.D., (1996). Ultrastructure, number, distribution and innervation of electroreceptors and mechanoreceptors in the bill skin of the platypus, Ornithorhynchus anatinus (part 1 of 2). *Brain, Behavior and Evolution*, *48*(1), pp.27-40.

Marçalo, A., Nicolau, L., Giménez, J., Ferreira, M., Santos, J., Araújo, H., Silva, A., Vingada, J. and Pierce, G.J. (2018). Feeding ecology of the common dolphin (*Delphinus delphis*) in Western Iberian waters: has the decline in sardine (*Sardina pilchardus*) affected dolphin diet?. *Marine Biology*, 165(3), pp.1-16.

Marcotte, M.M. and Lowe, C.G. (2008). Behavioral responses of two species of sharks to pulsed, direct current electrical fields: testing a potential shark deterrent. *Marine Technology Society Journal*, *42*(2), pp.53-61

Massos, A. and Turner, A. (2017). Cadmium, lead and bromine in beached microplastics. *Environmental Pollution*, *227*, pp.139-145

Mato, Y., Isobe, T., Takada, H., Kanehiro, H., Ohtake, C. and Kaminuma, T., (2001). Plastic resin pellets as a transport medium for toxic chemicals in the marine environment. *Environmental Science & Technology*, *35*(2), pp.318-324.

Mattson, E.E. and Marshall, C.D. (2016). Follicle microstructure and innervation vary between pinniped micro-and macrovibrissae. *Brain, Behavior and Evolution*, *88*(1), pp.43-58.

Mauck, B., Eysel, U. and Dehnhardt, G. (2000). Selective heating of vibrissal follicles in seals (*Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). *Journal of Experimental Biology*, *203*(14), pp.2125-2131.

May-Collado, L. and Agnarsson, I. (2006). Cytochrome b and Bayesian inference of whale phylogeny. *Molecular Phylogenetics and Evolution*, 38(2), pp.344-354.

Mazzoldi, C., Bearzi, G., Brito, C., Carvalho, I., Desiderà, E., Endrizzi, L., Freitas, L., Giacomello, E., Giovos, I., Guidetti, P. and Ressurreição, A. (2019). From sea monsters to charismatic megafauna: Changes in perception and use of large marine animals. *PLoS One*, *14*(12)

McGowan, D. W., & Kajiura, S. M. (2009). Electroreception in the euryhaline stingray, *Dasyatis sabina*. *Journal of Experimental Biology*, 212, pp.1544–1552

McGowen, M.R., Spaulding, M. and Gatesy, J. (2009). Divergence date estimation and a comprehensive molecular tree of extant cetaceans. *Molecular Phylogenetics and Evolution*, *53*(3), pp.891-906.

Mercado, E. (2014). Tubercles: What sense is there? *Aquatic Mammals*, 40, pp.95–103.

Michel, J., Dunagan, H., Boring, C., Healy, E., Evans, W., Dean, J.M., McGillis, A. & Hain, J. (2007) Worldwide Synthesis and Analysis of Existing Information Regarding Environmental Effects of Alternative Energy Uses on the Outer Continental Shelf. pp.

254. U.S. Department of the Interior, Minerals Management Service, Herndon, VA, MMS OCS Report 2007-038

Minton, G., Reeves, R. & Braulik, G. (2018). *Globicephala melas*. The IUCN Red List of Threatened Species 2018: e.T9250A50356171. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T9250A50356171.en. Downloaded on 24 September 2020.

Mitigation, C.C. (2011). IPCC special report on renewable energy sources and climate change mitigation. [Online] Available at: https://www.uncclearn.org/sites/default/files/inventory/ipcc15.pdf] [Accessed 20th April 2020)

Maughan, B. and K. Arnold. 2010. UK Royal Navy Marine Mammal Observations. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/64) on 2022-01-11. https://doi.org/10.15468/6zsrhp accessed via GBIF.org on 2022-01-11.

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature*, *558*(7708), pp.50-59

Muchlinski, M.N., Durham, E.L., Smith, T.D. and Burrows, A.M. (2013). Comparative histomorphology of intrinsic vibrissa musculature among primates: implications for the evolution of sensory ecology and "face touch". *American Journal of Physical Anthropology*, *150*(2), pp.301-312.

Muchlinski, M.N., Wible, J.R., Corfe, I., Sullivan, M. and Grant, R.A. (2020). Good vibrations: the evolution of whisking in small mammals. *The Anatomical Record*, *303*(1), pp.89-99.

Murray, R.W., (1960). Electrical sensitivity of the ampullae of Lorenzini. *Nature*, *187*(4741), pp.957-957.

Murray, R.W., 1962. The response of the ampullae of Lorenzini of elasmobranchs to electrical stimulation. *Journal of Experimental Biology*, *39*(1), pp.119-128.

