Edinburgh Napier
UNIVERSITY

SCHOOL OF LIFE, SPORT AND SOCIAL SCIENCES

ENV10100 Project Thesis

Honours

Project Title	**INTERACTIVE EFFECTS OF FACTORS INFLUENCING THE DIVING TIMES OF MINKE WHALES (BALAENOPTERA ACUTOROSTRATA) IN THE OUTER MORAY FIRTH, NORTHEAST SCOTLAND**
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Course	**ANIMAL BIOLOGY**
Year	**2010/2011**

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Acknowledgments

I would first thank my supervisor Dr. Alison Craig for her sound advice and guidance during the execution of this project and for providing expert knowledge to it.

Secondly, I would like to thank Dr. Kevin Robinson, director of the Cetacean Research and Rescue Unit, to share not only the data used for this project (without these my project could not been carried out), but also his enthusiasm, and passion for these animals. His dedication for the understanding and conservation of cetaceans and other animals has been my inspiration since I first put my foot in Gardenstown.

Lastly, I want to thank my mother Clara and my brother Pablo for without their endless support at all levels this project could have not been possible. Thanks for helping me fulfil my dreams.

List of Abbreviations:

cm	Centimetre
CRRU	Cetacean Research and Rescue Unit
d.f	Degrees of Freedom
e.g.	For example
GPS	Global Position System
ICW	International Whaling Commission
IQR	Interquartile Range
km	Kilometre
m	Meter
SAC	Special Area of Conservation
SD	Standard Deviation
sec	Seconds
SONAR	SOund Navigation And Ranging
SPWPH	Surfacing Per Whale Per Hour
UK	United Kingdom

Abstract

Minke whale (*Balaenoptera acutorostrata*) dive sequences were recorded between the months of May and October from 2006 and 2010 in the coastal waters of the outer southern Moray Firth, NE Scotland. A total of 31 focal follows of more than 20 minutes were extracted from these boat surveys. Data were categorised into groups: behaviour of the whale during the encounter, month in which the whale was recorded and age class of the animal. For all the groups, the frequency of the surfacing intervals (time between successive blows) was found to be positive skewed to short diving times. The relatively high interquartile ranges showed the large variability found in their surfacing intervals. A 3-way interaction between the three studied independent factors, i.e. behaviour, month and age class was determined using a General Linear Model (multiway ANOVA) test. This finding provides evidence that biotic and abiotic factors modify the surfacing intervals of minke whales, not only when acting singly but also when in combination. Consequently, the results of this study have a significant importance on the design of future researches, where the interaction effects of multiple factors should be considered.

1 Introduction

1.1. Taxonomy, morphology and distribution of minke whale

Minke whales (*Balaenoptera acutorostrata* Lacépède, 1804) are members of the family Balaenopteridae, also called rorquals. This family is a very diverse group of cetaceans composed of eight species including the blue whale (*Balaenoptera musculus*) and the humpback whale (*Megaptera novaeangliae*). The Balaenopteridae belong to the larger sub order Mysticeti or baleen whales. Instead of teeth, as in odontocetes, mysticetes possess a distinctive feeding structure composed of plates of baleen, a keratin-based structure. These plates hang from the upper jaw creating a sieve-like apparatus for effectively trapping prey when feeding.

Until just recently, only one species of *B. acutorostrata* was recognised. Since 2000, however, the International Whaling Commission (IWC) has acknowledged a separate species in Antarctic waters, *B. bonaerensis*. From the North Pacific population, a further subspecies has been described, *B.a. scammoni*. There may be even a third species, in the southern hemisphere a pygmy form of "dwarf minke whale", *B.a.spp*.) (Perrin and Brownell, 2008).

The minke whale is the smallest and most abundant member of the rorqual whale family (Perrin and Brownell, 2008). As with all baleen whales, they present a sexual dimorphism, where females are larger than males (see Appendix 1 for morphology and life history details; Hoelzel and Stern, 2000). The species has a slender, fusiform body shape and two slim pectoral fins, on which a white pigmentation patch is typically present in most subspecies (Figure 1.1). The dorsal fin is located two thirds of the way back along the dorsal surface and it is approximately 30 cm long. The dorsal fin can be a variety of shapes, colorations and other characteristic markings that along with the white pigmentation found in the pectoral fins may assist in the identification of individual whales (Dorsey, 1983; Dorsey *et al*., 1990; Joyce and Dorsey, 1990, as seen in Baumgartner, 2008; Gill, 1994; Baumgartner, 2008). The minke whale also possesses a very narrow pointed rostrum with a single prominent ridge. The scientific name *acutorostrata* describes this characteristic head-shape of the species as it is literally translated from Latin as "sharp rostrum".

Figure 1.1. Surfacing minke whale at the outer Moray Firth. Note the white pigmentation on the pectoral fin, present in the North hemisphere species (Photo credit, Mike Tetley/CRRU).

Minke whales have approximately 50 to 70 throat grooves, characteristic features of the baleen whales. These grooves extend from under the lower jaw to just behind the pectoral fins to the navel; by greatly expanding, they allow these whales to engulf a large volume of water and prey. Minke whales possess approximately 230 to 360 baleen plates (Christensen *et al*., 1990). These plates, composed of keratin-filled cells, grow continuously, replacing the eroded ones (Pivorunas, 1979; Berta *et al*., 2006). With a length of approximately 25 cm and a width of 12 cm, minke whales possess the smallest plates compared with the other rorqual species (e.g. blue whales: 91 cm length). The colour of the baleen also differs between species, being creamy-white in the North Hemisphere species and gray-black in the posterior side of the plates in the Antarctic species (Christensen *et al*., 1990).

Widely distributed, the North Atlantic minke whale is the most abundant of the baleen whales in European waters and a significant component of the marine ecosystem (Perrin and Brownell, 2008; Robinson *et al*., 2009). Found in all the oceans of the world (Figure 1.2 for distribution map), the species is considered to frequent coastal habitat or iced edges areas more often than pelagic zones (Kasamatsu *et al*., 2002). In British waters these whales are generally sighted in coastal and inshore regions less than 200m. deep (Northbridge *et al*., 1995; Macleod *et al*., 2004; Weir *et al*., 2007; Robinson *et al*., 2009). This is especially true along the summer feeding grounds, such as the Hebridean Islands on the west coast of Scotland and the study area, the Moray Firth (Gill *et al*., 2000; Stockin *et al*., 2001; Robinson *et al*., 2009). The winter breeding range is poorly documented, but seasonal migrations may occur between the feeding and breeding grounds. In the North East Atlantic, some individuals are thought to reside in the same area year-round, however (Macleod *et al*., 2004).

For the remainder of this report, all of the biological characteristics described hereafter will be for the common North Atlantic species *Balaenoptera acutorostrata.*

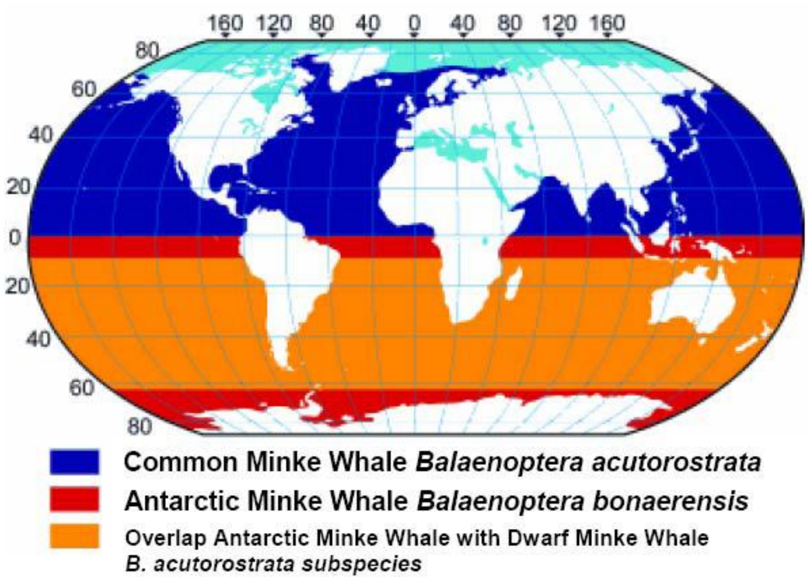

Figure 1.2. Distribution map of the study species, common minke whale *Balaenoptera acutorostrata*, the Antarctic minke whale *Balaenoptera bonaerensis* and the dwarf minke whale (unnamed *B. acutorostrata* subspecies). (Reproduced with permission from the American Cetacean Society).

1.2. Feeding behaviour of minke whales

Baleen whales are obligate batch feeders, meaning that they consume a large number of prey in a single event. Minke whales in particular are engulfers, swallowing prey concentrated in shoals deep in the water column (Hoelzel *et al*., 1989). Near the surface they can be seen lunge feeding on prey chased and herded from below, or feeding on prey congregated by piscivorous fish from below and sea birds from above, known as bird-associated feeding (Hoelzel *et al*., 1989; Gill *et al*., 2000; Robinson and Tetley, 2007). They filter the water back through the baleen plates, retaining the prey items. In the North Atlantic the diet of minke whales is composed by a range of demersal and pelagic fish such as sandeels (*Ammodytes* spp.), cod (*Gadus morhua*) mackerel (*Scomber scombrus*), haddock (*Melanogrammus aeglefinus*), sprat (*Sprattus sprattus*) capelin (*Mallotus villosus*) and whiting (*Merlangius merlangus*) (Haug *et al*., 1997; Macleod *et al*., 2004; Pierce *et al*., 2004; Perrin and Brownel, 2008). On the contrary, Antartic minke whales (*B. bonaerensis*) are stenophagous (feeding in a single type or limited variety of species), with a diet composed mainly by euphasiids (krill) (Kawamura, 1980; Ichii and Kato, 1991; Perrin and Brownel, 2008).

The anatomical features of the minke whale are adapted to this strategy: the short and coarse baleen, the disarticulation of the lower jaw from the upper jaw and the extraordinary expansion of the throat grooves, are all adaptations allowing these whales to engulf a large volume of water and prey items (Berta and Sumich, 1999) (Figure 1.3.).

