SCHOOL OF APPLIED SCIENCES

ENV10112 Scientific Research Project
Honours Thesis

Project Title: The diving ecology and foraging behaviour of coastal minke whales (*Balaenoptera acutorostrata*) in the outer Moray Firth, northeast Scotland.

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2. Abstract

The surfacing rates and diving ecology of minke whales have played an important role in the study of this species. Since respiration is a critical component of metabolic activity and feeding strategies employed by these whales, this knowledge is vital to their biology and behaviour. In the present study, the dive duration, surface duration and surfacing interval were investigated in the species, from a long-term dataset opportunistically collated between 2006 and 2019, within the coastal waters of the Moray Firth, in northeast Scotland. A total of 58 focal follows, of which 47 individual follows lasted more than 20 minutes, were examined in this study with respect to the behaviour, age class and the time of year. A one-way analysis of variance (ANOVA) detected a significant difference between dive duration, behaviour, and time of year, demonstrating that the whales modified their diving ecology with changing behaviours and at different times of the year. Specifically, it was found that traveling adult minkes performed longer dives in August, compared to June. The surface duration was also found to be statistically different between adults and juveniles, with adult whales spending longer at the surface recovering from longer and deeper dives than juveniles. These findings demonstrate a clear variation in dive rates between the different factors explored, which should be taken into consideration in future survey design to aid adaptive management efforts for the species.

3. Introduction

1.1 Taxonomic classification of the minke whales and the *Balaenopteridae*

The minke whale (Balaenoptera acutorostrata Lacépède,1804) belongs to the Suborder Mysticeti (the baleen whales) within the larger order of Cetacea. The Suborder comprises 14 species across four families; the Balaenopteridae being the largest family with 9 species over 2 genera (the Balaenoptera and Megaptera respectively) (Perrin et al., 2009). The members within this family are also referred to as rorqual whales, originating from a Norse word meaning ‘pleated’ or ‘tubed’ whale (Curnier, 2005). Rorqual species can be distinguished by their streamlined body shape and the presence of multiple ventral pleats (or throat grooves) on the underside of the lower jaw (Horwood, 1989). The family is further characterised by relatively short baleen plates in comparison to other baleen whales. They have short heads, less than a fourth of their body size, and have a small dorsal fin positioned to the rear of the body (Bannister, 2002).

Within the minke whales, it was thought that only one species occurred, known as the common minke whale. However, in the 20th century, the Antarctic minke whale (Balaenoptera bonaerensis) received full recognition as a second species of minke, from morphological and genetic evidence (Ohsumi et al., 1970, Satake & Omura, 1974, Zerbini & Castello, 2003). Currently, 3 further sub-species of common minke whale are also recognised, defined largely from their geographical location, but with each showing morphological and genetic differences (Milmann et al., 2021). These comprise the North Atlantic minke whale (Balaenoptera acutorostrata), North Pacific minke whale (Balaenoptera scammoni), and the unnamed dwarf minke whale (Balaenoptera unnamed subsp.) (Rice, 1998).

The research within this project was carried out on the common North Atlantic minke whale *B. acutorostrata* and as such all the biological traits discussed hereafter refer uniquely to this species.

1.2 North Atlantic minke whale’s morphological characteristics

The minke whale is the smallest member of the Balaenopteridae family. Estimated at 10.7 metres in length in females and 9.8 metres in males (Reeves et al., 2002), a distinctive feature of the whale is the narrow, pointed rostrum, with its single, longitudinal ridge (Figure 1.1).

Figure 1.1 Feeding minke whale displaying the single longitudinal ridge on the rostrum. Photo credit: Kevin Robinson (CRRU).

The species name describes this distinct feature ‘acutorostrata’ translating to ‘sharp snout’ (Reeves et al., 2002). Within the mouth, there are 230 to 360 cream-coloured baleen plates made from keratin (Perrin et al., 2018). These form comb-like structures which replace the customary teeth, hanging down from the upper jaw (Pivorunas, 1979) (Figure 1.2).

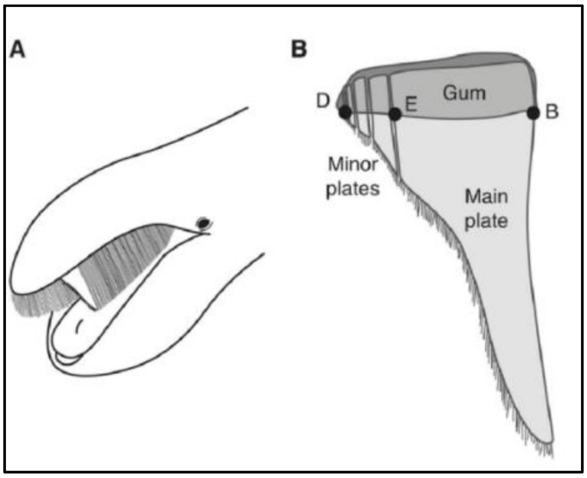

Figure 1.2 Morphology of baleen: (A) baleen rack of a generalised mysticete and (B) a single baleen plate (Adapted from Jensen et al., 2017).

Minke whales have the smallest baleen plates of all the rorqual species. In comparison to blue whales (Balaenoptera musculus) which have a baleen plate length of 91 cm, the minke whale plate length is just 25 cm with a breadth of 12 cm (Christensen et al., 1990). The minke whale also possesses a highly distensible throat with 50 to 70 throat grooves. The connective tissue and muscle of the grooves are extremely elasticated, enabling the throat to expand up to 4 times its original size when engulfing prey (Orton & Brodie, 1987).

Minkes have a falcate dorsal fin, located two thirds along the back (Perrin et al., 2018), which appears simultaneously with the blow hole as the whale surfaces. Adult body pigmentation is black or dark grey with a white underside, a grey band crossing behind the head, and a white stripe across the pectoral fins (Reeves et al., 2002) (Figure 1.3). The dorsal fin shape and characteristic pattern of nicks are often unique between adults and can be used for the recognition (photo-identification) of individual animals (e.g., Robinson et al., 2021).

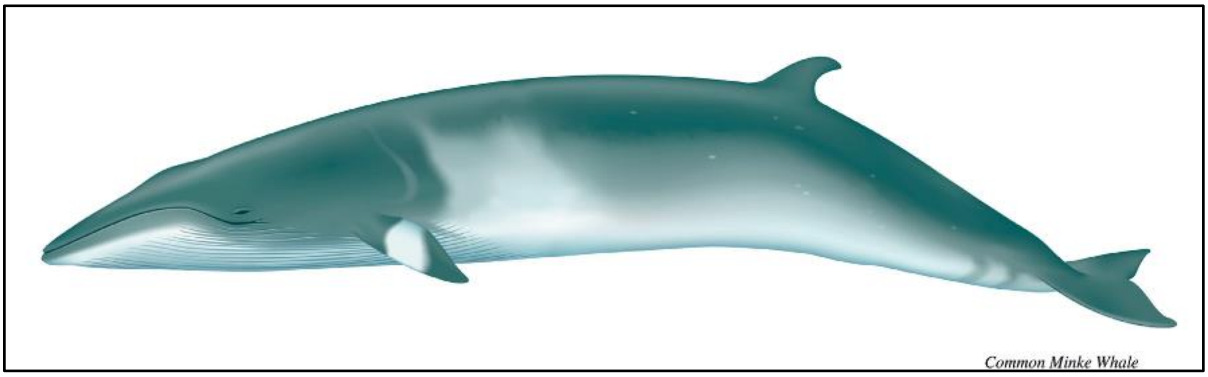

Figure 1.3 Illustration of a common minke whale depicting the pigmentation characteristics (from, Perrin et al., 2018).

1.3 Distribution and Abundance.

A highly cosmopolitan species, the common minke whale has been discovered in all oceans and at all latitudes, ranging from 70°S to 80°N (Cooke, 2018), thus making it an essential part of the marine ecosystem. During the summer months, the North Atlantic minke has been sighted as far north as Baffin Bay in Svalbard, Norway, and Franz Josef Land, off the North coast of Russia (Hansen et al., 2019). Wintering grounds are inadequately known but can range from the Strait of Gibraltar in the east, to the Caribbean in the west (Rice, 1998), and informal evidence suggests that minke whales may travel as far south as the Senegalese coast (Perrin et al., 2018) (Figure 1.4). The estimated abundance of animals within the east Northern Atlantic is 120,000, with 60,000 in the central Northern Atlantic (Haug, 1995). There is no complete abundance estimate for the west Northern Atlantic, however it is thought that a population of approx. 2,500 is present along the east coast of North America, from Virginia to the Bay of Fundy (Palka, 2012).

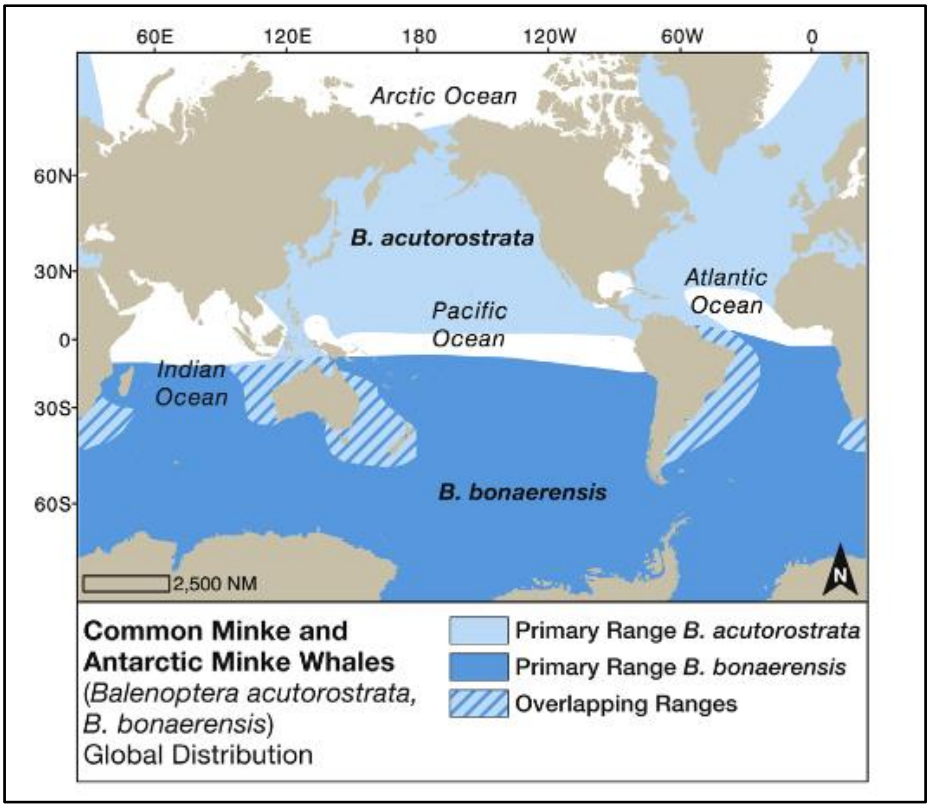

Figure 1.4 Map illustrating the distribution and ranges of the common and Antarctic minke whale, (from Webber et al., 2015).