Nakai, J., and Shida, T. (1948). Sinus-hairs of the sei-whale (*Balaenoptera borealis*). *The Scientific Reports of the Whales Research Institute*, Tokyo, 1, pp.41–47.

Nerini, M. (1984). A review of gray whale feeding ecology. *In* Jones, M.L., Swartz, S.L., Leatherwood, S., (eds). *The Gray Whale, Eschrichtius robustus*, Cambridge, MA, Academic Press. pp.423-450.

Newton, K.C., Gill, A.B. and Kajiura, S.M. (2019). Electroreception in marine fishes: chondrichthyans. *Journal of Fish Biology*, *95*(1), pp.135-154.

Nicol, C., Bejder, L., Green, L., Johnson, C., Keeling, L., Noren, D., Van der Hoop, J. and Simmonds, M. (2020). Anthropogenic threats to wild cetacean welfare and a tool to inform policy in this area. *Frontiers in Veterinary Science*, 7, pp.57.

Nishi, T., Kawamura, G. and Matsumoto, K., (2004). Magnetic sense in the Japanese eel, *Anguilla japonica*, as determined by conditioning and electrocardiography. *Journal of Experimental Biology*, *207*(17), pp.2965-2970.

NOAA Fisheries, n.d. *Sowerby's beaked whale*. Species directory. [Online] Available at: https://www.fisheries.noaa.gov/species/sowerbys-beaked-whale#overview [Accessed 21st December 2020]

Norfolk Biodiversity Information Service (2017). NBIS Records to December 2016. Occurrence dataset https://doi.org/10.15468/jca5lo accessed via GBIF.org on 2022-01-11.

North East Scotland Biological Records Centre (2017). NE Scotland marine mammal records 1800-2010. Occurrence dataset https://doi.org/10.15468/suphju accessed via GBIF.org on 2022-01-11.

Northridge, SP, Kingston, AR & Thomas, LJ., (2017), Annual report on the implementation of Council Regulation (EC) No 812/2004 during 2016. DEFRA, online. [Online] Available at: http://randd.defra.gov.uk/Document.aspx?Document=14086_UK812Reportfor2016.pdf [Accessed 17th November 2020]

Nowacek, D.P., Johnson, M.P. and Tyack, P.L. (2004). North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1536), pp.227-231.

NPower Renewables. (2005) North Hoyle Offshore Wind Farm. [Online] [Accessed 15th September] Available at: https://www.innogy.com/web/cms/mediablob/en/3170666/data/3170712/1/rwe-innogy/rwe-innogy-uk/sites/wind-offshore/in-operation/north-hoyle/environment/1.-Executive-summary-and-contents-.pdf

Nyqvist, D., Durif, C., Johnsen, M.G., De Jong, K., Forland, T.N. and Sivle, L.D. (2020). Electric and magnetic senses in marine animals, and potential behavioral effects of electromagnetic surveys. *Marine Environmental Research*, *155*, pp.104888.

O'Connor, S., Campbell, R., Cortez, H. and Knowles, T. (2009). Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare. Yarmouth MA, USA, prepared by Economists at Large, 228.

Officer, S. (2011). United Kingdom National Whale Stranding Database 1913-2008. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/731) on 2022-01-11.

Ogawa, T., & Shida, T. (1950). On the sensory tubercles of lips and of oral cavity in the sei and the fin whale. *The Scientific Reports of the Whales Research Institute*, 3, pp.1–16

Öhman, M.C., Sigray, P. and Westerberg, H. (2007). Offshore windmills and the effects of electromagnetic fields on fish. *Ambio*, 36(8), pp.630-633.

Orca. (2019) *The state of European cetaceans 2019*, University of Plymouth: Orca. [Online] Available at: https://www.orcaweb.org.uk/images/content/SOEC/ORCA_The_State_of_European_Cetaceans2019_Online.pdf [Accessed on 11th August 2020]

Ortega, J.C., Figueiredo, B.R., da Graça, W.J., Agostinho, A.A. and Bini, L.M. (2020). Negative effect of turbidity on prey capture for both visual and non-visual aquatic predators. *Journal of Animal Ecology*, *89*(11), pp.2427-2439.

Overholtz, W.J. and Link, J.S. (2007). Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977–2002. *ICES Journal of Marine Science*, 64(1), pp.83-96.

Overholtz, W.J. and Waring, G.T. (1991). Diet composition of pilot whales *Globicephala sp.* and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. *Fishery Bulletin*, 89(4), pp.723-728.

Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, 14(12), pp.483-488.

Pace, D.S., Tizzi, R. and Mussi, B. (2015). Cetaceans value and conservation in the Mediterranean Sea. *Journal of Biodiversity & Endangered Species*, 1(4).