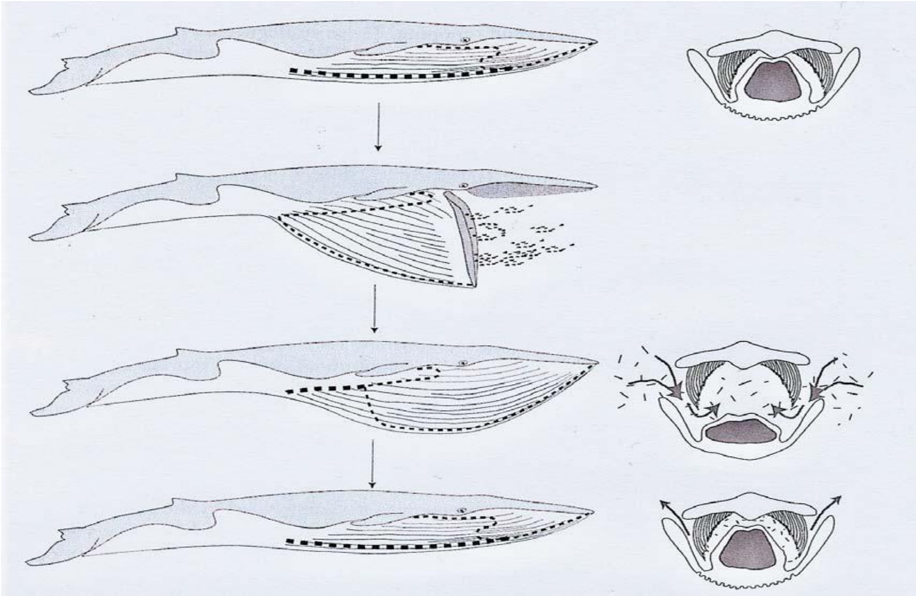

Figure 1.3. Lateral and cross sectional views of batch feeding of a baleen whale. Reproduced from Berta and Sumich (1999).

As well as variation between prey species, minke whales have been reported to adopt a variety of feeding strategies. These differences in feeding techniques are found in populations of the same or contiguous areas (Hoelzel *et al*., 1989). Other cetaceans, such as humpback whales have been also reported to specialise individually on particular foraging styles (Weinrich *et al*., 1985 as seen in Hoelzel *et al*., 1989). These intraspecific differences found in this and other species of animals might be forced by selective pressures such as prey availability, or experience of the animal. In the outer Moray Firth, an important summer feeding for minke whales and other marine animals, the main strategy shown by these cetaceans is the bird associated technique (explained above) with 76% of foraging cases observed between 2000-2005 adopting this strategy (Robinson and Tetley, 2007).

1.3. Diving behaviour of minke whales

Aquatic mammals and birds have evolved a number of physiological, morphological and behavioural adaptations that permit them to extend the time underwater, where to forage, reproduce or avoid predators. Larger blood volume (i.e. increased oxygen storage), decreased metabolic rate (i.e. decreased oxygen consumption) and formation of lactic acid in the muscles (i.e. anaerobic processes) are physiological modifications that cetaceans possess to live underwater. (Schmidt-Nielsen, 1997). In order to satisfy these physiological requirements, animals have to respond behaviourally. In general marine mammals exhale and inhale rapidly during surfacings, and make relatively short surface intervals (time spent in the surface between dives) after a long dive. These clusters of short dives of are thought to maximize the time spent submerged (Kramer, 1988). The typical dive sequence of minke whales is 5 to 8 blows (i.e. exhalation) at intervals of less than 1 minute, followed by a long dive of between 3 to 8 minutes. (Carwardine, 2000).

However, diving-surfacing patterns in these and other rorquals may evidently vary with different factors. For example, Dolphin (1987a; 1987b) investigated the respiratory and dive patterns of foraging humpback whales (*Megaptera novaeangliae*) in their feeding grounds of Alaska. He found that their dive duration, surface times and surface rates were correlated with the depth at which they foraged. Most of the dives of humpback whales in Alaska were of short duration (less than 3 minutes) and shallow (less than 60 metres). Dolphin suggested that these types of short and shallow dives would represent the aerobic dive limit (ADL), defined as "the longest dive that does not lead to an increase in blood lactate concentration", causing a degree of fatigue in the animal and requiring longer surfacing rates and periods. (Kooyman, 1985). Furthermore, Jahoda *et al*., (2003) compared the respiration activity of disturbed and undisturbed fin whales (*Balaenoptera physalus*) in the Mediterranean Sea. Foraging fin whales reacted to disturbance by changing their behaviour to travelling, spending less time at the surface. Commercial whale watching and other anthropogenic disturbances have subsequently been the focus of many studies and debates (e.g. Robinson *et al*., 2007a; Eisfeld *et al*., 2010). Humpback whales studied in Hervey Bay, Queensland, altered both their surfacing intervals and dive time when vessels were present (Corkeron, 1995); similar changes in respiratory patterns were shown in bowhead whales (*Balaena mysticetus*) feeding in the Canadian Beaufort Sea where drilling and dredging noise occurred (Richardson *et al*., 1990). Consequently, these findings may have direct implications when studying the diving behaviour and abundance of species (based on cue-count surveys, for example) as they demonstrate that ventilation rates and time spent at the surface by these animals may change according to vessel presence. Stockin *et al*. (2001) found that surfacing intervals of minke whales in the North-West coast of Scotland were affected by both time of year and time of day. They found significant differences between the lengths of surfacing intervals, being shortest at between 12:00 and 13:00 and during May and August. These findings were concluded to be directly relevant in the design of surveys used in abundance estimates for the species. The different behaviourial states of minke whales have also been shown to affect their respiratory patterns. Lynas and Sylvestre (1988) examined the ventilation rates (surface intervals, diving duration, number of dives and surface duration; see Figure 2.5 for illustration of the different terms) in travelling, foraging and feeding minke whales in St. Lawrence, Canada, and found significant differences between these behaviours. A further examination by Curnier (2005) subsequently classified these behaviours as near surface feeding, deep feeding and travelling and showed that respiratory patterns (surfacing intervals and dive duration in his study) were highly variable depending upon these behaviours. In her MSc thesis, Baumgartner (2008) also studied the breathing intervals of minke whales in the Moray Firth in northeast Scotland and found similar significant differences in dive duration with varying behaviour states. However, the study by Lynas and Sylvestre (1988) remains the only published study to assess the differences in ventilation characteristics over a range of behaviour types in these whales.

The sparseness of studies on North Atlantic minke whales is concerning at this time, as current estimations of the species abundance, for example Schweder *et al*. (1997) for Norwegian whaling operations are thought to be erroneous at this time. The estimates for 1989 and 1995 were resolved from surveys in the North-East Atlantic performed exclusively during the month of July. However, Stockin *et al*. (2001) demonstrated that the surfacing intervals in the species were shorter during this month, and therefore estimates based solely on this month may be over-estimated with concerns for the annual quotas for whaling from which these values were derived.

These are just some examples of the ecological and behavioural factors that may affect the ventilation patterns of whales. Other aspects associated with the methodology and research techniques employed during surveys may also have an effect when analysing the diving times of the animals. Furthermore, all these elements can interact between them. Statistical artifacs might emerge when all these factors and their possible interactions are not considered. As a result, the findings would not reflect the actual biology of minke whales and other marine mammals.

1.4. The outer Moray Firth

The Moray Firth, in the North East coast of Scotland, represents the largest firth or embayment on the Scottish coastline. Measuring some 5,230 km^2 (Wilson *et al*., 1997), it is divided into the Inner Moray Firth, a designated Special Area of Conservation (SAC), and the Outer Moray Firth. The study area along the southern outer Moray Firth from which the dataset used in this study was collected, measures approximately 1,200 km^2 and lies between the coastal ports of Lossiemouth and Fraserburgh (Figure 1.4).

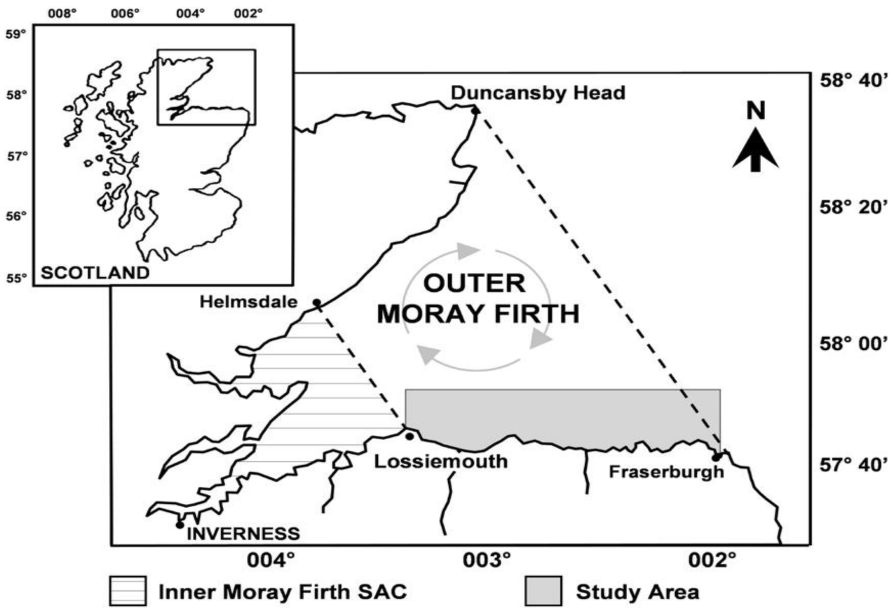

Figure 1.4. Map of the Moray Firth in northeast Scotland, showing the position of the study area adjacent to the SAC from where the present dataset used in this study was collected. The clockwise arrows indicate the direction of the Dooley current (reproduced from Robinson *et al*., 2009).

With a combination of coastal and oceanic mixed waters, the Moray Firth is a region of high productivity. Nutrient-rich waters are circulated by the local Dooley current (Svendsen *et al*., 1991), concentrating plankton which attracts high numbers of fish species, especially sandeels (*Ammodytes* spp.). These small eel-like fish are an important prey item for a variety of species including other fish, sea birds and marine mammals although they have further been targeted by industrial fisheries to their detriment. The distribution of sandeels is very much dependent upon the sediment type, with sandy gravel sediments providing their optimal habitat into which they burrow for protection (FRS, 2003). The type of sediment found in the Moray Firth is predominantly sandy (Figure 1.5) (Eleftheriou *et al.,* 2004). Sandeels emerge from their burrows between April and October, the period when minke whales are most typically sighted in UK coastal waters, especially in the North Sea (Northridge *et al*., 1995; Robinson *et al*., 2007b; Weir *et al*., 2007). Pierce *et al*. (2004) examined the stomach contents of stranded minke whales in Scotland. He found that around two-thirds of their diet by number and weight is comprised of sandeels. In the last two decades, sandeels have been targeted by industrial fisheries; in 1993 a sandeel fishery located off the Firth of Forth landed 100,000 tonnes of this fish an amount that caused seabird breeding failures in this area (FRS, 2003). In order to prevent the depletion of this important prey, management of the fisheries would be essential in areas where predators congregate for feeding. Robinson *et al*. (2009) found that the distribution of minke whales in the Moray Firth was significantly different across different sediment types with their highest density in areas characterised by sandy gravel sediments, where sandeels shelter.