12,800 minke whales are estimated to populate within UK waters, approximately 9,000 of which are within the North Sea (Hammond et al., 2017). Minke whales are typically encountered in coastal shelf waters lower than 200 meters deep. This is especially true within the rich productive waters surrounding the west coast of Scotland and the Moray Firth study area (57° 41′ N, 2° 40′ W), which attract higher-than-average numbers of minke whales as compared to the surrounding and wider Scottish waters (Paxton et al., 2014). The Moray Firth provides rich feeding areas for these whales during the summer and autumnal months (Robinson & Tetley 2007, Robinson et al., 2009). As a result, the Southern Trench in the outer Moray Firth was newly designated as a Marine Protected Area (MPA) for the conservation of these coastal whales (Marine Scotland, 2019).

Many of the population abundance estimates quoted above have been calculated from line transect surveys from dedicated vessels and aircraft (e.g., Palka, 2012; Hammond et al., 2017). These transects allow sampling of population densities within defined areas, unlike mark-recapture studies which focus on individual abundance. Firstly, the population abundance estimates are estimated from the density of animals per unit area, and then the density is extrapolated to the entire seas. As a result, abundance is defined as the expected number of animals in a specific area during the time the survey was conducted (Hammond et al., 2021). The assumption made when conducting a transect line survey is that all animals can be seen directly (Glennie et al., 2015). However, this cannot be assumed when studying marine mammals, as many remain underwater and move independently of the transect line, so may not be counted during a search. This is known as ‘availability bias’ (Rankin et al., 2020). When conducting line-transect survey work, the likelihood of locating a whale within the area of observation is referred to as g(0) (Stern, 1992). Since whales and dolphins spend the majority of their time submerged (during which time they cannot be detected), g(0) is usually <1 (Thomsen et al., 2004). Reliable data on surfacing rates thus provide correction factors to recalibrate the counts of undetected (subsurface) animals, which are critical to the credibility of whale population estimates derived from "cue-counting" census surveys (Brakes & Dall, 2016).

Another form of bias that occurs when performing a line transect survey is ‘perception bias’, which occurs when the animals are at the surface but cannot be seen due to observation conditions or chance (Marsh & Sinclair, 1989). Estimates of marine mammal abundance which are not adjusted for individuals lost on the transect line are consequently negatively skewed to an undetermined degree (Hammond et al., 2021), therefore leading to inaccuracies in population estimates. This can be avoided by using a double observer team system, where data are collected from two independent viewing platforms, which allows for correction of this perception bias (e.g., Martin et al., 2020).

Due to inaccuracies in cue counts used for the determination of abundances in dedicated surveys, definitive data on surfacing rates and behaviours can aid in the correction of biases leading to over-estimations in populations (Sucunza et al., 2018). The data on surfacing rates are also critical in determining how whales respond to industrial disturbances such as maritime activity and resource extraction (Kavanagh et al., 2016) and other possible sources of disruption like the intrusive presence of whale-watching ships.

1.4 Conservation status and threats.

The International Union for Conservation of Nature (IUCN) Red List currently lists the common minke whale as a species of Least Concern (Cooke, 2018). However, these whales are of conservation priority: regionally (under the Northeast Scotland Biodiversity Action Plan), nationally (under the United Kingdom Biodiversity Action Plan); and globally (under the European Union Habitats Directive, and the Convention on the International Trade in Endangered Species) (Baumgartner, 2008). Research shows there is a stable population of the species in the North Sea (Sigurjónsson, 1995). However, current population estimates contain a degree of ambivalence due to increasing anthropogenic threats impacting these cetaceans, e.g., acoustic pollution, entanglement in fishing gears and ship strikes (Evans et al., 2008; Leaper et al. in press). As minke whales have great trophic status and are at risk from anthropogenic effects, thereby they are a principal indication of ecosystem change (Hooker & Gerber, 2004).

One of the most controversial threats still facing the species is commercial whaling. In the 1970s, many whaling countries moved to targeting these smaller rorquals after the decline of larger species (Horwood, 1989). Commercial whaling is currently still practiced in Norway, Iceland and Greenland. Each of these countries are part of the International Whaling Commission and are under the legal framework, which includes regulations on whaling to aid the conservation of the ocean’s whale stock (Conrad & Bjørndal, 1993). Since International Whaling Commission records began in 1985, commercial, special permit and aboriginal whaling programmes have reportedly killed 43,799 minke whales to date (Risch, et al., 2019).

Another threat affecting these whales is underwater noise, which occurs in oceans all over the world. A study by Kvadsheim et al. (2017) found that minke whales perform unusual dive behaviour in order to avoid the underwater noise from naval activity, resulting in a 5-fold increase in horizontal speed away from the source, which in turn increases metabolic activity. Off the west coast of Scotland, there is a considerable amount of naval activity, causing lethal and sublethal effects on the minke whale populations in these waters as well (e.g., Parsons et al., 2000).

Entanglement in fishing gear (ropes/creels) is another immediately recognised threat to these animals (Leaper et al., in press). An investigation by Northridge et al. (2010) found that 50% of all minke whale strandings in Scotland are caused by entanglement, and 22% of sighted animals bore scars from previous entanglement events. Leaper et al. (in press) estimated that 32 minkes become entangled in fishing gears each year and, when found, 87% of these whales will already be deceased. Subsequently, entanglement is perhaps the greatest anthropogenic threat to minke whales and should be considered a major cause for concern.

Ship strikes are also a further cause for concern. Since the 1950s, ships have become larger and faster, resulting in an increasing number of strikes (McKenna et al., 2012). Mortality from ship strikes is caused by blunt trauma from the ship impacting with the animal, or from lacerations by the propeller. A study by Van Der Hoop et al, (2012) investigating the injury and fatality of large whales along the east coast of the United States from 1970 to 2009, and found that ship strikes were responsible for 4.3% of confirmed minke whale deaths. However, the number of ship strikes is known to be under-reported, which suggests that there will be many more deaths due to strikes than are presently documented (Peel et al., 2018). More detailed reporting techniques, as well as mandated reporting, are predicted to enhance awareness of this critical problem affecting whale populations, especially minke whales.

Minke whales face many threats, and therefore sounder management strategies are necessary. Better understanding of the general ecology and behaviour of these whales, as well as further knowledge of the role of these animals in the marine ecosystem, is believed to be essential to provide the future protection these cetaceans need (Baumgartner, 2008).

1.5 Diet, foraging strategies and feeding techniques of minke whales.

Amongst the baleen whale species, minkes are described as consuming the greatest number of fish (Macleod et al., 2004). In the North Atlantic, minke whales feed on a large range of pelagic shoaling and ground dwelling fish species such as sand eel (*Ammodytes sp.*), herring (*Clupea harengus*) mackerel (*Scomber scombrus*) and sprat (*Sprattus sprattus*) (Eerkes-Medrano et al., 2021). A study by Markussen et al. (1992) showed that an estimated daily intake of fish for an adult female minke whale was 277 kg, and for males a value of 204 kg was calculated.

The minke whale is a diverse feeder targeting many different prey. When one prey is in insufficient supply, prey switching occurs (Lindstrøm, 2002, Robinson et al., 2021). In the Moray firth, lesser sandeel, herring and sprat are predominantly targeted; these three prey species comprising 86% of the total fish biomass within these northeast waters (Greenstreet et al., 1998). However, Robinson et al. (2021) observed demographic differences in dietary preferences between adults and juvenile minkes, with juveniles, almost exclusively targeting year 0-1 sandeels, whilst adults showed more seasonal plasticity in their dietary choice.

As predators, minke whales are vital members of the Northeast Atlantic ecosystem. With regards to understanding their diet and role in the food-web, research by Folkow et al. (2000) and Windsland et al. (2007) looked at the stomach contents of whales caught from whaling vessels within the summer months. Revealing similar findings to Robinson et al. (2021), they found that the minke whales diet varied due to prey availability. However, this is not the most effective method of exploring the whale’s diet, as it only provides information on what prey the animal has been consuming. A more effective method involves the use of biopsy darts to collect skin samples for the study of naturally-occurring isotopes and trace elements (Lesage et al., 2010). This technique provide further information than just diet, and are being utilised in the study of minke whales, to elucidate the trophic relationships, migratory patterns, and habitat use, to aid in the understanding of these elusive whales (Eerkes-Medrano et al., 2021).

As flexible feeders, minke whales are seen to employ a variety of feeding strategies. Hoelzel et al. (1989) described two main feeding methods that individuals utilise which are termed as bird-associated feeding (passive feeding) or lunge feeding (active feeding). Bird-associated feeding is well documented in Scottish waters (Robinson & Tetley, 2007; Anderwald et al., 2011), and is more predominantly observed in juvenile animals (Robinson et al., 2021). The species of birds that minke whales have a strong association with have been found to be common guillemots (*Uria aalge*), kittiwakes (*Rissa tridactyla*), manx sheerwaters (*Puffinus puffinus*) and razorbills (*Alca torda*) (Evans, 1982). The whales rely on the congregation of small fish condensed at the water's surface by schooling predatory fish, from below, and by flocks of feeding birds, from above, hence the term passive feeding, as the whales exploit these ephemeral bait balls of prey without expending any energy to corral the food themselves (Robinson & Tetley, 2007). Conversely, active feeding involves a focused effort by the whale to actively corral together the prey by itself. Different manoeuvres and techniques are performed by individual whales which may involve aerial lunges, as seen in Figure 1.5. A study by Robinson & Tetley (2007) found that from June to October 2000 to 2005, 76% of all encounters with foraging minke whale were recorded as bird associated feeding. The utilisation of different feeding techniques by individual minkes may contribute to the stability of populations through evolutionary diversification (Robinson et al., 2021).