Palmer, E., & Weddell, G. (1964). The relationship between structure, innervation and function of the skin of the bottle nose dolphin (*Tursiops truncatus*). *Mammal Research Institute Polish Academy of Sciences*. 143 (4), pp.553-568

Parsons, E.C.M., Warburton, C.A., Woods-Ballard, A., Hughes, A. and Johnston, P. (2003). The value of conserving whales: the impacts of cetacean-related tourism on the economy of rural West Scotland. *Aquatic Conservation.* 13(5), pp.397-415.

Parsons, E.C.M. (2012). The negative impacts of whale-watching. *Journal of Marine Biology*, 2012, pp.1-9

Parsons, E.C.M., Baulch, S., Bechshoft, T., Bellazzi, G., Bouchet, P., Cosentino, A.M., Godard-Codding, C.A.J., Gulland, F., Hoffmann-Kuhnt, M., Hoyt, E. and Livermore, S. (2015). Key research questions of global importance for cetacean conservation. *Endangered Species Research*, *27*(2), pp.113-118.

Peel, D., Smith, J.N. and Childerhouse, S. (2018). Vessel strike of whales in Australia: The challenges of analysis of historical incident data. *Frontiers in Marine Science*, *5*, pp.69.

Perrin, W.F., Mallette, S.D. and Brownell Jr, R.L., 2018. Minke whales: *Balaenoptera acutorostrata* and *B. bonaerensis*. In Würsig,B., Thewissen J.G.M *Encyclopedia of marine mammals*. 3rd ed., pp.608-613. Cambridge, MA. Academic Press.

Perrow, M.R., Gilroy, J.J., Skeate, E.R. and Tomlinson, M.L. (2011). Effects of the construction of Scroby Sands offshore wind farm on the prey base of Little tern *Sternula albifrons* at its most important UK colony. *Marine Pollution Bulletin, 62*(8), pp.1661-1670.

Perrow, M.R., Skeate, E.R., Lines, P., Brown, D. and Tomlinson, M.L. (2006). Radio telemetry as a tool for impact assessment of wind farms: the case of Little Terns *Sterna albifrons* at Scroby Sands, Norfolk, UK. *Ibis, 148*, pp.57-75.

Peters, R.C., Eeuwes, L.B. and Bretschneider, F. (2007). On the electrodetection threshold of aquatic vertebrates with ampullary or mucous gland electroreceptor organs. *Biological Reviews, 82*(3), pp.361-373.

Pettigrew, J.D. (1999). Electroreception in monotremes. *Journal of Experimental Biology*, 202(10), pp.1447-1454.

Piantadosi, C.A. and Thalmann, E.D. (2004). Whales, sonar and decompression sickness. *Nature, 428*(6984), pp.1-2.

Pitman, R.L., and Durban, J.W. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (Orcinus orca), type B, in Antarctic Peninsula waters. *Marine Mammal Science.* 31, pp.16–36

Pollard, R.T., Salter, I., Sanders, R.J., Lucas, M.I., Moore, C.M., Mills, R.A., Statham, P.J., Allen, J.T., Baker, A.R., Bakker, D.C. and Charette, M.A. (2009). Southern Ocean deep-water carbon export enhanced by natural iron fertilization. *Nature*, 457(7229), pp.577-580.

Porter, D.G. (1992). Ethical scores for animal experiments. *Nature, 356*(6365), pp.101

Proske, U., Gregory, J.E. and Iggo, A. (1998). Sensory receptors in monotremes. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1372), pp.1187-1198.

Putman, N.F., Meinke, A.M. and Noakes, D.L. (2014). Rearing in a distorted magnetic field disrupts the 'map sense' of juvenile steelhead trout. *Biology letters*, 10(6), p.20140169.

Ragnarsson S.Á. et al. (2017) The Impact of Anthropogenic Activity on Cold-Water Corals. In: Rossi S., Bramanti L., Gori A., Orejas C. (eds) Marine Animal Forests. Cham, Springer. https://doi.org/10.1007/978-3-319-21012-4_27

Read, A.J., Drinker, P. and Northridge, S. (2006). Bycatch of marine mammals in US and global fisheries. *Conservation Biology*, *20*(1), pp.163-169.

Reeves, R., Berger, J. and Clapham, P.J. (2006). Killer whales as predators of large baleen whales and sperm whales. *In* Estes, J., DeMaster, P., Doak, D., Williams, T.,

Brownell, R. (eds) *Whales, whaling and ocean ecosystems*, California, University of California Press, pp.174-187.

Reeves, R., Pitman, R.L. & Ford, J.K.B. (2017). *Orcinus orca.* The IUCN Red List of Threatened Species 2017:
e.T15421A50368125. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T15421A50368125.en. Downloaded on 24 September 2020

Reijnders, P.J. (1992). Harbour porpoises (*Phocoena phocoena*) in the North Sea: Numerical responses to changes in environmental conditions. *Netherland Journal of Aquatic Ecology*, 26(1), pp.75-85.