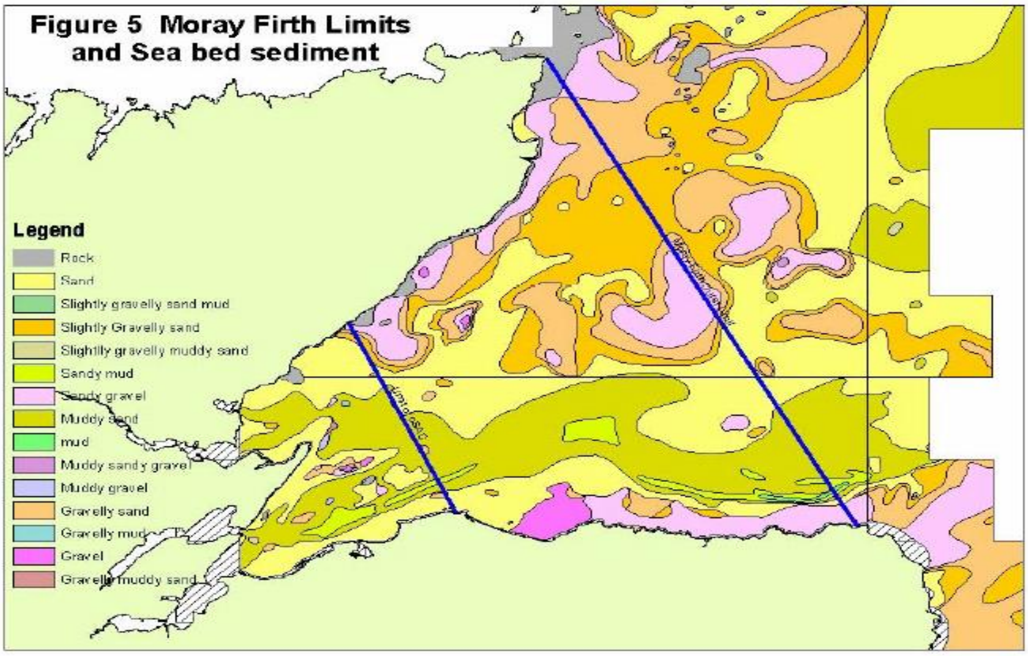

Figure 1.5. Map of seabed sediment types found in the Moray Firth in north east Scotland. Blue lines indicate the division between the Inner and the Outer Moray Firth. Note that sand and sandy-gravel are the most common type of sediment found in the study area. Reproduced from Eleftheriou *et al.*, 2004.

The Moray firth is also an important area for many other commercial fish species, including herring (*Clupea clupea*), sprats (Sprattus sprattus) mackerel (*Scombrus sombre*) haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangus merlangius*) (Greenstreet, 1998). This high number and diversity of species attract a variety of seabirds, making the outer Moray Firth internationally important, with various Sites of Special Scientific Interest (SSSI) and Special Protection Areas (SPA) designated areas. Gannets (*Morus bassanus*), puffins (*Fratercula arctica*), shags (*Phalacrocorax aristotelis*) kittiwakes (*Rissa tridactyla*), razor bills (*Alca torda*) and guillemots (*Uria aalge*), are some of the seabirds species that inhabit the cliffs and seas of the study area (Mudge and Crooke, 1986; Tasker, 1996; Eisfeld *et al*., 2009; Thompson *et al*., 2010).

The outer Moray Firth is also recognised for many other marine mammal species. Grey (*Halicherus grypus*) and harbour seals (*Phoca vitulina*) are common pinnipeds seen in the region and a large number of cetacean species have been recorded in the waters of the study area (Table 1.1.) (e.g. Robinson et al., 2007b; Robinson and MacLeod, 2009; Robinson *et al.,* 2010). Along with bottlenose dolphins and harbour porpoises, minke whales are the most commonly observed cetaceans in the outer Moray Firth (Robinson *et al*., 2007). (Figure 1.7).

The outer Moray Firth is a region of high ecologically importance. The gas and oil activities, fisheries industry and tourism, are some of the anthropogenic pressures that, if not managed with comprehensive knowledge, may threaten this outstanding area. Therefore it is essential that more studies concerning abundance, distribution ecology and behaviour of species found in the outer Moray Firth are conducted.

Table 1.1. List of cetaceans recorded in the Moray Firth. Species in bold characters indicate the most commonly sighted in the study area. (Robinson *et al*., 2007b; Robinson and MacLeod, 2009; Robinson *et al*., 2007).

	Common name	Scientific name
Mysticetes		
	Humpback whale	*Megaptera novaeangliae*
	Fin whale	*Balaenoptera physalus*
	Minke whale	***Balaenoptera acutorostrata***
Odontocetes		
	Sperm whale	*Physeter macrocephalus*
	Cuvier's beaked whale	*Ziphius cavirostris*
	Northern bottlenose whale	*Hyperoodon ampullatus*
	Pilot whale	*Globicephala melas*
	Killer whale	*Orcinus orca*
	Risso’s dolphin	*Grampus griseus*
	Bottlenose dolphin	***Tursiops truncatus***
	White-beaked dolphin	*Lagenorhynchus albirostris*
	White-sided dolphin	*Lagenorhynchus acutus*
	Common dolphin	*Delphinus delphis*
	Harbour porpoise	***Phocoena phocoena***

Figure. 1.6. Most commonly observed species of cetaceans in the Moray Firth. A) harbour porpoise (*Phocoena phocoena*) B) minke whale (*Balaenoptera acutorostrata*) C) bottlenose dolphin (*Tursiops truncatus.* (Photographs by Kevin Robinson /CRRU).

1.5. Aims of the study

The current project aims to investigate the sufacing and ventilation patterns of coastal minke whales (*Balaenoptera acutorostrata*) in northeast Scotland. With data collected during the summer months (May-October) from 2006 to 2010, the study intends to ascertain the source of variation in the respiratory rates of these animals. It is hoped that this information can provide an additional baseline necessary for impending estimations of the minke whale population in these and adjacent waters.

<u>Summary of aims</u>:

- Analyse the ventilatory rates of minke whales in the Southern Outer Moray Firth during the summer months (May-October) with data collected from 2006 to 2010.

- Determine whether the three studied factors, namely age class, behaviour and months interact between them, affecting therefore the surfacing intervals of minke whales in the outer Moray Firth.

- In the case of no interaction between the factors, examine surfacing intervals and surfacing rates of minke whales in the Moray Firth as a function of season, behaviour and age class.

- Compare surfacing intervals of minke whales found in the outer Moray Firth with those studied in other regions.

2 Materials and Methods

2.1. Survey Methodology

The datasets examined in the present investigation were collected between the months of May and October from 2006 to 2010 inclusive from dedicated boat surveys in a 1,200 km^2 coastal area comprising the outer southern Moray Firth in NE Scotland (57º41'N 2º40'W). The boat surveys were conducted by the Banff-based Cetacean Research & Rescue Unit (CRRU) using a crew of 1-2 experienced observers with up to 6 assisting volunteer observers trained by the qualified staff. The personnel were arranged equally around the boat to achieve full, 360° visual coverage of the surrounding waters during structured transects. All surveys were performed using 5.4 metre rigid inflatable boats (Figure 2.1) equipped with 90 horsepower outboard engines, full safety gear, GPS/SONAR units, binoculars, hand-held compasses and digital single reflex cameras (Nikon D700 body with a F2.8 300 mm zoom lenses). Observational towers attached to the boats provided an eye height of approximately 3.5 metres above the water when in movement, for spotting (Robinson *et al*. 2007).

Figure 2.1. One of the CRRU rigid inflatable boats stationary on sea surface, during a survey (photo credit: Kevin Robinson/CRRU).

All surveys were carried out at a mean speed of 7 knots (approximately 13 km per hour), at Beaufort sea state three or less and with visibility ≥ 1 km. Four selected line transect routes were used in the years 2006 and 2008: three parallel outer routes approximately 1.5 km apart in latitude and an inner coastal route (Figure 2.2). Since 2009, with a better knowledge of the area and a better understanding of the distribution of the animals, further offshore survey routes were introduced (Figure 2.3).

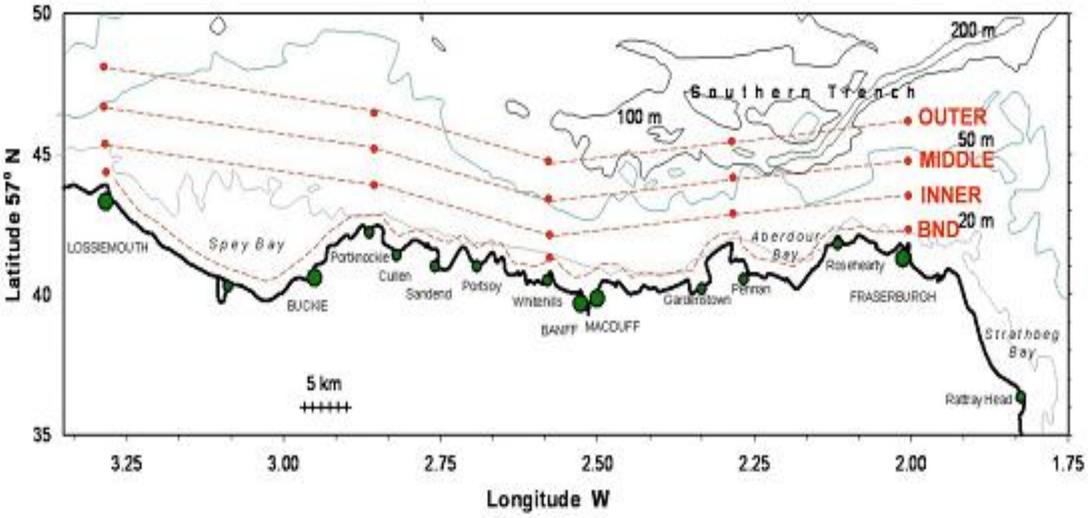

Figure 2.2. Map showing the transect routes used in 2006-2008 (from Robinson *et al*., 2007).

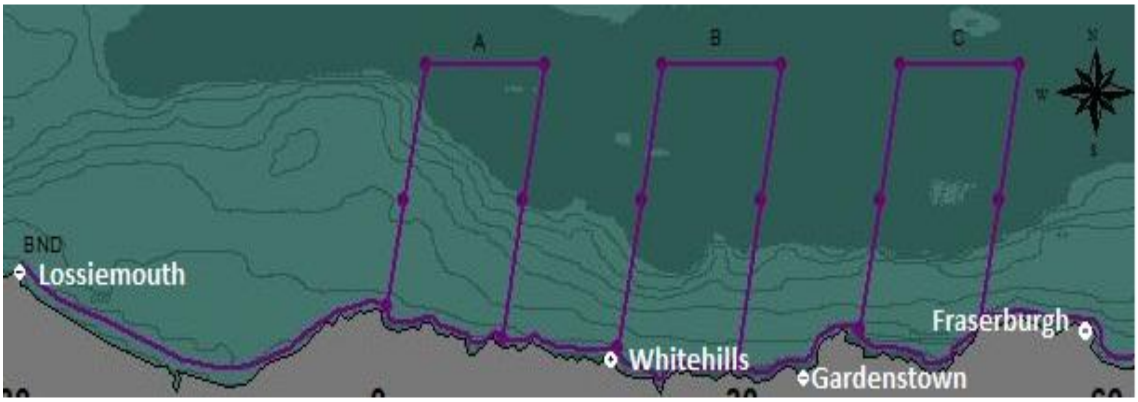

Figure 2.3. Map showing the new transect routes used post 2008 (adapted from Robinson, K.).