Figure 1.5 Arial behaviour of a common minke whale actively lunge-feeding in the St. Lawrence Estuary. Note the expanded throat grooves and the water being expelled through the baleen plates as the prey are trapped in the mouth (Photo credit: Mériscope / Brian Kot).

1.6 Ventilation and diving rates in minke whales.

Marine mammals have evolved to thrive in the underwater environment. Physiological, morphological and behavioural adaptations allow them to spend extended periods of time underwater, foraging, reproducing or avoiding predators (Fahlman, 2012). Physiological changes for living underwater include increased blood volume (enabling greater oxygen storage), slowed metabolism (i.e. lower oxygen intake), and the generation of lactic acid in the muscles (i.e. anaerobic activities) (Schmidt-Nielsen, 2010). More specifically, when performing a dive (the amount of time that has passed between two successive surface breaths), physiological responses are characterised by the halting of respiration (termed apnea), a reduction in heart rate (bradycardia), a simultaneous decrease in cardiac output, and narrowing of the arteries which keeps central arterial pressure constant (Davis, 2019). Although the necessity to dive is an important aspect of a whale's life history, these mammals remain tethered to the surface by the necessity to breathe air, and, as a result, all actions are subject to ventilatory patterns in a way that no other terrestrial creature is (Dolphin, 1987). Accordingly, whales have adapted behaviourally to meet the requirement to breathe.

Brief breath-hold, ventilatory rhythms are thought to optimise oxygen uptake in relation to the surface time (Kramer, 1988). However, diving and breathing rates in minkes are known to vary significantly respective to the sort of activity animals are engaged in and their differing behavioural states (Rosen et al., 2007), in addition to their geographical location, the depth of the water column and even the time of year (e.g., Baumgartner, 2008, Stockin et al., 2001). When investigating whether the surfacing sequence of minkes changed diurnally and/or seasonally, Stockin et al. (2001) found that surfacing intervals were shortest at 12am within June and July, and longest at 11am and 2pm during May and August, most likely as a result of a change in the foraging behaviour and habitat use of whales with respect to the availability of prey. These findings were determined to be useful for the design of surveys used to assess the species' abundance.

The minke whale has a typical dive sequence of 3 to 5 surfaces at intervals of 15 to 60 seconds, followed by a long dive lasting from 2 to 4 minutes. This cycle can be divided into several ventilation components: (i) the entire dive sequence (the complete dive with short and clustered surfacings and one long, possible deep dive interval), (ii) the surface interval (the time between successive blows), (iii) the surfacing duration (the sequential breath which are clustered blows, prior to long dive) and (v) the dive duration (total length of the long dive/breath hold) (see Figure 2.6 within methods for illustration and full definitions of different terms). There is seen to be lack of a standardised methodology in measuring the ventilation rates of whales, many studies such as Stockin et al., (2001), were not clear in their calculation of the choice in parameters. An example of the differences between studies can be seen in Christiansen et al., (2015), where they examine the short and long dives, compared to Stockin et al., (2001), who investigates dive duration. As there is no standardised way of calculating these parameters, researchers must base their choice from previous work which could lead to different calculations, causing contrasting results, that in turn could affect the applications of the results found. This study hopes to provide a clear outline of how the chosen parameters were calculated and measured. Furthermore, many of these studies previously mentioned (e.g., Stockin et al., 2001 & Lagerquist et al., 2000) have only focused on one ventilation parameter, compared to this study which is focusing on 3 different parameters – namely, the dive duration, surfacing duration and surface interval, in a hope to gain more in-depth knowledge on the minke whales dive structure within the Moray Firth.

Research into surfacing/diving rates can also provide useful baselines for assessing the effects of anthropogenic disturbances on these animals (Rojano-Doñate et al., 2018). Studies examining changes in surface duration, and surfacing intervals, subsequently provide an understanding of the strategic decisions made by individual animals in specific behavioural states in given environmental conditions, or in response to changing abiotic/biotic factors. Thus, a closer examination of the surfacing behaviour and dive rates in minke whales could provide a more thorough understanding of the underwater-related activities of these ecologically important whales.

1.8 Study Aims

This project aims to investigate the diving behaviour of coastal minke whales in the outer Moray Firth, in northeast Scotland, using a long-term dataset opportunistically collated between 2006 and 2019 by the Cetacean Research & Rescue Unit (CRRU). The objectives of this study are:

1. To better understand the surfacing and ventilation rates of minke whales within the Moray Firth,

2. To explore differences in diving rates in the species by age class (i.e., juveniles vs adults), behaviour and time of year (i.e. monthly differences).

3. To investigate the relationship between dive rates, dive duration, surfacing duration and surfacing intervals with respect to the above factors.

1.9 Alternative Hypothesis

To aid the investigation into surfacing and ventilation rates of coastally occurring minke whales within the Moray Firth, the following alternative hypotheses were explored:

H^1 - A significant difference will be described between diving rates and age class (i.e., juveniles vs adults), behaviour, and time of year (i.e., monthly differences).

H^2 - A significant relationship will be observed between the three calculated ventilation parameters.

4. Methods

2.1 Survey Methodology

The secondary datasets examined in this present report were collected from May to October, 2006 to 2019. A dedicated boat-based survey was used for data collection, within a 1980 km^2 area of the southern Moray Firth encompassing the recently designated Marine Protected Area (MPA), in the Southern Trench (57°39′54″N, 002°31′24″W) (Figure 2.1).

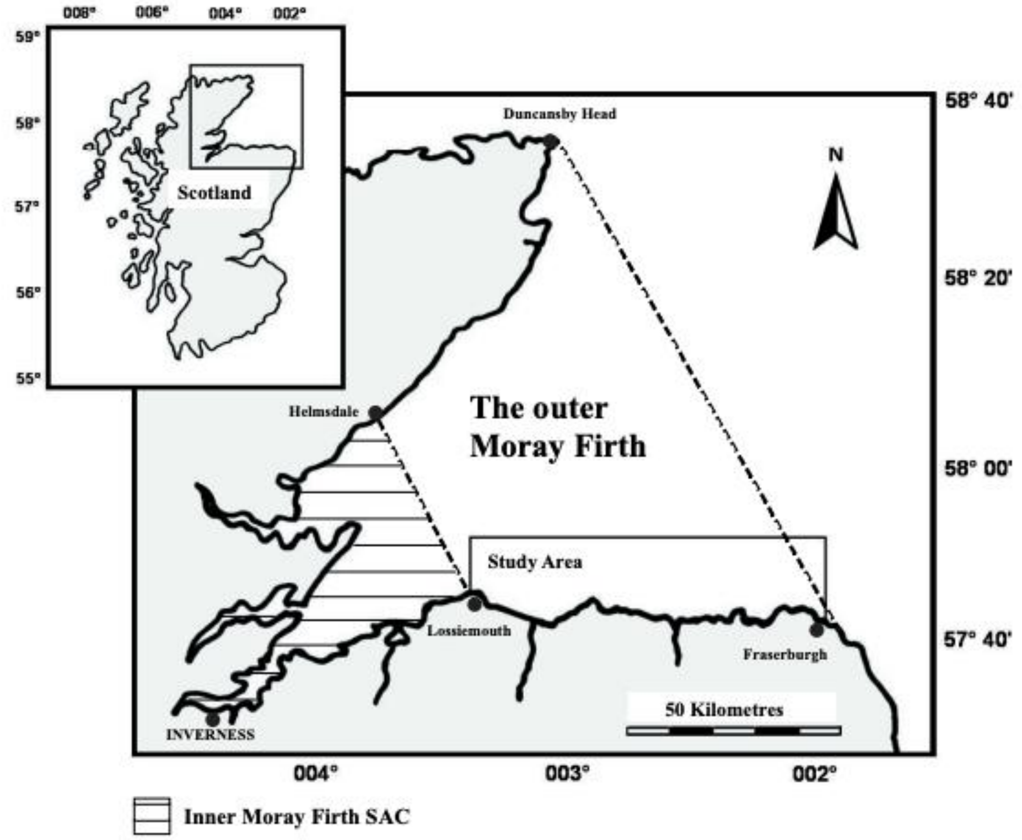

Figure 2.1 Map of Moray Firth, showing study area covering southern coastline from Lossiemouth to Fraserburgh (from, Robinson et al., 2007).

The data were provided for this study by the Banff-based Cetacean Rescue & Research Unit (CRRU), based out of Banff, with the surveys carried out using an 8 metre Humber ridged hulled inflatable boat (Figure 2.2), at a mean vessel speed of 15 to 20km per hour, at Beaufort Sea States ≤3, in visibility ≥1 km (after Robinson et al., 2009).

Figure 2.2 'Hermes', the CRRU's ridged inflatable survey boat used in the data collection provided for the present study. Photo credits: Kevin Robinson (CRRU).

