



BI4016 Research Project Thesis

2023/24 School of Biological Sciences

**Diving and surfacing characteristics of coastal minke whales (*Balaenoptera acutorostrata*)
in the Moray Firth, Scotland: Implications for visual estimates of population size**

Jade Rogers

Supervisors: Dr Joanna Kershaw & Dr Kevin Robinson

Work completed in partial fulfilment of the requirements for the degree BSc (Hons) Zoology

Word count (excluding references): 5034

Abstract

The common minke whale (*Balaenoptera acutorostrata*) is a protected species in the UK under the European Protected Species (EPS) Act. A greater understanding of the intraspecific variation in diving behaviour and surfacing patterns is needed for the species to provide more accurate criteria for cue count abundance surveys. The aim of this study was to investigate the factors influencing diving behaviour, and thus surfacing rates, by analysing the effect of age (adult *versus* juvenile) and behaviour (feeding *versus* travelling) in these whales. A total of 47 focal follows were collected between June and September 2006 to 2023 in the Moray Firth, Scotland. A one-way ANOVA was used to highlight initial differences in the mean number of surface events per hour, finding higher surfacing rates in adult and feeding whales. Generalised Linear Models (GLM) were used to determine which variables influenced diving and surfacing behaviour. No variables influenced dive duration, with a non-significant negative correlation shown between surface duration and dive duration, however both age and behaviour were found to significantly influence the time spent at the surface. Adults were shown to have longer pre-dive and post-dive surface durations than juveniles, and feeding whales were shown to have longer pre-dive surface durations than travelling whales, irrespective of the dive duration. A strong correlation was found between surface duration and the number of breaths taken, showing that the whales take more breaths when recovering for longer at the surface in order to replenish their oxygen stores. As surface duration and dive duration were found to be negatively correlated, this indicated that oxygen store management occurs over multiple dive cycles rather than single dives. Overall, the study concluded that age and behaviour significantly influenced the time the whales spent at the surface and therefore the probability that an animal would be detected during line transect survey work for species estimations. The key findings of this study will contribute to conservation and management strategies by updating current methodology for more accurate estimations of population sizes.

1. Introduction

The common minke whale (*Balaenoptera acutorostrata*) is the smallest and most abundant of the mysticetes (baleen whales) and of the balaenopterids (rorqual whales) in UK waters (Horwood, 1989) with, according to the latest SCANS survey, an estimated North Sea population size of almost 9,000 (Hammond *et al.*, 2017). The common minke whale migrates to high-latitude summer feeding grounds, often in shallow, coastal waters between 9-70m (Lechwar *et al.* 2023; Robinson *et al.*, 2009) and is most commonly sighted between June and October within the highly productive shelf waters of the outer Moray Firth, in northeast Scotland (Robinson *et al.*, 2009).

For decades now, human driven activities have threatened the global minke whale population. Entanglement has been responsible for 56% of stranded minke whales in Scotland

between 1990 and 2010, noise pollution masks up to 97% of cetacean communication signals, and interactions with vessels can significantly impact feeding (Lechwar *et al.*, 2023). Minke whales are also at risk from commercial whaling operations (Clapham *et al.*, 1999). Historically, minke whales were not favoured by large-scale whaling operations until the 1950s, when stocks of larger whale species such as blue (*Balaenoptera musculus*) and sei whales (*Balaenoptera borealis*) became severely depleted.

The International Union for Conservation of Nature (IUCN) currently lists the common minke whale as of 'Least Concern' (Cooke, 2018), primarily because they have been targeted less than other whale species. Despite multiple studies revealing a decline in minke whale populations (Lechwar *et al.*, 2023; Pike *et al.*, 2020), they are still hunted commercially today in the North Sea, surrounding Atlantic Ocean, and Norwegian Sea by Norway and Iceland (Wong *et al.*, 2023). The International Whaling Commission (IWC) estimates that Norway takes up to 900 individuals a year based on a self-allocated quota, however little is known as to how much this impacts upon the North Sea population (IWC, 2021). Quotas are based on population size; however, cetaceans are difficult to provide an accurate estimate of abundance for given that they predominantly spend their time submerged underwater. Therefore, it is essential to accurately determine population sizes to analyse population trends over time and assess the effectiveness of conservation initiatives to determine the impact of these threats.