In addition to direct sightings of the animals themselves, the presence of feeding birds was used as a visual cue to locate the targeted whales. When a whale was sighted, an approach was made until a distance of approximately 50 m when the speed of the boat was reduced or halted. On confirmation of the species, the time, position, age class (based on visual observations of size of the individual) behaviour (see 2.1.1. for categorization of both age class and behaviour) and environmental data were first recorded prior to attempting a focal follow of the whale to record its surface/diving behaviour. If the animal was deemed trackable, the surfacing rates were subsequently recorded using a digital stopwatch. All observers were responsible for tracking the sightings. The person with the stopwatch would call out the time between successive surfaces in minutes and seconds. A further observer with the hand-held compass would call out the distance and bearing of the whale from the boat and its direction of travel. A third nominated observer was responsible for recording all this information as relayed, plus any other significant data such as the age of the subject (calf, adult or subadult), the type of surface behaviour (see below for the different categories), presence or absence of birds when feeding and any other factor that could affect the analysis (e.g. presence of fishing or whale-watching vessels, etc). An example of a focal follow form as used during such an encounter is shown in Figure 2.4. To minimise the possibility of missing a surfacing animal during a follow, the vessel was continued in the same general direction and speed as the whale ahead. The information gathered in these encounters, along with all focal follows longer than 20 minutes formed the central data used available for analyses in this BSc project.

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							
4							
5							
6							
7							
8							
9							
10							
11							
12							
13							
14							
15							
16							

Figure 2.4. Focal follow form used to record information while on survey

2.1.1. Definition and Categorization of age and behaviour of minke whale for identification during surveys

The age of the subjects was categorized as calf, adult and subadult by visual observations of size and other characteristics:

- **Calf** minke whales are lighter than adults, measuring around 4 to 5 meters long and sometimes seen in company of the mother.
- **Adult** minke whales possess dark coloration and are approximately >7 m. long. The dorsal fins are tall and falcate (rounded) with numerous edge marks.
- **Subadult** minke whales by contrast are smaller than adults, have lighter coloration with smaller and typically triangular dorsal fins with fewer dorsal edge markings.

The behavioural activity was divided into two different categories:

- **Feeding/foraging:** detected movements were either swimming in circles in an area with short dives (suspected feeding) or observations of direct surface feeding. When direct observation of surface feeding, whales displayed lunging activity by opening the mouthparts and distending the throat grooves in a series of engulfing strikes. This type of lunges are also seen when bird-association feeding.

- **Travelling:** the direction of the animals was constant and predictably in a relatively straight bearing with slow movements through the water.

2.1.2. Definition of ventilation characteristics

There are different approaches for measuring the ventilation/ diving rates of whales and other marine mammals when studying their respiratory patterns. In order to clarify the different terminology, the following diagram was produced to illustrate graphically these diverse parameters (Figure 2.5).

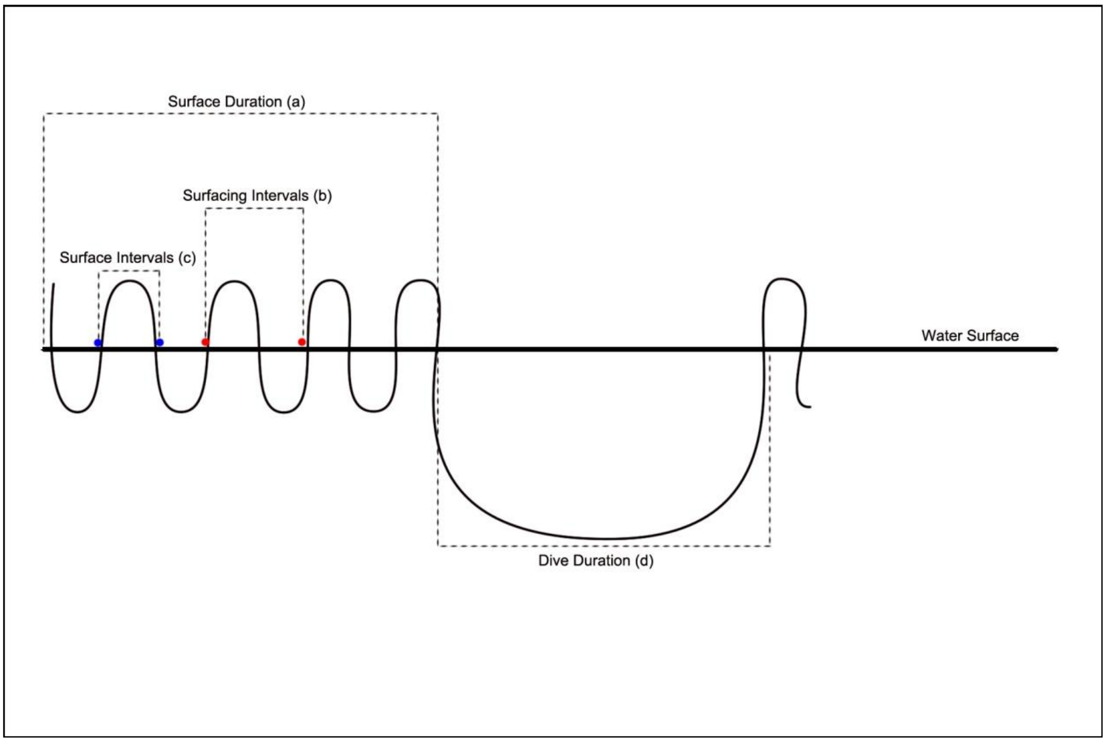

Figure 2.5. Graphic representation of the diving profile of minke whales and the different respiratory characteristics used for their investigation.

- Surface duration: time spent during the clustered series of blows (a).
- Surfacing interval: time between successive blows (b).
- Surface interval: time spent at the surface between dives (c).
- Dive duration: long dives that follow a series of short clustered blows; the arching of the dorsum of the whale would serve as an indication (d).
- Surfacing rate: numbers of surfacings per whale per hour (SPWPH).

Because most of the focal follows used for this study does not present an evident regular pattern, as Carwardine (2000) described (i.e. 5 to 8 blows at intervals of less than 1 minute, followed by a long dive of between 3 to 8 minutes) and no indication of long dive (i.e. arching of the dorsum) was recorded, only the surfacing intervals and surfacing rates were employed for the current study.

2.2. Statistical analysis

All survey information was entered into an Excel spreadsheet. Data were subsequently extracted for categorisation into groups (years, months, travelling/foraging, adults/subadults). In order to obtain representative results, focal follows for the analysis of the respiration patterns of less than 20 minutes were removed. Data was transformed to seconds for the analysis. To avoid biased results due to differences between individuals, the mean surfacing intervals values were obtained for each individual (N=31) and assessed for normality using a Shapiro-Wilk test. A Kruskal-Wallis non-parametric test was used to analyse the differences in the surfacing intervals between individuals.

In order to describe the linear association between the two dependent variables, i.e. surfacing intervals and surfacing rate, a Spearman correlation test was performed.

Overall surfacing interval sequences (N= 843) was tested for normality. Data values were replaced by their ranks in order to analyse it for variation. A General Linear Model was used to test the relationship between the studied different factors (age class, months and behaviour) and the dependent variable. First, a 3 way ANOVA was performed to assess the possible interactions between the three factors and their effects produced in the time spent by minke whales submerged. Groups were subsequently divided by subcategories by age class and activity of the whale (subadults * foraging; subadults * travelling; adults * foraging; adults * travelling) and analysed by months.

3. Results

Statistical result tables obtained from SPSS 18.0 can be found in Appendix 3.

3.1. Survey Effort

Between 2006 and 2010, a total of 237 encounters with minke whales were recorded during the summer months (Table 3.1.). The search effort (expressed in kilometres travelled) was seen to be variable between years with the highest effort being recorded in 2009 and 2010. The total encounter rate for all years was determined as 0.087 whales per km (Table 3.1).

Table 3.1. Survey effort, showing numbers of survey days, effort, number of encounters, cumulative number of minke whales and encounter rate recorded by CRRU in the outer Moray Firth from 2006 to 2010 inclusive.

Year	Number survey days	Effort (kms)	No. Minke whales encounters	Total minke whales	Encounter rate (whales/per km)
2006	64	2908.5	118	123	0.042
2007	50	2204.3	17	17	0.008
2008	49	2220.6	43	48	0.022
2009	39	4932.4	29	33	0.007
2010	51	3500.0	30	32	0.009
Total	**253**	**15765.8**	**237**	**253**	**0.087**

Only focal follows greater than 20 minutes could be used in the following analysis, resulting in a total of 31 samples: 18 from 2006, 6 from 2008, 4 from 2009 and 3 from 2010. As a result, 843 surfacing/diving sequences were extracted from these encounters.

3.2. Normality tests and analysis of variance of mean surfacing intervals per whale

The distribution of mean surfacing intervals per whale was analysed for normality using a Shapiro-Wilk test (*P*=0.017), which revealed that the data were not normally distributed. Figure 3.1 shows how the data were positive skewed, meaning that the majority of the minke whales encountered during surveys exhibited short surfacing intervals of less than 90 seconds. A Kruskal-Wallis non-parametric test was further performed to test for differences between individuals, but revealed that the mean individual surfacing intervals were not significantly different from one another (H_{30} =30; *P*=0.466). Because the individual differences were not significant, this would not have an effect on analysis of the overall dive sequences. Consequently, an analysis of the total dive sequences (N=843) was viable.