During boat surveys, a crew of 2 experienced observers and a maximum 6 trainee researchers searched the ocean using a continuous scanning method (after Mann, 1999). Observers were positioned around the vessel to provide a 360° coverage of the search area during surveys. In addition to direct observations of the minke whales traveling or feeding/suspected feeding (Robinson et al., 2009) (see below for behaviour definitions), the presence of feeding birds in groups on the surface of the water (bird rafts) were used as visual cues for locating the whales (Robinson & Tetley, 2007). Once a sighting was made, the whale was approached stealthily until within range to commence a focal follow. At this point, the time, geographic location, age class of the sighted animal (juvenile/adult; see below for age class definitions) and its behaviour (feeding and travelling; see below for behaviour definitions) (see Appendix 1 for an example survey form) were recorded prior to establishing whether a follow was possible. Once a focal follow commenced the boat maintained a distance of 50 to 300 meters from the subject and sampling was conducted for up to 30 mins. To reduce the chance of losing a surfacing animal throughout a follow, the vessel kept moving in the same direction and at the same pace as the whale ahead. If the whale was lost, the crew would either restart the follow or dismissed the data. All observers were involved in maintaining a visual on the whales. One observer would measure the time between successive surfacings with a digital stopwatch. Another observer would use a hand-held compass to record the bearing and distance of the surfacing animal from the vessel as well as its direction of travel. A third observer would record all the relayed information above, including the significant data on the age of the tracked animals, its surfacing behaviour, and the presence or absence of birds. Only focal follows longer than 20 mins were used in the subsequent analysis due to minke whales being known to dive down for up to 20-25 minutes (Christiansen et al., 2015). The approach and configuration of observers used throughout the surveys reduced heterogeneity in detection probability between individual species and/or group sizes (Palka, 2005), also allowing for standardisation and comparability.

2.2 Age and behaviour classifications and definitions of minke whales.

Samples were separated into the two behavioural categories, as defined in Table 2.1.

Table 2.1 Definitions of behavioural states used during surveys.

Behaviour	Definition
Feeding/Suspected feeding	A typical 2 to 3 surfacing with 2 min dive observed. The animal sighted swimming in circles within an area with brief dives (suspected feeding) or direct feeding observed, by lunging activities seen by whales. Mouthparts would be observed opened and throat grooves descending in a sequence of surface strikes. These surface lunges are often associated with birds feeding.
Travelling	The animal moved in a straight line throughout the behavioural sample, with the direction remaining constant, with an atypical surface pattern, with 30 seconds to a 1 min surfacing's.

Samples were also categorised by age class by visual observations of size and other traits to classify if the subjects were adult or juvenile, as defined in Table 2.2.

Table 2.2 Definitions and classification of age class used during surveys.

Age Class	Definition
Juvenile	Animals less than 6.5 meters, lighter olive-colour, with triangular dorsal fin with fewer edge markings from external obstacles.
Adult	Animals greater than 6.5 meters, dark in colouration, with tall and rounded (falcate) dorsal fins which have numerous edge markings.

2.3 Manipulation and Analysis of Data

When studying minke whales, there are variations of approaches to measuring diving and ventilation patterns. Within this project, the ventilation parameters were produced based on a comprehensive literature research (Dorsey et al., 1989; Stockin et al., 2001; Christiansen et al., 2015; Dombroski et al., 2021) and thorough data organisation. Multiple factors were investigated within this study to avoid bias which could occur when investigating only one factor. The collected data set was inputted into an Excel spreadsheet. To ensure that representative results were obtained when analysing the respiration patterns, focal follows less than 20 minutes were removed. The data was transformed into seconds and subsequently categorised into groups (months, travelling/feeding & suspected feeding, adult/juvenile). To ensure bias was avoided between individuals and to minimise error, the mean of each of the ventilation parameters was determined for each individual whale. For each sample, the following ventilation parameters were examined (Table 2.3)

Table 2.3 Definition of calculated ventilation parameters used in the present study.

Ventilation Parameter	Definition
Dive sequence (Figure 2.3, (a))	The complete dive with short, clustered surfacings and one long, possible deep dive interval. From this, the various ventilation parameters were calculated.
Surface duration (Figure 2.3, (b))	The sequential breath (clustered blows) prior to long dive. This parameter was calculated as mean number of blows per minutes per individual prior to true dive, seen in Lagerquist et al., (2000) study of dive characteristics of satellite-monitored blue whales (*Balaenoptera musculus*).
Surfacing interval (Figure 2.3, (c))	The time between successive blows; calculated as mean of the time between blows before each true dive as seen in Bowles et al., (1994) research into relative abundance and behaviour of marine mammals.
Dive duration (Figure 2.3, (d))	A long dive that follows a series of sequential breaths also known as a true dive. Calculated from true dive longer than 60 seconds within the dive sequence, as seen in Lagerquist et al., (2000).

To ensure clarity when discussing the different terminology, the following diagram was produced to visually portray the various parameters (Figure 2.3).

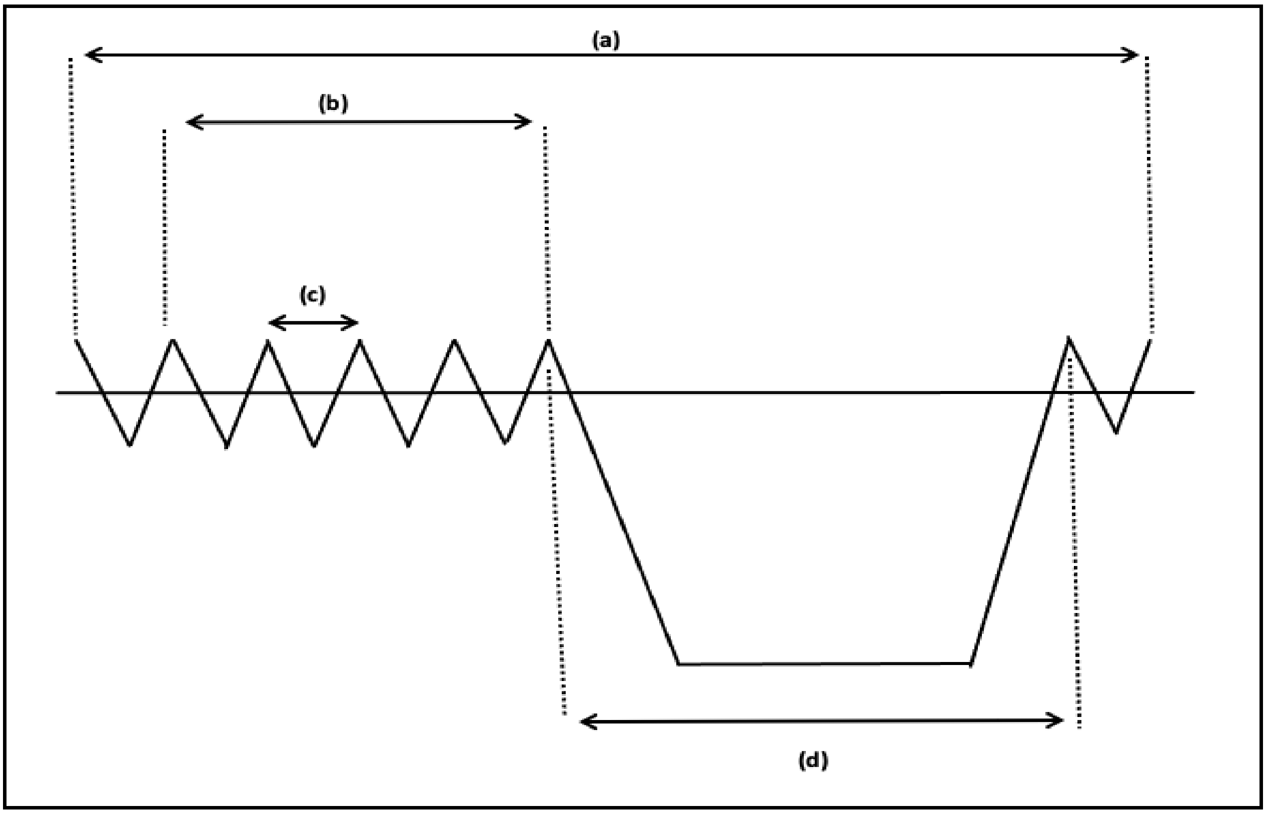

Figure 2.3 Graphic visualisation of the minke whales dive profile and varying respiration characteristics utilised.

After the manual calculation of the 3 chosen dive parameters (dive duration, surfacing interval and surface duration), data were subsequently analysed against each of the categories (behaviour, age class and month of year)

2.4 Statistical Analysis.

All data were analysed using R (R studio version 4.0.2) (R Core Team, 2020). The data sets were assessed for normality and then the data was plotted into frequency distribution graphs to allow visualisation of the ventilation parameters investigated.

2.4.1 Analysis of the differences between age class, behaviour, and time of year and the effects they have on the calculated ventilation parameters.

The aim was to explore the differences between the independent variables of month, behaviour (travelling/feeding) and age-class (adult/juvenile), and the dependent ventilation parameters. A General Linear Model was used and the parametric model of one-way analysis of variance (ANOVA) was utilised due to the large sample size. Initially, a three-way ANOVA was applied to see if an interaction occurred between the independent variables and the dependent variable. However, due to there being lack of replicate data points for each combination of age class/behaviour/month, a three-way ANOVA was unsuccessful, preventing the investigation into the interaction between the three variables. Therefore, a one-way ANOVA was used to test the dependent variables (dive duration, surface duration and surfacing interval) against each of the independent variables (age class, behaviour, and time of year), to explore if there was a significant difference between the mean values of the groups. The data was fitted into a linear model and the assumptions of homoscedasticity of the dependent variable was conducted using the Levene test, followed by the assumption of normality of the residuals. If the data did not fit the assumptions, a log transformation was utilised to conform the data to ensure the assumptions were met. The data was analysed separately for each dependent variable against each categorised independent variable, to aid in answering the specific study hypothesis. For further investigation into the differences between variables, age class and behaviour were grouped together (juvenile*travelling; juvenile*feeding/suspected feeding; adult*travelling; adult*feeding/suspected feeding) and each of the ventilation parameters was analysed against month using a one-way ANOVA. Results were then displayed for each ventilation parameter against behaviour, age class and month, as boxplots to allow the significant differences to be viewed.

2.4.2 Analysis of the relationships between ventilation parameters.

To aid the exploration into the relationships between the three calculated ventilation parameters, with the aim to establish a predictive relationship between the dependent variables, a single linear regression was performed i.e., dive duration was analysed against an independent i.e., surface duration and surfacing interval (also dependant), with the assumptions tested. This allowed a more in-depth examination of interconnections amongst the factors and the ability of one variable to predict a specific outcome i.e., how well the dependent variable (surface duration) was able to determine an independent variable (surfacing interval). The linear regression was presented as a scatter plot.