Studies on population size use a detection function known as $g(0)$ – the probability of detecting an object on a survey transect line (Thomsen *et al.*, 2004). Boat and aerial cue count surveys detect cues (usually a blow or dorsal fin sighting at the surface) and use them to estimate animal density (e.g. Hiby *et al.*, 1989). The main assumption of this method is that all animals on the transect line are detected (Barlow, 2015). However, cetaceans spend much of their time beneath the water, only appearing at the surface for a short interval to breathe. Cetacean dive times range from an average of 5 minutes for common dolphins (*Delphinus delphis*) to up to 90 minutes for sperm whales (*Physeter macrocephalus*) (Ridgeway, 1986) and so the detection function becomes unreliable if such differences are not accounted for. Surfacing behaviour significantly alters the probability of an individual being detected (known as availability bias). This heterogeneity in surfacing behaviour can be modelled by including variables such as age class and behaviour in the detection function to more accurately estimate abundance for those species that spend less time than others at the surface (Thomsen *et al.*, 2004). For example, parameters can be adjusted when estimating abundance in a known feeding area, or an area more commonly associated with a particular age class (e.g. Robinson *et al.* 2023).

Diving and surfacing behaviours can be subdivided into activities associated with feeding and travelling. Feeding behaviours recorded in minke whales include bird-associated feeding, in which whales exploit concentrations of fish compacted into 'bait balls' by seabirds at the sea

surface and by predatory fish from below; lunge feeding, where aggregated prey is engulfed at the air-water interface and corralling manoeuvres which aid in concentrating and capturing prey (Hoelzel *et al.*, 1989; Robinson and Tetley, 2007; Christiansen *et al.*, 2015). The specialised feeding behaviours of minke whales are thought to be a learned strategy for coping with patchy prey distributions and unpredictable variations in resource availability (Hoelzel *et al.*, 1989). Diving ability in cetaceans is most commonly hypothesised to vary by physiological constraints, as a result of the aerobic dive limit (ADL) (Croll *et al.*, 2001; Quick *et al.*, 2020). The ADL was originally defined by Kooyman *et al.* (1980) in Weddell seals as the maximum breath hold without an increase in blood lactate, however it is now considered to be the relationship between usable oxygen stores and the rate of oxygen consumption (Butler, 2006). As oxygen is the main limiting factor in air breathing vertebrates, oxygen stores determine ADL (Acevedo-Gutiérrez *et al.*, 2002). Studies into ADL have led to the question of whether variations in surfacing behaviour in cetaceans such as minke whales are associated with preparing for or recovering from a dive. To date, however the answer has remained undetermined, and this question is still highly debated.

The aim of the study is to better understand the intraspecific variation in diving and surfacing behaviours in the coastally occurring minke whale. Specifically, how the behaviours are affected by age class (adult *versus* juvenile) and behaviour (feeding *versus* travelling). The study will investigate the overall effect of age class and behaviour on surfacing rates to reveal differences in the probability of a minke whale being detected during line transect survey work. Furthermore, the study will aim to understand the drivers of diving and surfacing behaviour and to answer if the whales prepare for or recover from a dive. This information will overall provide excellent criteria for correcting biased population estimates and allow for more accurate decisions on future conservation and management strategies for minke whales.

The hypotheses for the study are as follows: firstly, adult minke whales dive for longer durations than juveniles, due to their larger oxygen stores, therefore requiring a longer surface duration to recover, and leading to a higher surfacing rate per hour. Secondly, feeding minke whales dive for longer than travelling minke whales, due to their need to access their prey, which therefore requires a longer surface duration for recovery, and predictably results in a higher surfacing rate per hour. Thirdly, there is a strong correlation between dive duration and surface duration.