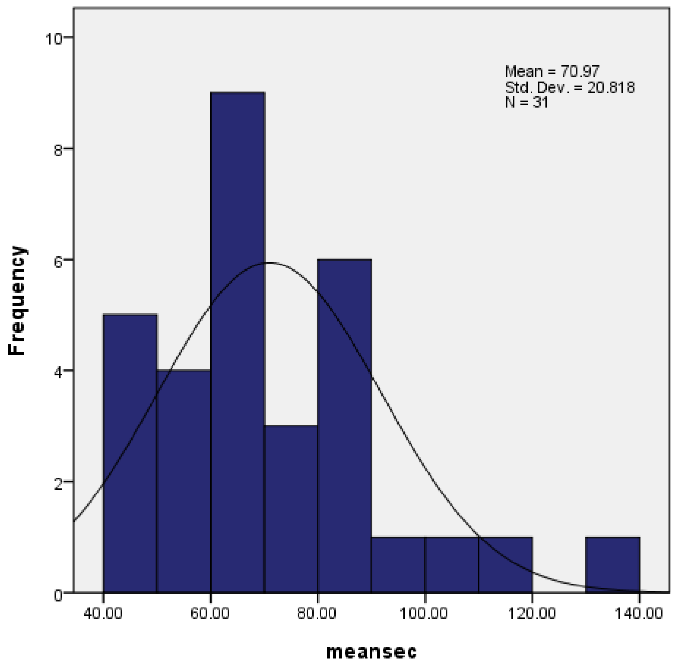

Figure 3.1. Histogram showing the frequency distribution of the mean surfacing interval for minke whales from the Moray Firth for which focal follows greater than 20 mins were possible. The distribution curve, mean value, standard deviation of the mean and sample size (N) can be also seen in the graph.

3.3. Descriptive statistics of overall surfacing intervals sequences

A total of 31 focal follows with a total of 843 sequences were recorded between the field study months (May to October) during the study time (2006-2010). The median value (42 sec IQR= 66sec) and a mean surfacing interval of 67.19 sec (SD= 66.16; min/max: 2/608 sec) was determined for the 31 minke whales sampled. The frequency histogram for the overall data shown in Figure 3.2 demonstrated a positive skew once again to short surfacing intervals and suggested that the data was not normal distributed. The Shapiro-Wilk test for normality further revealed that the assumption for normality on the distribution of the total data (2006-2010) for surfacing intervals was violated (*P*<0.0001).

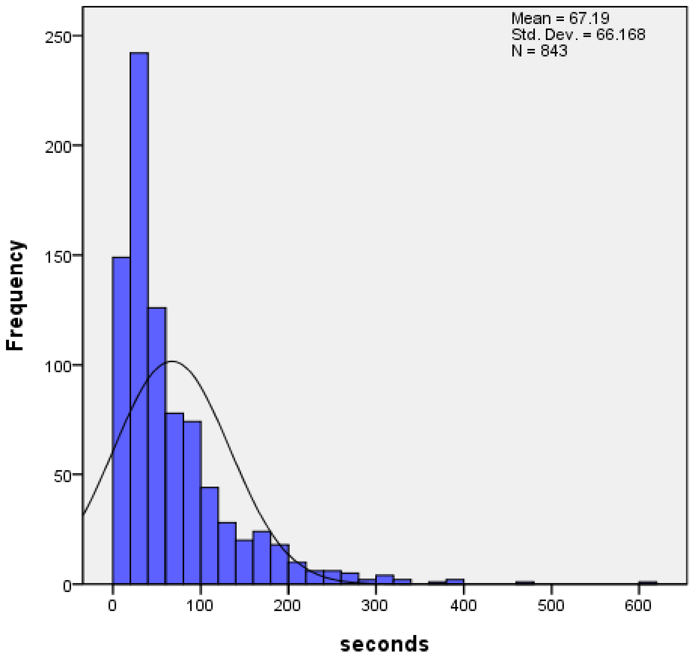

Figure 3.2. Frequency histogram showing the distribution curve, mean value, standard deviation of the mean and sample size (N) of the overall surfacing intervals of minke whales during the study period, 2006-2010.

The highest median value was found in foraging individuals (46.5 sec.; IQR= 65). On the contrary, when means were compared, the highest value was found to belong to travelling whales (69.15 sec.; SD= 72.15). The maximum and minimum sequences were also found in whales engaged in travelling (608 sec and 2 sec. respectively). The descriptive statistic values of minke whales engaged in the different behaviours are shown in Table 3.2 below.

Table 3.2. Showing the descriptive statistics for surfacing intervals (in seconds) of minke whales engaged in behaviours foraging and travelling respectively.

Behaviour	Foraging	Travelling
Median	46	40
Interquartile range	65	68
Mean	65.1	69.1
Standard deviation	58.1	72.5
Minimum	5	2
Maximum	397	608
N	400	443

The median and other descriptive values for surfacing intervals of minke whales were calculated for the different months (Table 3.3). The highest median value was determined in June (53 sec; IQR= 59 sec), although no focal follows were recorded in either May or September. The minimum median value was obtained in October (35 sec; IQR=67 sec). Both the minimum and maximum values were recorded in August (2 and 608 sec respectively).

Table 3.3. Table showing descriptive statistics for surfacing intervals (in seconds) of minke whales in the different months.

Months	June	July	August	October
Median	53	43	35	35
Interquartile range	59	66	72	67
Mean	67.7	63.3	77.1	67.5
Standard deviation	50.6	56.2	95.1	79.7
Minimum	13	4	2	8
Maximum	245	387	608	320
N	199	460	170	37

Both the mean and median values were higher for subadults, showing that, on average, younger minke whales recorded during the study period spent more time submerged than the adult ones(Table 3.4).

Table 3.4. Table showing descriptive statistical values for surfacing intervals (in seconds) of age class groups (subadults and adults).

Age class	Subadults	Adults
Median	50	37
Interquartile range	72	54
Mean	74.6	61.1
Standard deviation	70.1	61.9
Minimum	2	4
Maximum	608	97
N	383	460

3.4. Correlation between Surfacing Intervals and Surfacing Rate

In order to examine the relationship between the two dependent variables, namely surfacing intervals and surface rates (Surfacings Per Whale Per Hour, SPWPH) a Spearman's rank correlation test was performed. Mean surfacing intervals were obtained from each of the 31 focal follows recorded and plotted against the respective surfacing rates in a scatter plot (Figure 3.3). As the surfacing intervals increased, the surfacing rate decreased (r= -0.969; *P*< 0.0001) indicating a strong negative correlation between the two variables (i.e. minke whales that spent more time below the water, surfaced more times than those that dived longer). Because this relationship was established, and using both variables would be a redundancy, only the surfacing intervals were employed for the study of respiratory rates of minke whales in the following analyses.

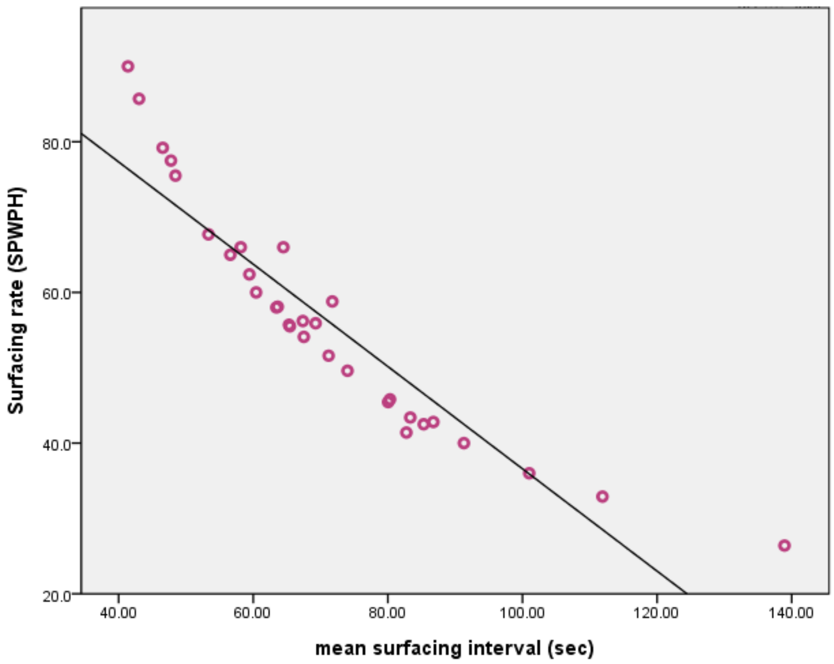

Figure 3.3. Scatter plot showing the relationship between surfacing rates and mean surfacing intervals of minke whales from focal follows >20 mins recorded between 2006 and 2010.

3.5. General linear model

A univariate analysis of variance on ranked data was performed to study the effects and interactions between the three independent variables, namely age class, behaviours and months. The test revealed a significant interaction between the three factors ($F_{[1,831]}$= 5.547; P= 0.019) (see ANOVA table for details; Table 3.5). A three-way interaction exists whenever a two-way interaction differs depending on the level of a third variable. In this case, surfacing intervals of minke whales are affected by the combination of the three factors: the effect of, for example, age class (subadult/adult) on the surfacing intervals of minke whales will differ depending on the level of the other variables in combination. Graphs were produced to ilustrate these interactions. Behaviours are represented in the horizontal axis, months are represented by different lines, leaving age class represented in different graphs (subadults and adults, Figure 3.4, A and B respectively). A table summarising the number of individuals encountered by months was also created to assist the reader (Table 3.6).

Table 3.5. ANOVA table showing the results of the General Linear Model. Degrees of freedom (df), *F* and *P* (Sig.) values for the effect of each factor singly and the interactions between two and the three factors are seen in the table.

Dependent Variable:Rank of seconds

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	3991995.087	11	362908.644	6.567	.000
Intercept	9.159E7	1	9.159E7	1657.320	.000
age	111624.073	1	111624.073	2.020	.156
behaviour	365.930	1	365.930	.007	.935
month	345998.446	3	115332.815	2.087	.100
age * behaviour	71648.923	1	71648.923	1.297	.255
age * month	757337.468	2	378668.734	6.852	.001
behaviour * month	787754.261	2	393877.130	7.127	.001
age * behaviour *month	306523.383	1	306523.383	5.547	.019
Error	4.592E7	831	55262.656		
Total	2.000E8	843			
Corrected Total	4.992E7	842			

Because the residual degrees of freedom left from the General Linear Model were not sufficient to perform a posteriori test (e.g. Tukey test) groups were separated by age class and behaviour (Subadults * Foraging; Subadults * Travelling; Adults * Foraging; Adults * Travelling) and analysed by months using a 2- way ANOVA test. A Tukey post-hoc analysis was performed for those groups with more than 2 levels. Significant differences were found between the surfacing intervals of subadult minke whales engaged in foraging in different months ($F_{[3,215]}$ = 4.081; P= 0.008), although no significant differences were determined for travelling subadults between months($F_{[2,161]}$= 2.768; P= 0.66). Adult minke whales were also affected by season when engaged in different activities. Only two levels were compared, as data for foraging adult minke whales were only available for the months of July and August. The difference in their surfacing intervals were however significant between these months ($F_{[1,179]}$= 8.974; P= 0.03). When travelling, the surfacing intervals of adult individuals were also affected by the different months when they were recorded ($F_{[2,276]}$= 11.992; P< 0.001). A summary of the results was produced to facilitate the understanding and to show the different *P* values obtained from the posterior Tukey tests. These are further illustrated in Figure 3.3 below.