5. Results

3.1 Survey Efforts.

Between May and October 2006 to 2019, a total of 6,436 km of survey effort was conducted by the CRRU research team, from which 774 minke whales were recorded from 657 encounters. Feeding/suspected feeding individuals were recorded in 84% of the encounters, with the remaining 16% recorded as travelling whales. A total of 58 focal follows were conducted by the CRRU, of which 47 individual follows were selected for the following analysis.

3.2 Analysis of Variance

3.2.1 Dive Duration

From the 47 selected follows, 129 ventilation/surfacing intervals were extracted for analyses. The dive duration was calculated from the long dive that follows a series of sequential breaths, also known as a true dive. The mean dive duration for minke whales from the Moray Firth, was found to be 143.4 sec (standard deviation (SD) = 56.64, min/max: 68.9/ 291.4), with a median value of 124.9 sec (inter-quartile range (IQR) = 48.10). Age class was found to be non-significant (F = 0.799, df = 1,43, *p* = 0.376), from the one-way ANOVA as performed between itself and dive duration. Although a non-significant result, variations were observed in the dive durations of adult vs juvenile minke whales respectively. Adult minkes preformed the longest dive duration (mean = 142.7 seconds; SD = 56.42; median = 130.6 seconds; IQR = 89.87). The mean dive duration in juvenile minkes was significantly lower (mean = 137.4 seconds; SD = 51.25; median = 119.6 seconds; IQR = 48).

Behaviour.

The dive duration was further compared in feeding/suspected feeding verses travelling animals, from which the following results were discovered.

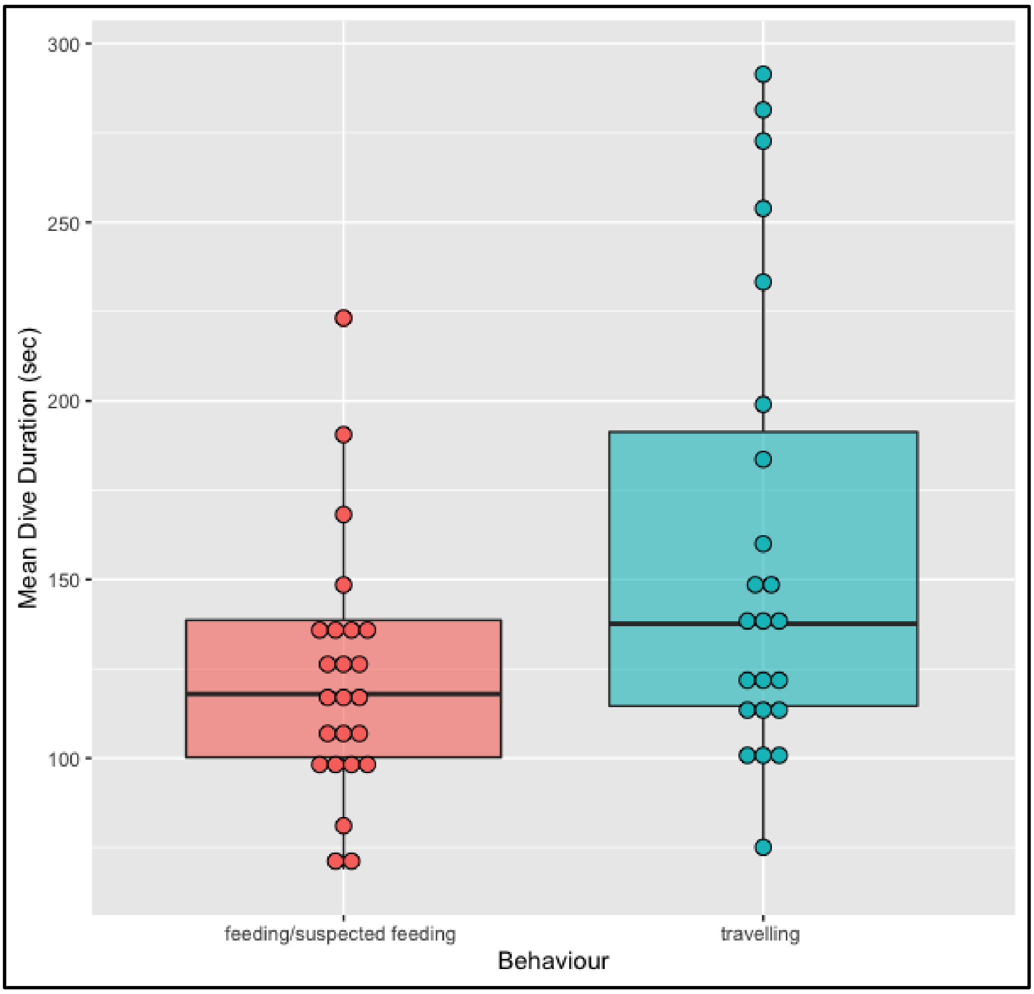

Figure 3.1 Box plot comparing mean dive duration in seconds against feeding/suspected feeding and travelling minke whales. Plot is presented with maximum (feeding/suspected feeding: 281.4 sec, travelling: 291.4 sec) and minimum values (feeding/suspected feeding: 81.1 sec, travelling: 68.9 sec). Plot includes the distribution of the data, upper and lower interquartile range (top and bottom horizontal line of boxplot) and median of data (represented as mid line in boxplot).

The dive duration was found to be significantly different between the two behaviours (one-way ANOVA, F = 6.788, df =1,42, *p* = 0.012; Figure 3.1). Therefore, minke whales dive duration is affected by the behaviour they are engaged in. The box plot demonstrates that travelling individuals (N=22), spend more time under the surface as they had a greater mean dive duration, (144.1 seconds.; SD= 59.37), in comparison to that of feeding/suspected feeding individuals (N=24) (136.2 seconds.; SD= 44.58).

Month.

Due to there being only one usable focal follow which was over 20 minutes in May, September and October, these follows were removed from the data analysis. The months of June (N=15), July (N=17), and August (N=11) were analysed against dive duration to determine whether a significantly different result would occur.

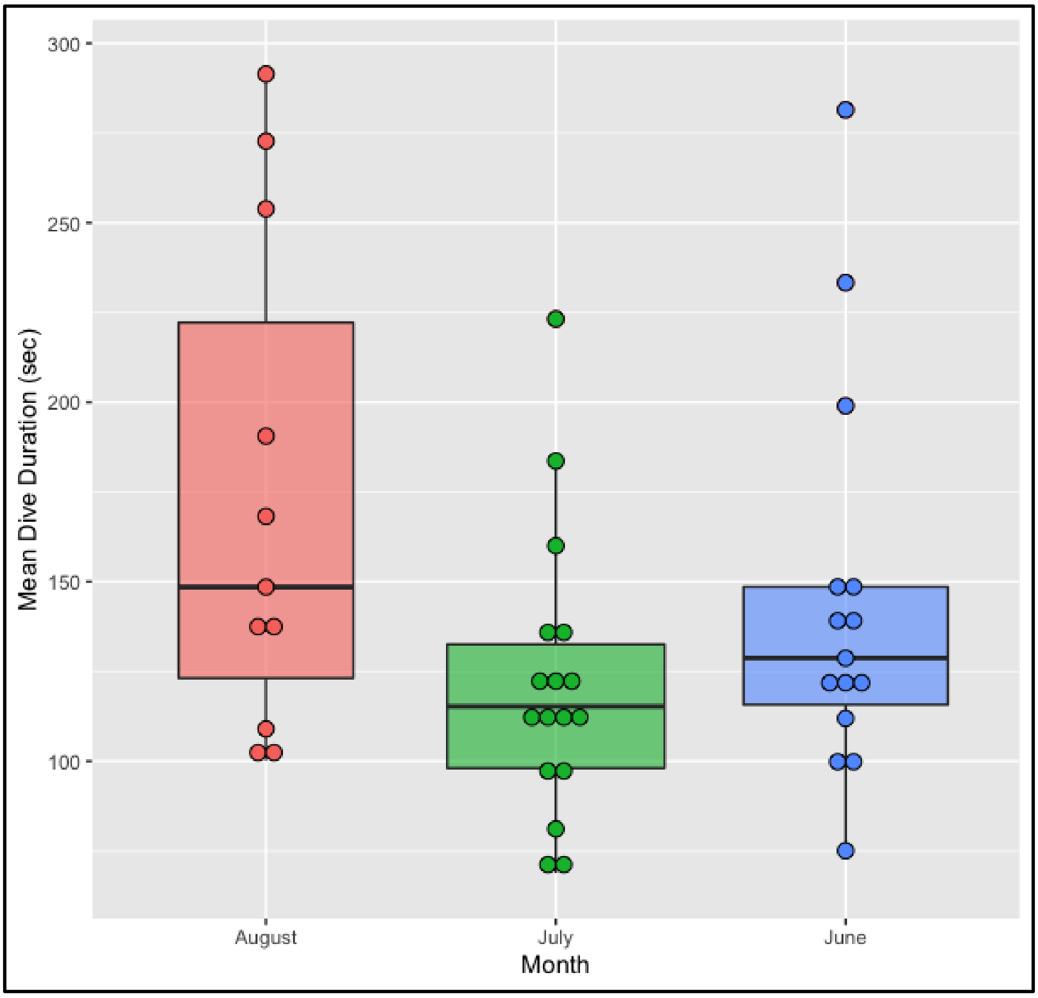

Figure 3.2 Box plot depicting the mean dive duration in seconds, visualised within a boxplot, across three months. Within the visualised data the maximum (August: 291.4 sec, July: 183.6 sec, June: 233.3 sec) and minimum (August: 104.6 sec, July: 68.9 sec, June: 73.5 sec) values are included, as well as the distribution of the data.