Renewable UK. (2018) Development rounds. [Online] Available at: https://www.renewableuk.com/general/custom.asp?page=DevelopmentRounds [Accessed 15th September 2020]

Rice, F.L., Mance, A. and Munger, B.L. (1986). A comparative light microscopic analysis of the sensory innervation of the mystacial pad. Innervation of vibrissal follicle-sinus complexes. *Journal of Comparative Neurology*, 252(2), pp.154-174.

Ritter, F. and Panigada, S. (2019). Collisions of vessels with cetaceans—the underestimated threat. *In* Sheppard, C., (ed). *World Seas: An Environmental Evaluation.* Cambridge, MA., Academic Press. pp. 531-547

Rivera-Vicente, A.C., Sewell, J. and Tricas, T.C. (2011). Electrosensitive spatial vectors in elasmobranch fishes: implications for source localization. *PLoS One*, *6*(1)

Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, U.R., Wilson, R.W. and Worm, B. (2017). Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences*, *114*(24), pp.6167-6175.

Robinson, K.P., Tetley, M.J. and Mitchelson-Jacob, E.G. (2009). The distribution and habitat preference of coastally occurring minke whales (*Balaenoptera acutorostrata*) in the outer southern Moray Firth, northeast Scotland. *Journal of Coastal Conservation*, 13(1), pp.39-48

Rockwood, R.C., Calambokidis, J. and Jahncke, J. (2017). High mortality of blue, humpback and fin whales from modeling of vessel collisions on the US West Coast suggests population impacts and insufficient protection. *PLoS One*, *12*(8),

Rodríguez-Pérez, M.Y., Ruiz-Cooley, R.I., Aurioles-Gamboa, D., Sánchez-Velasco, L., Lavín, M.F. and Gallo-Reynoso, J.P. (2021). Deciphering the trophic niche of the nearly extinct vaquita (*Phocoena sinus*) and its variability through time. *Progress in Oceanography*, 199, p.102694.

Rolland, R.M., Graham, K.M., Stimmelmayr, R., Suydam, R.S. and George, J.C., 2019. Chronic stress from fishing gear entanglement is recorded in baleen from a bowhead whale (*Balaena mysticetus*). *Marine Mammal Sciences*, 35, pp.1625-1642.

Rolland, R.M., Parks, S.E., Hunt, K.E., Castellote, M., Corkeron, P.J., Nowacek, D.P., Wasser, S.K. and Kraus, S.D. (2012). Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society B: Biological Sciences*, 279(1737), pp.2363-2368.

Roman, J. and McCarthy, J.J. (2010). The whale pump: marine mammals enhance primary productivity in a coastal basin. *PloS One*, 5(10).

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J.B., Nicol, S., Pershing, A. and Smetacek, V. (2014). Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment*, 12(7), pp.377-385.

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B. and Tryjanowski, P. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature, 453*(7193), pp.353-357.

Rossbach, K.A. and Herzing, D.L., (1997). Underwater observations of benthic-feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Marine Mammal Science, 13*(3), pp.498-504.

Rossi-Santos, M.R. and Wedekin, L.L. (2006). Evidence of bottom contact behavior by estuarine dolphins (*Sotalia guianensis*) on the eastern coast of Brazil. *Aquatic Mammals, 32*(2), p.140.

Ryan, C., Leaper, R., Evans, P.G., Dyke, K., Robinson, K.P., Haskins, G.N., Calderan, S., van Geel, N., Harries, O., Froud, K. and Brownlow, A. (2016). Entanglement: an emerging threat to humpback whales in Scottish waters. *Paper SC/66b/HIM/01 submitted to the International Whaling Commission Scientific Committee.*

Samarra, F.I., Bassoi, M., Béesau, J., Elíasdóttir, M.Ó., Gunnarsson, K., Mrusczok, M.T., Rasmussen, M., Rempel, J.N., Thorvaldsson, B. and Víkingsson, G.A. (2018). Prey of killer whales (*Orcinus orca*) in Iceland. *PloS One,* 13(12), p.e0207287.

Sandler, R. (2012). Intrinsic value. ecology and conservation. *Nature Educational Knowledge*, 3(4). pp.1-7

Santos, M.B., Saavedra, C. and Pierce, G.J. (2014). Quantifying the predation on sardine and hake by cetaceans in the Atlantic waters of the Iberian peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography*, 106, pp.232-244.

Saulitis, E., Holmes, L.A., Matkin, C., Wynne, K., Ellifrit, D. and St-Amand, C. (2015). Biggs killer whale (*Orcinus orca*) predation on subadult humpback whales (*Megaptera novaeangliae*) in Lower Cook Inlet and Kodiak, Alaska. *Aquatic Mammals*, 41(3), p.341.