Table 3.6. Number of focal follows of minke whales encountered by months and classified by behaviour and age class.

Month / Behaviour+ Age class	June	July	August	October
Foraging subadults	2	3	2	1
Travelling subadults	2	4	1	0
Foraging adults	0	4	2	0
Travelling adults	3	5	2	0

A) Subadults foraging ($F_{[3,215]}$ = 4.081; *P*= 0008). *P* values of Tukey test.

*** indicates a significant difference.**

Months	June	July	August	October
June	-	0.664	0.018*	0.042*
July	0.664	-	0.146	0.251
August	0.018*	0.146	-	1.000
October	0.042*	0.251	1.000	-

B) Subadults travelling, no significant differences ($F_{[2,161]}$= 2.768; *P*= 0.066)

C) Adults foraging, July*August ($F_{[1,179]}$= 8.974;*P*= 0.003)

D) Adults travelling, overall, ($F_{[2,276]}$= 11.992; *P*< 0.001). *P* values from Tukey test.

*** indicates a significant difference.**

Months	June	July	August
June	-	0.001*	0.689
July	0.001*	-	0.000*
August	0.689	0.000	-

A) **B)**

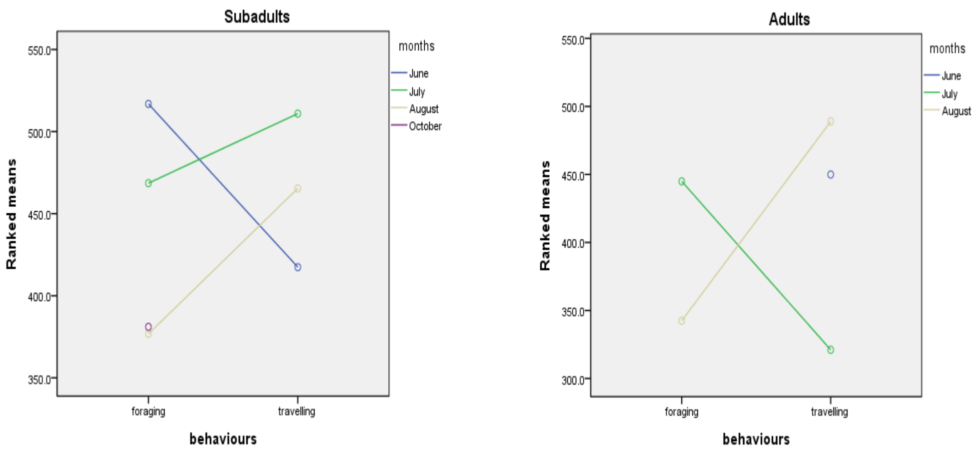

Figure 3.4. Graphs showing the ranked means (Y axis) of surfacing intervals for (A) subadult and (B) adult minke whales engaged in different behaviours (X axis) in different months.

The presence of a triple interaction between the factors regulates and modifies the effects on the surfacing intervals of the factors taken singly. As a result, it would not be valid to analyse the differences on the time the whale spent submerged as a function of season or behaviour or age class separated.

From the first graph (Figure 3.4. A), it can be observed that subadult minke whales spent more time below the surface when foraging than when travelling during June. The surfacing intervals found in June are the highest of all the values. On the contrary, during the other months, subadult minke whales spent less time submerged when foraging than when travelling (i.e. they have an “additive effect”, with no interaction). No subadults were found engaged in travelling during October. The distances between the ranked means (represented by circles in the graphs) seen in the graph, indicate the difference between their ranked means. During June, foraging subadults spent significantly more time submerged than those foraging in August and October, confirming the results obtained by the Tukey test. When travelling, subadult minke whales did not spend a significantly different time below the surface during the different months.

The surfacing intervals of adult minke whales (Figure 3.4. B) were also affected by the interaction of the different months and the different behaviours. The graph shows a clear interaction, where the main effect for the different behaviours is modified by the different months. Foraging adults spent more time below the surface than those travelling individuals during July, but the opposite pattern can be seen during August. No focal follows were recorded during October and three individuals (with the same mean rank of surfacing intervals) were recorded foraging in June.

When the third factor is considered graphically (i.e. both of the 2-way interactions graphs are compared), it can be seen that the 2-way interaction between months and behaviour is also affected by age class. During August, both age class groups had higher mean surfacing intervals when travelling than when foraging. In the case of July, the patterns are the opposite when compared both age class groups. Subadults spent longer intervals submerged during travelling, whilst adults spent less time during travelling.

3.6. Summary of results

- The total encounter rate recorded between 2006 and 2010 was determined as 0.087 minke whales per km.

- A total of 31 focal follows > 20 min. with a total of 843 surfacing/diving sequences were collected.

- The majority of individuals had short surfacing intervals of <90 sec.

- The mean surfacing intervals per whale were not significantly different between individuals.

- The mean surfacing interval of minke whales in the outer Moray Firth was determined as 67.1 sec (SD= 66.1; min/max : 2/608 sec). The median for the total period was determined as 42 (Interquartile range = 66).

- There was a strong negative correlation between surfacing intervals and surfacing rate (SPWPH) ($r=-0.969$; $P<0.0001$). As the surfacing intervals increased, the surfacing rate decreased.

- A 3-way interaction was determined between the three independent variables (i.e. age class, behaviour and month) (3-way ANOVA test: $F_{[1,831]} = 5.547$; $P= 0.019$).

- Significant differences in surfacing intervals were found between June and August and between June and October when subadults were foraging, but not when travelling

- Significant differences in surfacing intervals were found between June and August when adults were foraging. Significant differences were found between June and July and between July and August when adults were travelling.

4. Discussion

The findings extracted from the current study provide evidences that factors such as behaviour or month not only have an effect on the surfacing intervals of minke whales when acting separately, as other studies revealed, but also when acting in combination. The synergistic interaction effect found between behaviour, months and age class taken together shows the complexity existing in nature as well as when studying behavioural ecology. Thus, the relation between these different factors should be taken in consideration for the remainder of this report.

The data collected in this study were found to be strongly positive skewed and very variable as indicated by the high standard deviation and interquartile ranges. This can be due to the fact that most of the data have a lower bound (i.e. minke whales had fewer long surfacing intervals). The large number of extreme values also affected the distribution of the data. In a non normal distributed dataset, mean value is not a good indicator of measuring average, as it can be affected by extreme values. In this study, the median (42 sec; IQR= 66) was used to locate the typical surface interval value across the different datasets and its posterior statistical analysis. However, even those studies on minke whales where their authors transformed the data in order to use parametric tests and those that used non-parametric tests (i.e. comparing medians instead of means) only reported the mean surfacing intervals (e.g. Joyce, 1982; Stockin, 2001; Curnier, 2005). In order to meet the objectives of comparing respiration rates across different regions, the mean surfacing interval observed in this study will be used for comparison. This was determined of 67.19 (SD= 66.16), what it makes it comparable to those found in other studies performed in other locations (Table 4.1).

Table 4.1. Table showing the mean surfacing intervals of minke whales from studies in different regions.

Mean Surfacing Interval (seconds)	Study Area	Author/s
54.7	Canada	Curnier (2005)◊
74.6	Norway	Folkow & Blix, (1993)*○
68.3	Iceland	Gunnlaugsson (1989)*◊
90.0	Antarctic	Joyce (1982)◊
68.7	Norway	Joyce, *et al*. (1989)*◊
54.1	Iceland	Joyce *et al*. (1990)*○
85.7	Norway	Øien *et al*. (1990)*○
93.26	California	Stern (1992)*◊
66.1	Scotland	Stockin *et al*. (2001)

* The authors analysed the surfacing rate (SPWPH). Mean surfacing intervals were calculated by dividing 3600 (1hour) by the SPWPH.

◊ Observational method for collecting data.

○ Radio tagging method for collecting data

The high variability on mean surfacing intervals across the different regions can have several explanations. As well as the mean values, the methodology employed in these studies also varied considerably between locations. Most investigations have been performed using visual observations, whereas other studies (e.g. Folkow and Blix, 1993; Joyce *et al*., 1990) collected their data from radio-tagged individuals. Both methods have advantages and disadvantages (see Joyce *et al*., 1990 for a complete examination). Whales may react when tagged by changing their behaviours (e.g. spending more time below the surface than usual, Folkow and Blix, 1993), giving inaccurate values. On the contrary, whales tracked by observational vessels may respond by modifying their behavioural state with respect to the proximity of the research vessel. For example, feeding fin whales (*B. physalus*) disturbed by boats in the Ligurian Sea changed their behaviour to travelling, increasing their swimming velocity and reducing their time at the surface (Jahoda *et al*., 2003). The surfacing signals received from a radio tagged whale may be erroneous as sometimes the antenna clears the water without the whale breathing. Signals from radio tags can also be lost, as in the tagged minke whale reported by Joyce *et al*. (1990). Modern monitoring tags have been developed to avoid such inaccuracies. Despite potential errors, radio tagging presents the possibility of study marine mammals during the night. Folkow and Blix (1993) managed to track two of the four tagged minke whales by night. They found that whales during night just break the surface to respire very rarely. The minke whale tracked by Joyce *et al*. (1990) in the Antarctic, had a significantly higher mean surfacing interval during the night (59.65 sec.) compared to that during the day (48.36 sec). This difference between the lengths of dives and surfacing of minke whales, should be considered when study the respiration patterns of this and other species of marine mammals, as it might give a large variability in the data and consequently imprecise averages.

In the present study observational methods were used to gather the data exclusively. Regardless of the possible errors in data obtained with this method, such as the inexperience of observers and sea state (surveys were performed in a sea state of ≤3; at sea state of 3, whitecaps start to appear, potentially missing surfaces of the whales), the results are comparable with those studies performed with the same methodology. Two exceptions of studies carried out through observational methods, can be observed in the table of mean values of surfacing intervals, with remarkably large mean values (Stern, 1992 and Joyce, 1982). Stern (1992) reported the highest value of mean surfacing intervals of minke whales to date. This result may be biased upwards, as he collected his data from mainly travelling individuals. The activity in which the whale is engaged inevitably affects the ventilatory patterns recorded, as demonstrated in the present study. In aerobic respiration, oxygen is required to generate chemical energy in the form of ATP (adenosine triphosphate) during the electron transport chain (Schmidt-Nielsen, 1997). Therefore, surfacing and diving intervals are known to be reliable indicators of energy expenditure. The activities related to the foraging/feeding behaviours (searching, pursuing, corralling and trapping prey) require high expenditure of energy, and thus, more oxygen. A decrease in the surfacing intervals is expected to occur when marine mammals are engaged in this type of behaviour. Studies with minke whales (Lynas and Sylvestre, 1988; Curnier, 2005, Baumgartner, 2008) and other cetaceans

(Dorsey, 1983; Würsig *et al*., 1984; Jahoda *et al*., 2003) support this information by giving evidence of these changes in respiration patterns on animals engaged in different behaviours. For example, Acevedo-Gutiérrez *et al*. (2002) compared the rates at which blue (*B. musculus*) and fin (*B. physalus*) whales recovered from foraging dives to those from non-foraging dives, as a measure of energy costs. They found that when foraging, these whales increased twice the time spent for recovering at the surface.