A statistically significant difference was discovered between the three months and dive duration in minke whales within the Moray Firth (one-way ANOVA, F = 3.1778, df =2,40, *p* = 0.052; Figure 3.2). Demonstrating that minke whales show variation in dive durations within different months. Due to there being more than two categories, a post hoc test was performed. The Tukey test found that the mean monthly values were significantly different between July and August (*p* = 0.042, 95% C.I. = -0.646, -0.0097). Within the month of

August, minke whales demonstrated the longest mean dive duration at 195.5 seconds (SD = 71.25). In contrast, the mean dive durations in July were the shortest at 120.3 seconds (SD = 26.86). To investigate this data further, the data were categorised into age class and behaviour (feeding juvenile, travelling juvenile, feeding adult and travelling adult) for subsequent analyses by month.

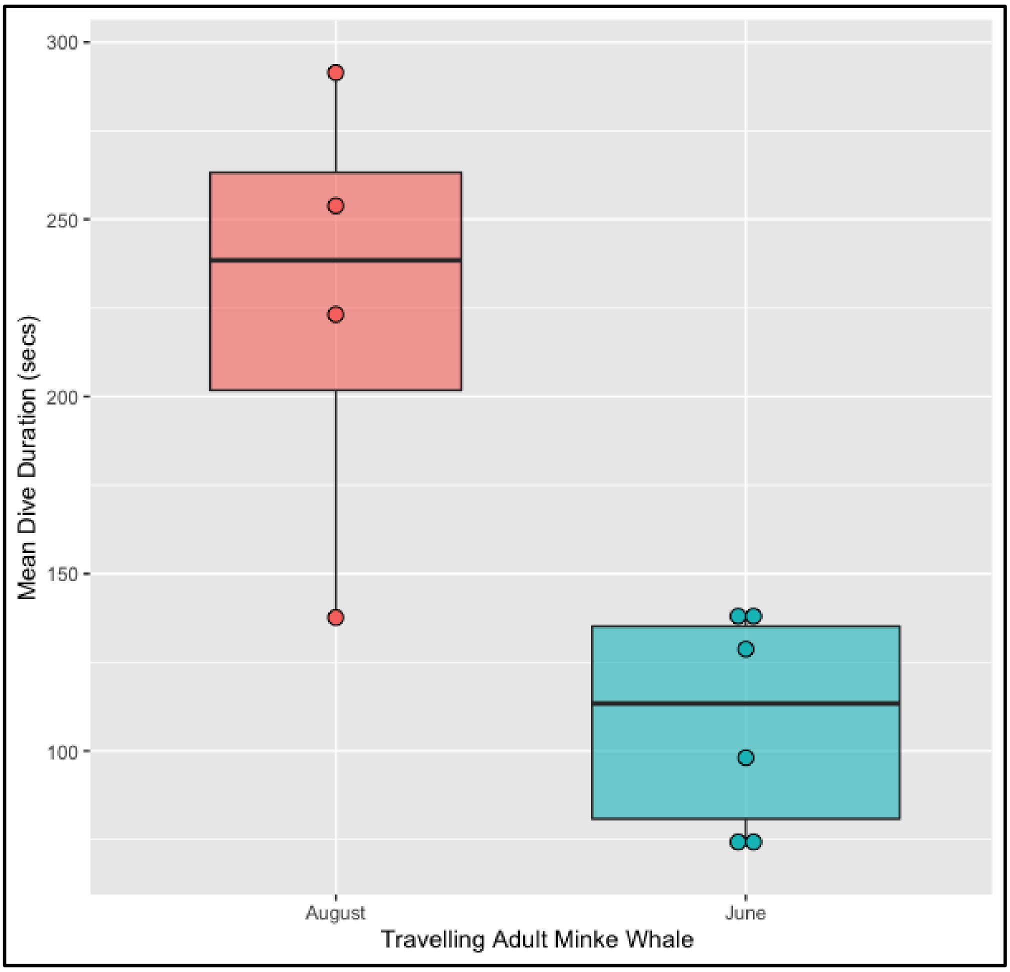

Figure 3.3 Box plot visualising surface duration of travelling adult minke whales within the months of August and June. Maximum (August: 291.4 sec, June: 138.75 sec) and minimum (August: 137.636 sec, June: 73.5 sec) values are presented within the plot alongside the distribution of the data.

Which showed a clear significant result in the dive duration of travelling adult whales (one-way ANOVA, F = 15.29, df =1,8, *p* = 0.0044; Figure 3.3). Travelling adult minke whales display changes in dive duration between August and June. The greatest mean dive duration in travelling adults minke whale was seen in August (N= 4) at 226 seconds (SD = 65.4), compared to adults travelling in June (N=6), the mean dive duration was 108.5 seconds (SD = 30.3). All other categories were non-significant (*p* = >0.05).

3.2.2 Surface duration

The mean surface duration was calculated as the mean number of surfaces per min per individual prior to the true dive. A mean value of 1.38 surfaces per minute (SD = 0.355) and median of 1.333 (IQR = 0.436) was determined for the species. Surface duration was tested against the three independent variables (behaviour/age-class/month). However, ‘month’ resulted in a non-significant outcome (one-way ANOVA, F = 0.731, df =2,40, p = 0.487), and was therefore not included in the following results.

Behaviour

A one-way ANOVA of the surfacing duration (number of surfaces per minute) between travelling (N = 24) verses feeding/suspected feeding (N = 23) was carried out. A non-significant result occurred (Kruskal-Wallis test, H = 3.133, df =1, p = 0.077; Figure 3.4). However, marginal difference were observed between the means. Feeding/suspected feeding individuals showed a higher mean surfacing interval at 1.430 surfaces per minute (SD = 0.302) compared to travelling individuals, with a mean of 1.208 surfaces per minute (SD =0.230).

Age Class

An analysis of surface duration between adult and juvenile minke whales was made.

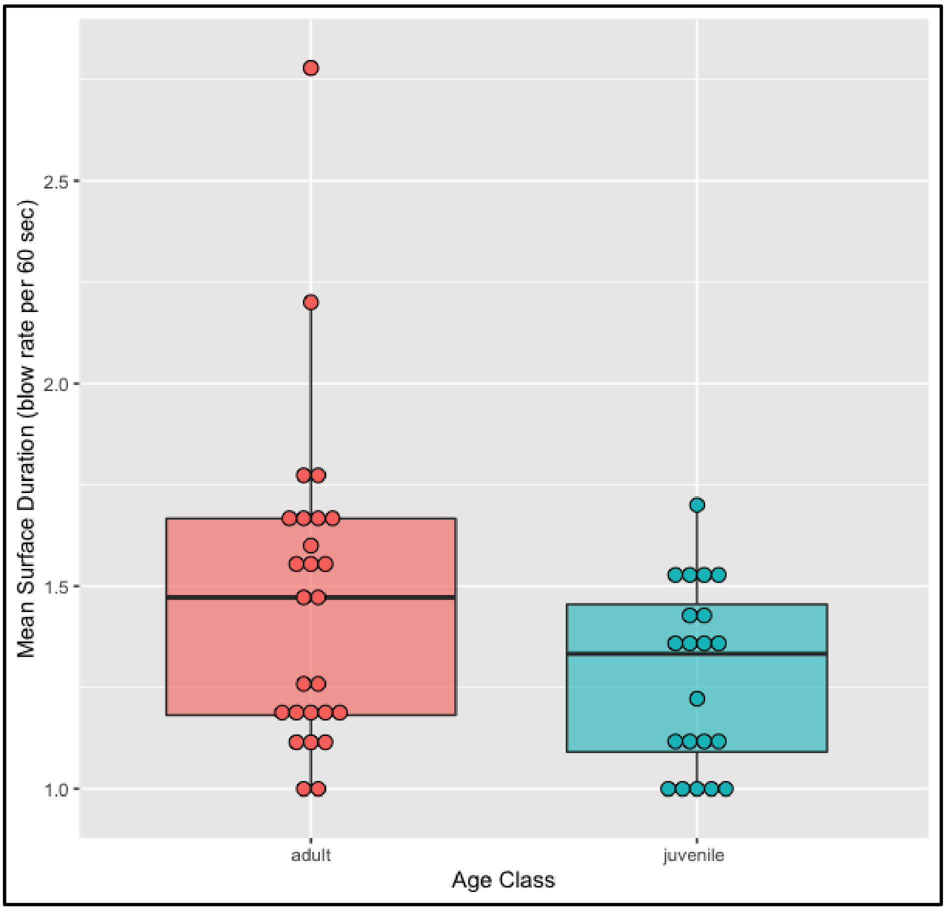

Figure 3.4 Box plot illustrating the significant difference in mean surfacing duration (blow rate /60 secs) between age classes. Plot also depicts maximum (adult: 2.200 blow/ 60 sec, juvenile: 1.700 blow/ 60 sec) and minimum (adult: 1.000 blow/ 60 sec, juvenile: 1.000 blow/ 60 sec) value, also includes data distribution.

The one - way ANOVA of surface duration between adult (N= 21) and juvenile (N= 26) whales showed a marginal significant difference between age-classes (one-way ANOVA, F =3.913, df =1,45, p = 0.054; Figure 3.4). The box plot displays that adult minke whale have a greater mean surface duration (1.359 blows/60 sec.; SD = 0.326) in comparison to juveniles (1.267 blows/60 sec.; SD = 0.233). Therefore, adult minke whale will perform more blows at the surface after a dive, in comparison to juveniles.

3.2.3 Surfacing Interval.

From the 41 minke whales sampled, a total mean surfacing interval of 30.13 seconds (SD = 6.934) and a median surfacing interval of 31.34 seconds (IQR = 10.508) was determined. The surfacing was tested for a significance. The mean surfacing interval was tested against each of the three categories, however the results for each of these tests came back as statistically non-significant; Behaviour = one-way ANOVA, F = 0.861, df =1,45, p = 0.358; Age class = one-way ANOVA, F = 0.955, df =1,45, p = 0.333; Month = one-way ANOVA, F = 1.04, df =2,40, p = 0.407.

3.3. Relationship between dependent variables.

To examine the relationship between the three dependent variables of dive duration, surface duration and surfacing interval, a simple linear regression was performed.