Schultz, I.R., Woodruff, D.L., Marshall, K.E., Pratt, W.J. and Roesijadi, G. (2010). *Effects of Electromagnetic Fields on Fish and Invertebrates*. Richland, WA. Pacific Northwest National Lab (PNNL). PNNL-19883

Scott, M.D., Wells, R.S. and Irvine, A.B. (1990). A Long-Term Study of Bottlenose Dolphins on the West Coast of Florida 11. *In* Leatherwood, s., Reeves*, R., (eds) The bottlenose dolphin*, Amsterdam, Elsevier, pp.235-244.

Sergio F, Caro T, Brown D, Clucas B, Hunter J, et al. (2008) Top predators as conservation tools: ecological rationale, assumptions, and efficacy. A*nnual Review of Ecology Evolution and Systematics*, 39, pp.1-19.

Shane, S. H. (1994) Pilot whales carrying dead sea lions. *Mammalia*, 58, pp.494–498

Simmonds, M.P. and Eliott, W.J. (2009). Climate change and cetaceans: concerns and recent developments. *Journal of the Marine Biological Association of the United Kingdom*, *89*(1), pp.203-210.

Simmonds, M.P. and Brown, V.C. (2011). Is there a conflict between cetacean conservation and marine renewable-energy developments? *Wildlife Research*, *37*(8), pp.688-694.

Sisneros, J.A., Tricas, T.C. and Luer, C.A. (1998). Response properties and biological function of the skate electrosensory system during ontogeny. *Journal of Comparative Physiology A*, *183*(1), pp.87-99.

Sisneros, J.A. and Tricas, T.C. (2000). Androgen-induced changes in the response dynamics of ampullary electrosensory primary afferent neurons. *Journal of Neuroscience*, *20*(22), pp.8586-8595.

Skeate, E.R., Perrow, M.R. and Gilroy, J.J. (2012). Likely effects of construction of Scroby Sands offshore wind farm on a mixed population of harbour *Phoca vitulina* and grey *Halichoerus grypus* seals. *Marine Pollution Bulletin*, *64*(4), pp.872-881.

Slater, M., Schultz, A., Jones, R. and Fischer, C. (2017). Effects of electromagnetic fields on marine species-A literature review. Oregon Wave Energy Trust. [Online] Available at: https://ir.library.oregonstate.edu/concern/technical_reports/9w032369d [Accessed 15th September 2020]

Smeenk, C. (1987). The harbour porpoise *Phocoena phocoena* in the Netherlands: stranding records and decline. *Lutra*, 30(1), pp.77-90.

Smetacek, V., Klaas, C., Strass, V.H., Assmy, P., Montresor, M., Cisewski, B., Savoye, N., Webb, A., d'Ovidio, F., Arrieta, J.M. and Bathmann, U. (2012). Deep carbon export from a Southern Ocean iron-fertilized diatom bloom. *Nature*, 487(7407), pp.313-319.

Snyder, D.E. (2003). Invited overview: conclusions from a review of electrofishing and its harmful effects on fish. *Reviews in Fish Biology and Fisheries*, *13*(4), pp.445-453.

Soares-Ramos, E.P., de Oliveira-Assis, L., Sarrias-Mena, R. and Fernández-Ramírez, L.M. (2020). Current status and future trends of offshore wind power in Europe. *Energy*, p.117787.

Soulé ME (1985) What is conservation biology? *Bioscience* 35, pp.727-734.

Spitz, J., Ridoux, V., Trites, A.W., Laran, S. and Authier, M. (2018). Prey consumption by cetaceans reveals the importance of energy-rich food webs in the Bay of Biscay. *Progress in Oceanography*, *166*, pp.148-158.

Stern, S.J. and Friedlaender, A.S. (2018). Migration and movement. *In* Perrin, W.F., Wursig, B., Thewissen, J.G.M., (eds) *Encyclopedia of marine mammals*. Cambridge MA. Academic Press. pp. 602-606

Sumaila, U.R. and Tai, T.C., (2020). End overfishing and increase the resilience of the ocean to climate change. *Frontiers in Marine Science*, *7*, pp.523.

Sutton, S.J., Lewin, P.L. and Swingler, S.G. (2017). Review of global HVDC subsea cable projects and the application of sea electrodes. *International Journal of Electrical Power & Energy Systems*, *87*, pp.121-135.

Switzer, T. and Meggitt, D. (2010). *Review of literature and studies on electro-magnetic fields (EMF) generated by undersea power cables and associated influence on marine organisms.* Seattle. 20th September 2010. IEEE. pp.1-5

Taormina, B., Bald, J., Want, A., Thouzeau, G., Lejart, M., Desroy, N. and Carlier, A. (2018). A review of potential impacts of submarine power cables on the marine environment: Knowledge gaps, recommendations and future directions. *Renewable and Sustainable Energy Reviews*, *96*, pp.380-391.

Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G, Notarbartolo di Sciara, G., Wade, P. & Pitman, R.L. (2008a). *Hyperoodon ampullatus*. The IUCN Red List of Threatened Species 2008: e.T10707A3208523. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T10707A3208523.en. Downloaded on 24 September 2020.

Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G, Notarbartolo di Sciara, G., Wade, P. & Pitman, R.L. (2008b). *Mesoplodon bidens*. The IUCN Red List of Threatened Species2008: e.T13241A3424903. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T13241A3424903.en. Downloaded on 24 September 2020.

Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G, Notarbartolo di Sciara, G., Wade, P. & Pitman, R.L. (2008c). *Ziphius cavirostris*. The IUCN Red List of Threatened Species 2008: e.T23211A9429826. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T23211A9429826.en. Downloaded on 24 September 2020.

Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G, Notarbartolo di Sciara, G., Wade, P. & Pitman, R.L. (2019). *Physeter macrocephalus* (amended version of 2008 assessment). The IUCN Red List of Threatened Species 2019: e.T41755A160983555. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en. Downloaded on 24 September 2020.

Taylor, D. (2004) Wind energy. *In* Boyle, G., (ed) *Renewable Energy: Power for a sustainable future*, Oxford, Oxford University Press. pp. 244–293.

The Wind Power. (2019) *UK Statisitics – production statistics*. [Online] Available at: https://www.thewindpower.net/country_en_8_united-kingdom.php [Accessed 5th August 2020]

Thewissen, J.G. and Nummela, S. (2008). *Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates*. Los Angeles, California. University of California Press.

Thewissen, J.G.M., Cooper, L.N., George, J.C. and Bajpai, S. (2009). From land to water: the origin of whales, dolphins, and porpoises. *Evolution: Education and Outreach*, *2*(2), pp.272-288.

Thompson, K.F., Miller, K.A., Currie, D., Johnston, P. and Santillo, D. (2018). Seabed mining and approaches to governance of the deep seabed. *Frontiers in Marine Science*, *5*, pp.480.

Thompson, P.M., Lusseau, D., Barton, T., Simmons, D., Rusin, J. and Bailey, H. (2010). Assessing the responses of coastal cetaceans to the construction of offshore wind turbines. *Marine Pollution Bulletin*, 60(8), pp.1200-1208.

Thomsen, F., Lüdemann, K., Kafemann, R. and Piper, W. (2006). Effects of offshore wind farm noise on marine mammals and fish. *Biola, Hamburg, Germany. COWRIE Ltd*.

Tomanová, K. and Vácha, M. (2016). The magnetic orientation of the Antarctic amphipod *Gondogeneia antarctica* is cancelled by very weak radiofrequency fields. *Journal of Experimental Biology*, *219*(11), pp.1717-1724.

Tønnesen, P., Oliveira, C., Johnson, M. and Madsen, P.T. (2020). The long-range echo scene of the sperm whale biosonar. *Biology letters*, 16(8), p.20200134.

Torres, L.G. and Read, A.J. (2009). Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Marine Mammal Science*, *25*(4), pp.797-815.

Torres, L.G. (2017). A sense of scale: Foraging cetaceans' use of scale-dependent multimodal sensory systems. *Marine Mammal Science*, *33*(4), pp.1170-1193.

Tricas, T.C., Michael, S.W. and Sisneros, J.A. (1995). Electrosensory optimization to conspecific phasic signals for mating. *Neuroscience Letters*, *202*(1-2), pp.129-132.

Tricas T.C. (2001) The neuroecology of the elasmobranch electrosensory world: why peripheral morphology shapes behavior. In: Tricas T.C., Gruber S.H. (eds). *The Behavior and Sensory Biology of Elasmobranch Fishes: An Anthology in Memory of Donald Richard Nelson. Developments in Environmental Biology of Fishes*. Dordrecht, Springer. pp.77-92

Tricas T.C., Sisneros J.A. (2004) Ecological Functions and Adaptations of the Elasmobranch Electrosense. In: von der Emde G., Mogdans J., Kapoor B.G. (eds) *The Senses of Fish*. Dordrecht, Springer. pp.308-329

Tricas, T. and Gill, A. (2011). Effects of EMFs from undersea power cables on elasmobranchs and other marine species. *US Dept. of the Interior, Bureau of Ocean Energy Management, Regulation, and Enforcement, Pacific OCS Region, Camarillo, CA. OCS Study BOEMRE*, *9*.

Tyack, P.L. (2000). Functional aspects of cetacean communication. *In* Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H., (eds). *Cetacean societies: Field studies of dolphins and whales*, Chicago, University of Chicago Press. pp.270-307.