Although not significant when not interacting with other factors, in the present study the mean surfacing intervals of foraging whales was higher than travelling whales (69.1sec versus 65.1sec). Other studies on minke whales (Lynas and Sylvestre, 1988; Tetley, 2004; Curnier, 2005; Baumgartner, 2008) have found the same pattern: animals make longer dives when travelling. In order to obtain unbiased results, the behaviour of the animals during the data collection should be taken in consideration. The samples used in the present study were from travelling animals (18 individuals; 443 surfacing sequences) and foraging animals (14 individuals; 400 surfacing sequences), what it makes a good representation for the analysis of surfacing intervals in this area. However, not only the behaviour of the animal affects their respiratory patterns but the combination of behaviour with other factors. In this study, the effects of behaviour, age class and time of year (month) in combination, affect the time the whales spent below the sea surface. Therefore, in studies where only single factors were considered, the results may have biased by other factors.

The optimal foraging theory asserts that organisms chose their food resources in a way that maximises individual or species fitness (Krebs and Davies, 1997). By adopting different feeding strategies for different species of prey found at different depths, the respiratory behaviour of minke whales are subsequently expected to change. Ichthyophagous minke whales have been reported to feed on a number of different prey species which may require a variety of adopted feeding strategies (e.g. Helzel, 1989; Gill *et al*., 2000; Curnier, 2005; Robinson and Tetley, 2007). Depending on location and prey availability, they utilise diverse specialisations such as lunge feeding and bird-associated feeding techniques. Hoelzel (1989) provided the first descriptions of foraging specialisations in minke whales and reported that most individuals used one of two distinguishable surface feeding strategies. One technique, the lunge feeding technique, consisted on the whale "actively concentrating the prey against the air/water interface, with no feeding birds involved". The other technique, bird-association feeding technique, occurs when the whales exploit concentrations of fish herded by feeding sea birds from above and other predators such as piscivorous fish from below. Because whales employing the lunge feeding technique need to actively corrall the fish before engulfment, this requires higher energy expenditure (and therefore greater oxygen consumption) than the opportunistic bird-associated technique. Therefore, a lengthening of the dive duration of the animals engaged in the later is expected. In the outer Moray Firth, minke whales have been observed foraging in the presence of birds in as much as 78% of recorded encounters (Robinson and Tetley, 2007). On the contrary, minke whales in the St. Lawrence estuary, Canada mostly employ active, lunge feeding techniques. In this study, Curnier (2005) found that feeding individuals, especially those feeding in the surface, have the lowest surfacing intervals (43.4 sec) compared to the other behaviours (travelling 71.1 sec and deep feeding 52.4 sec). The differences between the surfacing intervals of feeding minke whales in these two different regions, therefore, appear to be due, among other different factors, to the different respective feeding techniques used. Water depth, might also be a source of variation, as the St. Lawrence estuary are shallower than the coastline of Moray Firth.

Dive times frequently increase with depth of air-breathing aquatic mammals and birds (Kramer, 1988). In his study, Kramer (1988) studied the respiratory ecology of marine mammals and other aquatic animals restricted to surfacing in order to breath. The study illustrated the principles of acquiring oxygen and the regulation of respiration on air breathing aquatic vertebrates. Along with important statements, such as the "theory of optimal breathing", Kramer explained that in order to optimize the utilisation and storage of oxygen, individuals diving in shallow waters will have relatively shorter surfacing durations than those deep divers. Humpback whales (Dolphin, 1987a; 1987b), fin whales (Baird, 2002), Cuvier's (*Ziphius cavirostris*) and Blainville's

(*Mesoplodon densirostris*) beaked whales (Baird *et al*., 2006) are some of the cetaceans species that show this respiratory adaptive pattern. Some authors suggested that minke whales found in shallower areas are more likely to have shorter surfacing intervals than those found in pelagic waters (Gunnlaugsson, 1989; Øien *et al*. 1990). Baumgartner (2008) found that the surfacing intervals of feeding minke whales in the outer Moray Firth were affected by the water depth at which they were found. In the current study, depth at which minke whales were found was recorded for some of the samples. In this present study, all sampled whales from which focal follows were achieved were encountered in water depth between 9.6m and 71m with a mean depth of 29m. Because the distribution of minke whales depends on the distribution of their prey (as with other baleen whales: e.g. Whitehead and Carscadden, 1985, Payne *et al*., 1990, Woodley and Gaskin 1996; Macleod *et al*., 2004) it is not surprising that minke whales were encountered in relatively shallow waters where sandeels (*Ammodytes* spp) occur at larger densities (between 20 to 45m depth; Wright *et al*., 2000). Because water depth may affect the duration of surfacing intervals of minke whales, this information should be considered as an important variable when investigating their respiratory patterns.

The geographical variations on mean surfacing intervals of minke whales between the different studies may be due to the low sample size employed in some of the studies (e.g. Joyce *et al*., 1990, where only one minke whale was analysed). As Stockin (2001) suggested, individual differences such as body size, may cause the differences found between the regions. In the present study, 31 focal follows were recorded between 2006 and 2010 providing a good number of observations for analysis. In order to prevent inaccurate results due to individual differences, the mean surfacing intervals were analysed for variances between whales. However, the mean surface interval was not significantly different between individuals demonstrating that individual variability had no affect on the overall surfacing intervals.

The different time of the year at which minke whales and other marine mammals are found, may also affect their respiratory patterns. For example, Jaquet *et al*. (2000) provided evidences that the diving behaviour of male sperm whales (*Physeter macrocephalus*) was significantly different between summer and winter, diving for longer during summer. These changes in surfacing intervals can be interpreted as the cause of an ecological change in their foraging strategies. These strategies will change as a function of prey availability. Consequently, prey availability will determine distribution of minke whales, both horizontally (i.e. geographically) or vertically (i.e. within the water column). Since depth as explained above, affects the diving behaviour of minke whales and other marine mammals, the vertical location of prey items will ultimately affect the time spent below the sea surface. Sandeels (*Ammodytes* spp.) comprise the majority of the diet of minke whales in Scottish waters (Pierce *et al*., 2004); the time when sandeels emerge to feed, from April to October is coupled to the feeding season of minke whales (Northridge *et al*., 1995; Robinson et al., 2007b; Weir *et al*., 2007). Stockin *et al*. (2001) found significant differences in surfacing intervals of minke whales in the northwest coast of Scotland recorded between months. They analysed a total of 1,367 dive sequences recorded between May and September, and concluded that minke whales spent longer periods of time submerged during May and August. They also found that their surfacing intervals varied significantly depending on the time of the day (e.g. shortest from 12:00 to 13:00, and longest from 13:00 to 14:00). These findings were interpreted as a result of ecological changes, in particular, prey availability, assuming therefore that all recorded individuals were foraging and/or feeding. As the present study established, the effect of seasonality (i.e. months) on the respiratory patterns of minke whales is modified by the behaviour in which the individual was found and the age class of the individual. Differences in surfacing intervals and rates between daytime and nigh-time have been observed in minkes and other species of cetaceans (e.g. Joyce *et al*., 1990; Folkow and Blix, 1993; Baird *et al*., 2005). This can be the result of physical activity changes (e.g. resting by night; Folkow and Blix, 1993) to avoid predators (Baird *et al*., 2008; Ford *et al*., 2005) or as in the case of mysticetes feeding on zooplankton, diel vertical migration of the prey (Bollens *et al.*, 1992). The results found by Stockin *et al*. (2001) for both seasonal and diel differences, on such a fine-scale may be caused by many artifacts that were not considered. The behaviour and age class of the whale (found to possess effects on surfacing intervals when combined in this study) or the differences in the experience of the observers (found to have a strong correlation with the number of sightings, e.g. Mori *et al*., 2003) are some of the factors to be considered when studying diving behaviours of minke whales and other marine mammals.

The respiratory patterns of minkes and other marine mammals are known to vary as a function of the size of the animal. Since subadult and adult marine mammals differ on size, age class of the studied individual should be an important factor to include when studying their respiratory patterns. Because oxygen consumption correlates with heat production, is utilised as a measure of metabolic rate. The “specific metabolic rate”, unlike the Kleiber’s law, which assesses the total oxygen consumption of the organism, analyses the rate of oxygen consumption per gram of body mass. As different tissues have different metabolic requirements, it is more convenient to analyse the metabolic rates per unit of body mass rather than per total body mass of the animal (Schmidt-Nielsen, 1997). Interspecific analysis (i.e. between different species or taxonomic groups) such as the one carried out by Schreer and Kovacs (1997) showed that the diving capability (maximum diving depth and duration) of air-breathing vertebrates increases with body size. This was found to be particularly true for mysticetes, which showed a strong relationship between maximum deep duration and body mass. The ability to remain beneath the surface is not only influenced by the mode of oxygen utilisation (i.e. metabolic rate), but also the ability to storage oxygen. In cetaceans, a large proportion of the percentage of oxygen is stored in the muscles, and as muscle mass increases with body mass, larger individuals have a higher aerobic dive limit (Kooyman 1989; as seen in Mori, 2002). Consequently, an increase in surfacing intervals would be expected with increasing body size of minke whales. For example, Folkow and Blix (1993) contemplated the possibility of having biased results when conducting studies with tagged animals. Since most of the minke whales that approached to the vessels are young and curious animals, and young mammals require higher specific metabolic rates, the surfacing rates may not be representative of a general diving behaviour of the species.

Contrary to the expectations, when age class was analysed singly (i.e. with no interaction effect with other factors), subadult minke whales recorded during the present study spent longer times submerged than the adults. This finding may be caused by the fact that subadult minkes are smaller than adults, and are thus more difficult to sight during surfaces. Age of the individual and thus, size should be considered when analyzing the data as a possible source of variability.

The triple interaction found in this study has important implications for the interpretation of the effects caused by the different studied factors. The so called "independent" variables cannot be considered independent between them, as they have an interactive effect on the surfacing intervals when combined. For example, the effect of different months is modified by the effect of the different behaviours that in turn is affected by age class. During June, subadult minke whales spent less time below the water when travelling than when foraging (please refer to Figure 3.4. for an illustration of these results). During the remainder months this pattern was found in the opposite direction. These results can be interpreted as a switch between feeding techniques. Young subadults may spend longer time submerged pursuing prey in deeper locations (depth feeding at the scattering layer) during June, changing to surface feeding during the other months. During surface feeding events, subadult whales may employ bird-associated feeding methods, exploiting easy prey corralled by piscivorous fish such as mackerel (*Scomber scombrus*), from below and seabirds from above, reducing therefore energy costs and maximizing fitness.