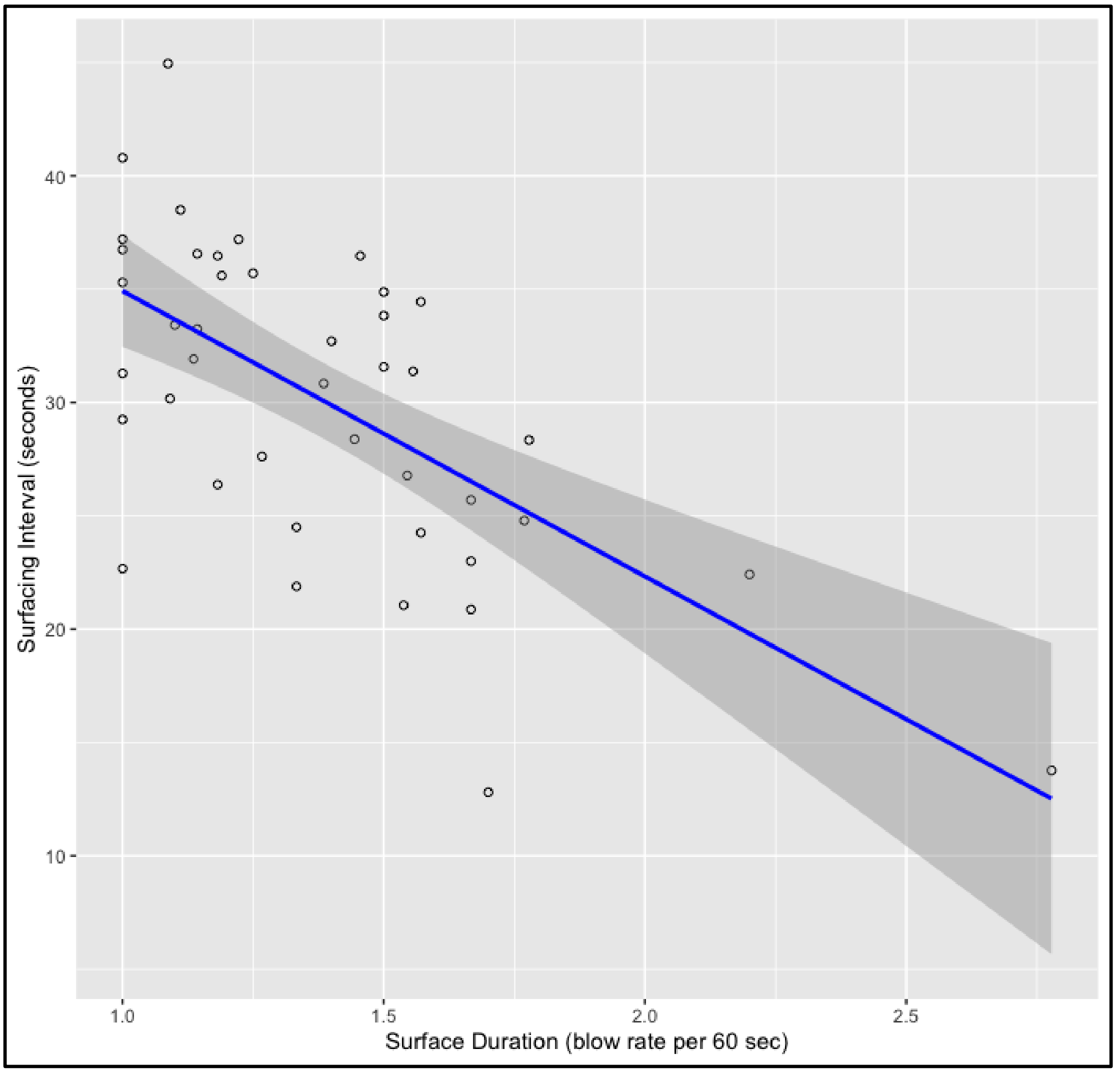

Figure 3.5 Scatter plot with a regression line and 95 % confidence interval visualising the relationship between surfacing interval and surface duration.

When testing surfacing interval vs dive duration (linear regression; $F = 1.521$, df = 1, 41, $p = 0.224$, adjusted $r^2 = 0.012$) and surface duration vs dive duration (linear regression; $F = 0.035$, df = 1, 41, $p = 0.851$, adjusted $r^2 = -0.023$), a non-significant relationship was discovered. The measured variables accounted for 40.3% of the variability in surfacing interval. However, a strong significant negative relationship between surfacing interval and surface duration was detected (linear regression; $F = 32.08$, df = 1, 45, $p = >0.001$, adjusted $r^2 = 0.403$; Figure 3.5). The adjusted r^2 value indicates that the surfacing interval will decrease by 12% for every incremental increase in the surface duration. Thus, as the surfacing interval of a whale decreases, the surface duration increases, demonstrating that whales will increase the number of breaths taken prior to a long dive. The regression equation of ($y = 47.6 + 12.94x$) was used to plot the graph.

6. Discussion

The aims of this study were to better understand the surfacing and ventilation rates of minke whales within the Moray Firth. Minke whales within the Moray Firth were found to show significant variability in their dive rates according to their age class, behaviour and the time of year, in particular in the length of their dives and surface durations. As hypothesised, an overall conclusion can be made from the ANOVA results: length of dive rates, particularly dive duration and surfacing duration, significantly differed according to the factors examined.

In the present findings, behaviour (i.e. feeding/suspected feeding versus traveling whales) was shown to be a significant predictor of dive duration. Traveling minkes were seen to show longer dive durations, spending a larger amount of time underwater compared to feeding individuals, as similar to findings by Stern (1992), Baumgartner (2008) and Christiansen et al. (2015). Christiansen et al. (2015), investigated the structure and dynamics of minke whale ventilation within the Gulf of St Lawrence, Canada. Examining how duration and surfacing patterns changed with different activity types over a 20-year period, and found that the whales will change their surfacing patterns, depending on the specific activity type they are engaged in. They found that feeding minkes showed considerable changes in their dive patterns when performing near-surface feeding versus depth feeding, increasing the number of sequential surface breaths with increasing dive duration. Traveling individuals likely spend longer periods at depth to minimise the cost of transport, since staying submerged reduces drag and energy expenditure (Christiansen et al., 2015). Conversely, feeding whales in the present study performed shorter dives due to the greater oxygen intake required when performing high energy lunges, at higher speeds and with rapid changes in direction. However, when feeding at depth, as opposed to surface feeding, longer dives were also recorded, indicating variations in prey entrapment manoeuvres (e.g. Robinson et al., 2022) and possibly even prey capture success. Alternative studies by Curnier (2005), Vacquié-Garcia et al. (2019), Fortuna et al. (2020) and Ogloff et al. (2021) also confirm these changes in ventilation rates when animals were engaged in different behaviours. Similar findings have also been reported for blue whales and humpback whales (Megaptera novaeangliae) respectively (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2008). The study by Christiansen et al. (2015) provides extremely useful data regarding the dive sequences within different behavioural patterns, however the research did not discuss the age ranges seen within the minkes studied and whether a difference would be found between dive sequences and behaviour between age ranges. This could have provided further information regarding minke whale dive sequences.

Dive durations were also found to be affected by the time of the year, as measured by ‘month’, in the present study. According to the optimal foraging hypothesis by Krebs and Davies (1997), organisms will choose prey in such a way that an individual’s or species’ fitness is maximised. As in other species of baleen whale, minke whales are opportunistic feeders that alter their foraging behaviour according to the seasonal availability and/or abundance of prey (Robinson & Tetley, 2007; Robinson et al., 2021). The respiratory behaviour of these whales is therefore likely to shift respective to the relative availability and distribution of targeted prey species. The longest dive durations were recorded during August in the present investigation and the shortest in July. Stockin et al. (2001) conducted a short-term study of minke whales on the west coast of Scotland and remarkably described the very same patterns observed herein. In July, minke whales primarily target sandeels in the Moray Firth (e.g. Robinson & Tetley, 2007). With increasing water temperatures, the sandeels move into the water column during the early summer (Winslade, 1974), and are driven to the surface by predatory fish, making them more easily accessible to the whales (Robinson & Tetley, 2007). Later in the year, however, herring and sprat are thought to be more widely available (Robinson et al., 2022). Sprat show a less complex schooling behaviour and weaker predator-avoidance than herring (Maraveliasl et al., 2000) and minkes have been seen targeting sprat from August onwards (Robinson et al., 2022). Since the species is a shoaling, mid-water fish, living in deep, shelf areas (Daewel et al., 2008), whales targeting this prey may need to perform longer, deeper dives, which would certainly explain the greater number of longer dives observed in the study later in the year.

Investigation into prey switching, could aid in the management of fisheries, to prevent the deaths which occur due to entanglement. Pathological evidence consistent with entanglement in shellfish creels has been documented in as many as 50% of stranded minke whales in Scottish waters (Northridge *et al*., 2010). Minkes show a strong association with sediment type (e.g. Macleod et al., 2004b; Robinson et al. 2009), and juveniles may typically occur in shallower waters than adults (Robinson et al., 2022), where higher numbers of creel pots are found, thereby inflating the likelihood of entanglement (Leaper et al., in press). Mitigation suggestions advise the exclusion of static fishing gears, including creels, between May and October when minke whales are most abundant (Donnan, 2019). A further strategy suggested is the use of line with a maximum breaking strength of 273 kg to allow the whales to break free from entangled ground lines (Northridge et al., 2010). Encouragingly, however, Scottish creel fishermen have shown willingness to engage in entanglement mitigation

(MacLennan et al., 2020) and have suggested measures such as the introduction of sinking lines, which should be pursued with some urgency.

Dive duration was also found to vary within travelling adult minke whales between June and August. This may be explained due to changes in the distributions of prey during the later summer months when the whales may already be well-fed, implying they spend more time resting than foraging, hence the longer dive durations observed. This data clearly shows changes in dive duration throughout the year, and as commercial whaling quotas are essentially derived from population estimations from line-transect surveys conducted in July, from which cue counts are adjusted using a standardised dive time of 2 minutes, these quotas may be erroneous due to evident overestimations (Stockin et al., 2001). Accordingly, population estimates should give consideration to the changes in diving behaviour as noted above, to ensure they are indeed accurate. A clear difference was found in the dive durations recorded in June, July and August respectively, in the present study. However, these only represent half of the months surveyed, since not enough focal follows were collected during May, September and October, largely due to more inclement sea states in the study area at these times of year. Therefore, further investigation into dive duration of minke whales in the later summer months could provide additional knowledge of the monthly variation found within their diving ecology.