Tyack P.L., Clark C.W. (2000) Communication and Acoustic Behavior of Dolphins and Whales. In: Au W.W.L., Fay R.R., Popper A.N. (eds) Hearing by Whales and Dolphins. Springer Handbook of Auditory Research, vol 12, New York, NY Springer. pp.156-224

UN Environment, (2018) *Progress Report on Relevant Activities Undertaken within the Framework of ASCOBANS for the United Nations Process on Oceans and the Law of the Sea. Germany, UN. A/RES/73/124*

United Nations Conference on Trade and Development. (2018) *Trade and Development report 2018 – Power, Platforms and The Free Trade Delusion* [Online] Available at: https://unctad.org/en/PublicationsLibrary/tdr2018_en.pdf [Accessed 11th September 2020]

Van Bressem, M.F., Raga, J.A., Di Guardo, G., Jepson, P.D., Duignan, P.J., Siebert, U., Barrett, T., de Oliveira Santos, M.C., Moreno, I.B., Siciliano, S. and Aguilar, A. (2009). Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. *Diseases of Aquatic Organisms*, *86*(2), pp.143-157.

Vanselow, K., Jacobsen, S., Hall, C., & Garthe, S. (2018). Solar storms may trigger sperm whale strandings: Explanation approaches for multiple strandings in the North Sea in 2016. *International Journal of Astrobiology*, 17(4), pp.336-344

Vanselow, K.H. & Rickles, K. (2005). Are solar activity and sperm whale strandings around the North Sea related? *Journal of Sea Research*. 53, pp.319–327

Vanselow, K.H., Rickles, K. & Colijn, F. (2009). Solar driven geomagnetic anomalies and sperm whale (*Physter macrocephalus*) stranding around the North Sea: an analysis of long-term datasets. *Open Marine Biology* Journal. 3, pp.89–94

Vinther, M. and Larsen, F. (2004). Updated estimates of harbour porpoise (Phocoena phocoena) bycatch in the Danish North Sea bottom-set gillnet fishery. *Journal of Cetacean Research and Management*, 6(1), pp.19-24.

Visser, I., (1999). Benthic foraging on stingrays by killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science*, *15*(1), pp.220-227.

von Benda-Beckmann, A.M., Aarts, G., Sertlek, H.Ö., Lucke, K., Verboom, W.C., Kastelein, R.A., Ketten, D.R., van Bemmelen, R., Lam, F.P.A., Kirkwood, R.J. and Ainslie, M.A. (2015). Assessing the impact of underwater clearance of unexploded ordnance on harbour porpoises (*Phocoena phocoena*) in the Southern North Sea. *Aquatic Mammals*, *41*(4). pp.340-341

Walker, M.M., Dennis, T.E. and Kirschvink, J.L. (2002). The magnetic sense and its use in long-distance navigation by animals. *Current Opinion in Neurobiology*, 12(6), pp.735-744.

Walker, M.M., Kirschvink, J.L., Ahmid, G. & Dizon, A.E. (1992). Evidence that Fin Whales respond to the geomagnetic field during migrations. *Journal of Experimental Biology*. 171, pp.67–78.

Waltman, B. (1966). Electrical properties and fine structure of the ampullary canals of Lorenzini. *Acta physiologica Scandinavica*. Supplementum, 264, pp.1.

Wang, M., Walker, W.A., Shao, K.and Chou, L. (2002). Comparative analysis of the diets of pygmy sperm whales and dwarf sperm whales in Taiwanese waters. *Acta Zoologica Taiwanica*, 13 (2), pp.53-62.

Wang Y, Pan Y, Parsons S, Walker MM and Zhang S. (2007) Bats respond to polarity of a magnetic field. *Proceedings of the Royal Society B.* 27, pp.2901–2905

Weilgart L. (2017) Din of the Deep: Noise in the Ocean and Its Impacts on Cetaceans. In: Butterworth A. (eds) Marine Mammal Welfare. Animal Welfare, vol 17. Cham, Springer. pp.111-124

Weiss, M.N., Franks, D.W., Balcomb, K.C., Ellifrit, D.K., Silk, M.J., Cant, M.A. and Croft, D.P. (2020). Modelling cetacean morbillivirus outbreaks in an endangered killer whale population. *Biological Conservation*, *242*, pp.108398.

Weller, D. W., Würsig, B., Whitehead, H., Norris, J. C., Lynn, S. K., Davis, R. W., Clauss, N. & Brown, P. (1996) Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. *Marine Mammal Science,* 12, pp.588–594

Wells, R.S., Natoli, A. & Braulik, G. (2019). *Tursiops truncatus* (errata version published in 2019). The IUCN Red List of Threatened Species 2019: e.T22563A156932432. https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T22563A156932432.en. Downloaded on 24 September 2020.