Although all uncertain data with possible anomalies were discarded, some irregular results might be caused by sampling artifacts. The fact that during June subadult minke whales spent more time submerged could be also may be explained by the variability caused by other factors such as the sea state. It could be that the focal follows of foraging minke whales during June were recorded in a 3 sea state, what it could hinder blows from the surfacing animal. Records of sea state for each sample are recommended in order to avoid biased results. Other form of bias might be the observer experience. Observer experience is defined "as the number of past sighting surveys in which the observer participated” (Mori *et al*., 2003). At the beginning of the season is therefore expected that observers are not as well practised as at the end of the season, what it may have an impact in the sightings of blows, lengthening in some cases the surfacing intervals.

In the case of the adults group (Figure 3.4.B) the pattern seen during July is the opposite of that in the subadults. Those travelling adults recorded in August spent a significant longer time submerged than those found in July, and the opposite occurred when foraging. The small sample size obtained for foraging adults (4 individuals during July, 2 individuals during August, Table 3.6), with no follows for either June or October, may give unrepresentative results. With only two focal follows of foraging adult minke whales, the population is underrepresented and possible bias, such as individual difference should be considered. The two individuals found in August (number 19 and 20 of the summarising table found in Appendix 2) have very different mean values and, especially number 19, a large deviation from the mean, indicating a high variability of the surfacing intervals (Individual 19: 71.2 sec; SD= 95.4. Individual 20: 46.55 sec; SD= 39.4).

5. Conclusion

This study has shown that the interaction between the three studied factors in combination, have a synergetic effect on the surfacing intervals of minke whales at the outer Moray Firth. These findings provide evidences that the effects of factors singly are important, but these effects may be modified for another/s factor/s and consequently not representative. The behaviour of the animal, the month at which they were recorded and age class of the individuals might on the contrary, not affect the surfacing intervals of minke whales when studied separately, but as this study determined, they interact between them influencing therefore the dive times of the animals.

In addition to the analysed factors, the methodology used to obtain the data might have an effect on the surfacing intervals of minke whales. A standardisation between studies in relation to methodology and terminology would be recommendable to comprehend the respiratory behaviour of these and other animals.

The information obtained from this study adds more knowledge to the relatively insufficient material on this species, especially in these productive feeding grounds. These findings have a high significance for the understanding of the diving behaviour of these and other marine mammals, as it considered the effect of the different factors acting in combination. It is recommended that future studies concerning the ventilation characteristics of minke whales examine the possible interactions of these and other biotic or abiotic factors, such as depth, diel period or feeding strategies. This is important not only for our understanding of the diving behaviour of these species, but also to improve the approaches to manage and conserve them. The IWC Scientific Committee recommends that more data on the dive behaviour of minke whales and the evident factors affecting their dive times should be collected. Because this information is essential for the studies of species abundances, the lack of these crucial data could lend to erroneous estimations of minke whales population size.

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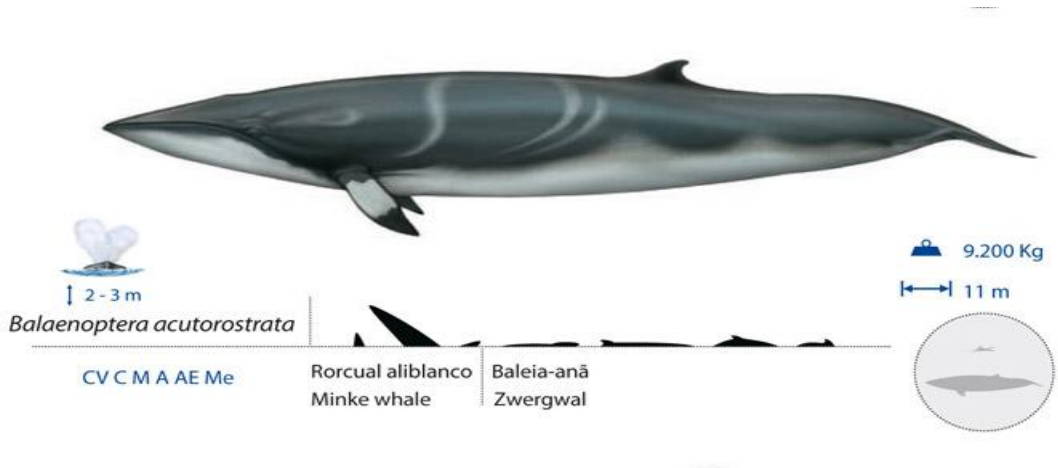
APPENDIX 1



Common name	minke whale, pikehead, lesser rorquals, little piked whale
Scientific names	*Balaenoptera acutorostrata*, *B. bonaerensis*

***B. acutorostrata* (northern hemisphere)**

	Female	Male
Maximum Adult Length	9.1m.	8.8m.
Average length at Sexual Maturity	7.4m.	6.9m.
Average Weight at Sexual Maturity	4-5 tonnes	4-5 tonnes
Gestation	10 months	
Age at Maturity	7-8 years	7-8 years
Longevity	up to 60 years	

***B. bonaerensis* (southern hemisphere)**

	Female	Male
Maximum Adult Length	10.7m.	9.8m.
Average length at Sexual Maturity	7.9m.	7.9m.
Average Weight at Sexual Maturity	4-5 tonnes	4-5 tonnes
Gestation	10 months	
Age at Maturity	7-8 years	7-8 years
Longevity	up to 60 years	

APPENDIX 2

Table showing descriptive statistics for the 31 focal follows recorded between 2006 and 2010. The table shows the subadults (SA) and adults (A).

	MEDIAN Surfacing Intervals (seconds)	**Interquartile range** Surfacing Intervals (seconds)	**MEAN** Surfacing Intervals (seconds)	**Standard deviation** Surfacing intervals (seconds)	**Surfacing rate** (SPWPH)
1 SA	57	61	64	35	66
2 SA	68	52	74	40	49
3 SA	37	70	63	48	58
4 SA	40	54	69	86	55
5 SA	15	85	97	109	56
6 SA	53	59	71	52	58
7 SA	68	66	86	52	42
8 SA	35	66	67	79	54
9 SA	41	90	80	85	45
10 SA	76	66	85	54	42
11 SA	33	183	138	180	26
12 SA	33	91	59	57	62
13 SA	50	62	65	44	55
14 SA	93	86	101	77	36
15 SA	56	65	65	40	55
16 A	81	80	91	69	40
17 A	74	81	82	54	41
18 A	34	34	41	28	90

19 A	30	48	71	95	51
20 A	26	55	46	39	79
21 A	56	20	53	18	67
22 A	62	40	58	24	66
23 A	23	108	60	60	60
24 A	34	64	56	44	65
25 A	40	219	111	115	32
26 A	47	43	80	82	45
27 A	31	64	63	65	58
28 A	39	30	43	20	85
29 A	13	49	47	67	77
30 A	14	25	48	76	75
31 A	73	69	83	60	43

APPENDIX 3

Statistical results (SPSS 18.0)

1) Spearman's rank correlation (mean surfacing interval per whale and SPWPH)

Correlations

			meansec	SPWPH
Spearman's rho	meansec	Correlation Coefficient	1.000	-.969**
		Sig. (2-tailed)	.	.000
		N	31	31
	SPWPH	Correlation Coefficient	-.969**	1.000
		Sig. (2-tailed)	.000	.
		N	31	31

2) Subadults foraging

Tests of Between-Subjects Effects

Dependent Variable:Subadults foraging

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	692980.395[a]	3	230993.465	4.081	.008
Intercept	3.846E7	1	3.846E7	679.472	.000
months	692980.395	3	230993.465	4.081	.008
Error	1.217E7	215	56607.475		
Total	5.618E7	219			
Corrected Total	1.286E7	218			

TUKEY test for subadults foraging

Multiple Comparisons

Subadults foraging

Tukey HSD

(I) months	(J) months	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
June	July	48.2790	42.27840	.664	-61.1898	157.7477
	August	140.1001*	47.36940	.018	17.4495	262.7507
	October	135.7978*	51.17164	.042	3.3023	268.2933
July	June	-48.2790	42.27840	.664	-157.7477	61.1898
	August	91.8211	43.05940	.146	-19.6699	203.3121
	October	87.5189	47.21006	.251	-34.7191	209.7569
August	June	-140.1001*	47.36940	.018	-262.7507	-17.4495
	July	-91.8211	43.05940	.146	-203.3121	19.6699
	October	-4.3023	51.81878	1.000	-138.4733	129.8688
October	June	-135.7978*	51.17164	.042	-268.2933	-3.3023
	July	-87.5189	47.21006	.251	-209.7569	34.7191
	August	4.3023	51.81878	1.000	-129.8688	138.4733

3) Subadults travelling

Tests of Between-Subjects Effects

Dependent Variable:subadults travelling

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	295789.014[a]	2	147894.507	2.768	.066
Intercept	2.013E7	1	2.013E7	376.907	.000
monthsII	295789.014	2	147894.507	2.768	.066
Error	8600882.242	161	53421.629		
Total	4.632E7	164			
Corrected Total	8896671.256	163			

4) Adults foraging

Tests of Between-Subjects Effects

Dependent Variable:Adults foraging

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	434136.917[a]	1	434136.917	8.974	.003
Intercept	2.565E7	1	2.565E7	530.139	.000
monthsIII	434136.917	1	434136.917	8.974	.003
Error	8659290.774	179	48375.926		
Total	3.932E7	181			
Corrected Total	9093427.691	180			

5) Adults travelling

Tests of Between-Subjects Effects

Dependent Variable:Adults travelling

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.425E6	2	712390.554	11.922	.000
Intercept	3.641E7	1	3.641E7	609.270	.000
monthsIIII	1424781.108	2	712390.554	11.922	.000
Error	1.649E7	276	59755.387		
Total	5.822E7	279			
Corrected Total	1.792E7	278			

Tukey test for adults travelling

Multiple Comparisons

Adults travelling

Tukey HSD

(I) months	(J) months	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
June	July	128.8606*	34.39374	.001	47.8142	209.9070
	August	-38.9884	47.34252	.689	-150.5477	72.5708
July	June	-128.8606*	34.39374	.001	-209.9070	-47.8142
	August	-167.8490*	42.27422	.000	-267.4652	-68.2328
August	June	38.9884	47.34252	.689	-72.5708	150.5477
	July	167.8490*	42.27422	.000	68.2328	267.4652