Minke whales, as well as other marine animals, are further recognised to show different ventilation/surfacing rates according to their size, as demonstrated by Schreer & Kovacs (1997). As the size of minke whales differs with age, the age-class (adults versus juveniles) of animals in this study was considered when examining their respiratory rates. Schreer & Kovacs (1997) study into the diving capabilities of mammals showed that as body size increased, so did the anaerobic dive limit (ADL)—defined as the length of time an animal can stay submerged before having to rely on anaerobic metabolism (Kooyman et al., 1983). The ability to stay below the surface is determined by not only method of which oxygen is consumed (metabolic rate), but also by the muscles' capacity to store oxygen. Thus, greater body/muscle mass allows for increased oxygen storage, and hence a greater aerobic dive limit (Kooyman & Ponganis, 1998). Schreer & Kovacs (1997) also discovered a clear link between ultimate deep dive duration and body size in baleen whales. Consequently, the increased dive times seen in adult animals due to their larger body mass have cause for longer surface recovery times compared to smaller sized juveniles. When analysing the surface duration of adult versus juvenile minkes, a significant difference was indeed found between these two age classes. Adult minkes spent a greater time at the surface compared to juveniles. This may be due to the adult whales having to spend a longer surface period recovering from the oxygen debt incurred during their deeper/longer dive cycles (e.g. Acevedo-Gutiérrez et al., 2002).

The second hypothesis investigating the relationship between the study factors of dive duration, surface interval and surfacing duration showed a non-significant relationship when dive duration was tested against surface interval and surface duration. However, a significant negative relationship was found between surface interval and surface duration, such that as the surfacing interval (time between blows before a true dive is performed) decreased, the surface duration (the sequential breath taken at surface) increased. This likely represents an increase in the number of breaths taken at the surface whilst recovering from a long/deep dive. However, an increased breath rate could also indicate an animal is preparing for a long dive. To better understand this, Christiansen et al. (2015) investigated this very question in the Gulf of St Lawrence, Canada, and found that the association between dive duration and the number of subsequent breaths (i.e., short dives) displayed that minke whales were recovering from, instead of planning for, a long dive. A similar conclusion has also been reached by Goldbogen et al. (2008) when investigating humpback whales (*Megaptera novaengliae*). Hence, the relationship between surface duration and surfacing interval is thought to serve as an indicator of gaseous exchange and long-dive recovery (e.g. Baird et al., 2006). Further investigation into the surfacing rates of these whales, especially small, isolated populations can aid in the implementation of mitigation strategies to reduce the number of ship strikes (McWhinnie et al., 2018). Mitigation strategies in place, such as up to date whale activity, speed restrictions and narrowing of shipping lanes have all been successfully utilised in other geographic locations to prevent ship strikes or reduce the likelihood of whale mortality should a ship hit occur (Lagueux et al., 2011).

Although the influence of anthropogenic effects was not investigated in the present study, changes in respiratory rates have been further documented due to the presence of whale watching vessels. A study by Sprogis et al. (2020), in the Exmouth Gulf off Western Australia, investigated the effects of vessel noise levels upon female humpback whales and the behavioural responses of mothers and calves. Resting times were seen to decrease by 30% and respiratory rates were doubled when vessel noise was played nearby. This shows that the energy attained for nursing, fending off males/predators and returning back to polar foraging grounds, is necessarily lowered as a result of noise-induced disturbance (Braithwaite et al., 2015). Similar findings were observed causing Mediterranean fin whales to change their surfacing intervals and dive times (Jahoda et al., 2003). Indeed, a plethora of studies and debates have been conducted on commercial whale watching vessels, as well as other anthropogenic disruptions (e.g. Santos-Carvallo et al., 2021 & Currie et al., 2021), with similar results. Further investigation into the effects of whale watching vessels upon minke whales in the Moray Firth could help understand the effect that boat operators might have on the behaviour of these whales to aid in adaptive management process within the recently designated Southern Trench MPA.

7. Conclusion

The findings of this study add to the relatively limited information available on UK minke whales, particularly within the Moray Firth. These coastal whales show variation in diving patterns, according to their behaviours, age class/size and the time of year, which may be influenced by biotic/abiotic and anthropogenic factors. To better understand the respiratory behaviour of this, and other species, investigations need to be standardised, in terms of methodology and terminology, to ensure quality and replicability is accomplished.

The International Whaling Commission Scientific Committee currently advises that more data on the dive profiles of minke whales should be collected to elucidate potential dissimilarity due to area, behaviour, and diurnal patterns. Such knowledge is understood to be crucial for studies on the breathing and foraging ecology of these small balaenopterids, and key for the calibration of cue counts and sighting probabilities used to estimate species abundances (Pike et al., 2008). Indeed, the current lack of data suggests that latest population estimates, from which whaling quotas are derived, are erroneous for the species.

For studies on ventilation rates and diving ecology, it is crucial to understand the surfacing patterns and behaviour of these aquatic, air-breathing mammals, as this can aid in the design and improvement of survey techniques and the quality of collated datasets. The present findings add to our existing knowledge of the behaviour and ecology of these coastally - occurring mysticetes. The protection and recognition of critical habitat is known to be notoriously challenging in marine environments, thus, there is a strong need to incorporate behavioural and demographic data into spatial models to inform management objectives for these whales in our coastal UK waters.

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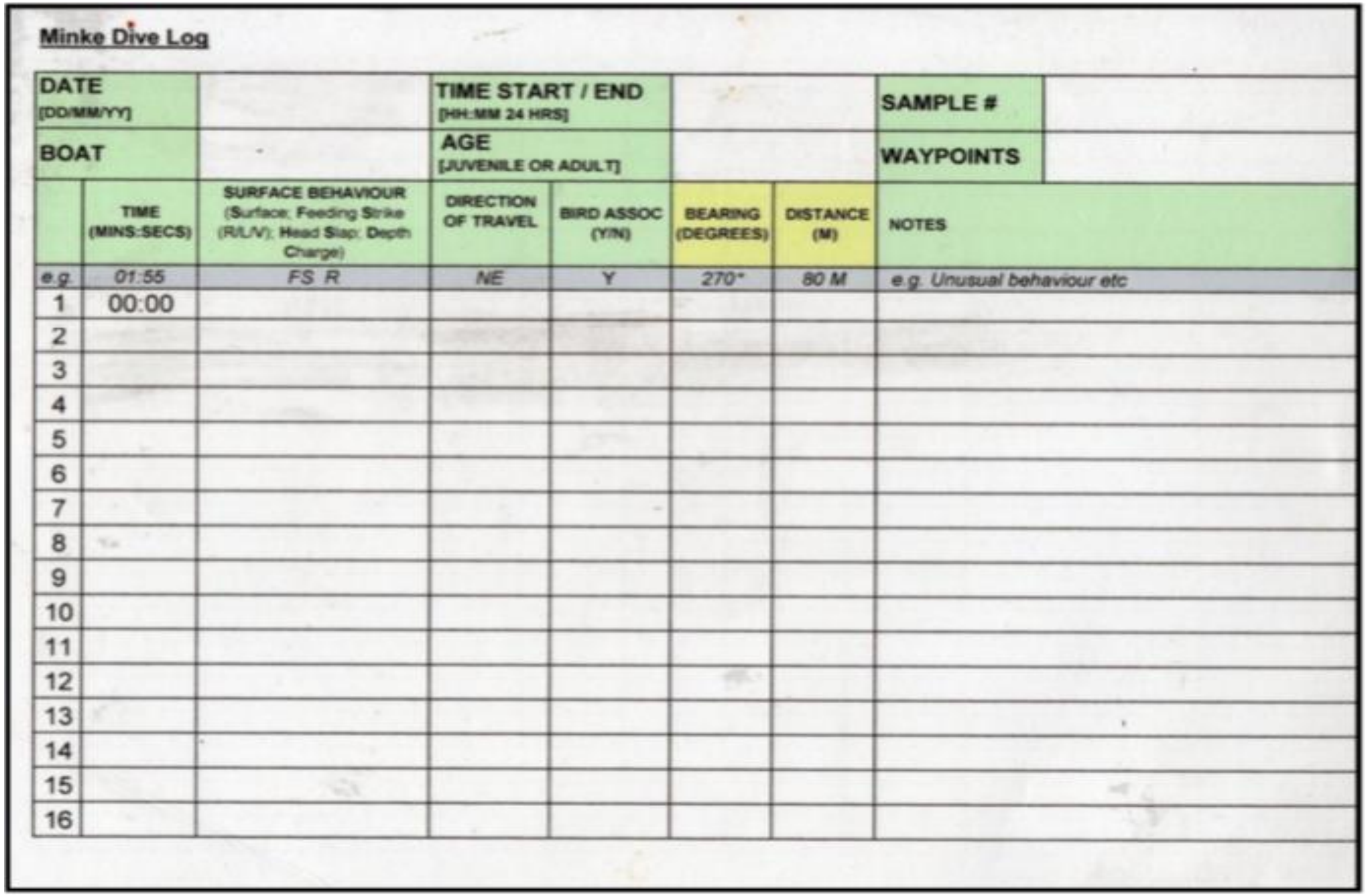
9. Appendices

Appendix 1

Survey form utilised to record focal follows of individual minke whales.



Minke Dive Log

DATE [DD/MM/YY]		TIME START / END [HH:MM 24 HRS]		SAMPLE #	
BOAT		AGE [JUVENILE OR ADULT]		WAYPOINTS	

	TIME (MINS:SECS)	SURFACE BEHAVIOUR (Surface; Feeding Strike (R/L/V); Head Slap; Depth Charge)	DIRECTION OF TRAVEL	BIRD ASSOC (Y/N)	BEARING (DEGREES)	DISTANCE (M)	NOTES
e.g.	*01:55*	*FS R*	*NE*	*Y*	*270°*	*80 M*	*e.g. Unusual behaviour etc*
1	00:00						
2							
3							
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