H. Westerberg, M.L. Begout-Anras (2000) Orientation of silver eel (*Anguilla anguilla*) in a disturbed geomagnetic field. A. Moore, I. Russell (Eds.), Advances in Fish Telemetry, CEFAS, Lowestoft, pp. 149-158.

West Wales Biodiversity Information Centre (2018). Seatrust Cetacean Records West Wales. Occurrence dataset https://doi.org/10.15468/ecsmqh accessed via GBIF.org on 2022-01-11

Whale and Dolphin Conservation (2021). WDC Shorewatch Sightings. Occurrence dataset https://doi.org/10.15468/9vuieb accessed via GBIF.org on 2022-01-11.

Whitehead, H., 2018. Sperm whale: Physeter macrocephalus. *In* Würsig, B., Thewissen, J.G.M., Kovacs, K. (eds) *Encyclopedia of marine mammals,* 3rd edition Cambridge MA, Academic Press. pp. 919-925.

Whitehead, D. and Collin, S. (2004). The functional roles of passive electroreception in non-electric fishes. *Animal Biology, 54*(1), pp.1-25

Williams, R. and O'Hara, P. (2010). Modelling ship strike risk to fin, humpback and killer whales in British Columbia, Canada. *Journal of Cetacean Research and Management*, 11(1), pp.1-8.

Willows, A.D. (1999). Shoreward orientation involving geomagnetic cues in the nudibranch mollusc *Tritonia diomedea*. M*arine & Freshwater Behaviour & Phy*, 32(2-3), pp.181-192.

Wilson, J.C., Elliott, M., Cutts, N.D., Mander, L., Mendão, V., Perez-Dominguez, R. and Phelps, A. (2010). Coastal and offshore wind energy generation: is it environmentally benign? *Energies, 3*(7), pp.1383-1422.

Wiltschko, W. and Wiltschko, R. (1995). Migratory orientation of European robins is affected by the wavelength of light as well as by a magnetic pulse. *Journal of Comparative Physiology A,* 177(3), pp.363-369.

Wiltschko, W. and Wiltschko, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *Journal of Comparative Physiology A*, 191(8), pp.675-693.

Winklhofer, M. (2010). Magnetoreception. *Journal of The Royal Society Interface,* 7, pp.131–134

Wood, M. P. and Carter, L. (2008). Whale entanglements with sub-marine telecommunication cables. *Journal of Oceanic Engineering,*33, 445–450

Wright, A.J., Soto, N.A., Baldwin, A.L., Bateson, M., Beale, C.M., Clark, C., Deak, T., Edwards, E.F., Fernández, A., Godinho, A. and Hatch, L.T. (2007). Do marine mammals experience stress related to anthropogenic noise? *International Journal of Comparative Psychology*, 20(2), pp.274-316.

Wueringer, B.E., Jnr, L.S., Kajiura, S.M., Tibbetts, I.R., Hart, N.S. and Collin, S.P. (2012). Electric field detection in sawfish and shovelnose rays. PLoS ONE 7(7). p.e41605-e41605.

Würsig, B., Wells, R.S. and Croll, D.A., (1986). Behavior of gray whales summering near St. Lawrence Island, Bering Sea. *Canadian Journal of Zoology*, *64*(3), pp.611-621.

Yablokov, A. V., Bel'kovich, V. M., & Borisov, V. I. (1972). Kity i del'finy. Nauka, Moscow, Russia: Whales and Dolphins

Yablokov, A. V., & Klevezal, G. A. (1969). Whiskers of whales and seals and their distribution, structure and significance. Morphological Characteristics of Aquatic Mammals, pp.48–81 Izdatel'stvo Nauka

Yadav, S.S. and Gjerde, K.M. (2020). The ocean, climate change and resilience: Making ocean areas beyond national jurisdiction more resilient to climate change and other anthropogenic activities. *Marine Policy*, *122*, pp.104184.

Young, D.D. and Cockcroft, V.G. (1994). Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: opportunism or specialization? *Journal of Zoology*, 234(1), pp.41-53.

Yu, Q., Liu, K., Teixeira, A.P. and Soares, C.G. (2020). Assessment of the influence of offshore wind farms on ship traffic flow based on AIS data. *Journal of Navigation*, 73(1), pp.131-148.

Zapetis M. and Szesciorka A. (2018) Cetacean Navigation. In: Vonk J., Shackelford T. (eds) *Encyclopedia of Animal Cognition and Behavior*. 14, Cham, Springer.pp.1-7

Zellar, R., Pulkkinen, A., Moore, K., Rousseaux, C.S. and Reeb, D. (2021). Oceanic and Atmospheric Correlations to Cetacean Mass Stranding Events in Cape Cod, Massachusetts, USA. *Geophysical Research Letters*, 48(20), pp.e2021GL093697.

Zoeger, J., Dunn, J.R. and Fuller, M. (1981). Magnetic material in the head of the common Pacific dolphin. *Science*, pp.892-894.