2. Methods

2.1. Survey method and data collection

The dataset used in this study was provided by the Cetacean Research & Rescue Unit (CRRU), based in Banff, Scotland. Dedicated boat surveys for minke whales were carried out between June and September 2006 to 2023, within a 1980 km² area along the southern coastline of the outer Moray Firth in NE Scotland (Figure 1) which was recently designated as a Marine Protected Area (MPA) (Marine Scotland, 2020).

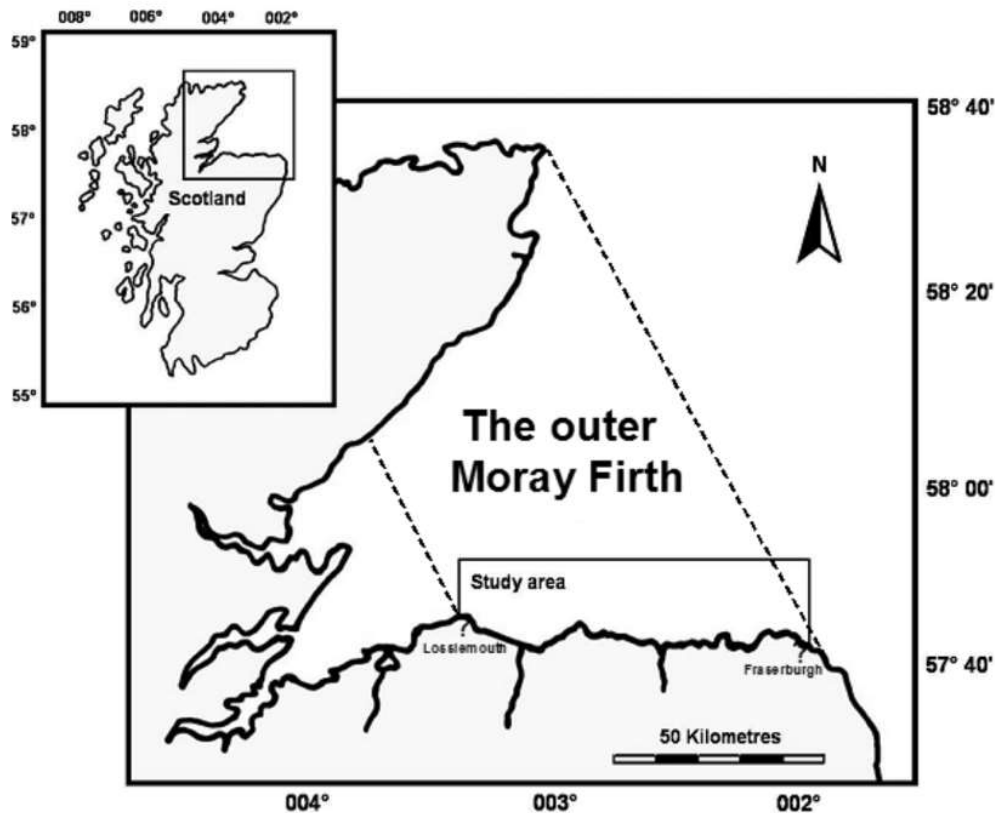


Figure 1. The outer Moray Firth in NE Scotland and the 1980km² study area between Lossiemouth and Fraserburgh (Robinson and Tetley, 2007).

The boat surveys were carried out using an 8-metre rigid hulled inflatable boat (RHIB) with up to eight trained observers in Beaufort sea state ≤ 4 and visibility ≥ 1 km). When a minke whale was located, standard information for all whale sightings was taken including the geographic position, water depth (m), and sea-surface temperature (°C) and the behaviour (travelling, feeding) and age class (adult, juvenile) of the whale (Table 1).

Focal follows (the practice of observing an individual for a period of time), from which the dive intervals were recorded, were only conducted on solitary minke whales in order to prevent unintentionally following two whales during the focal follow. If the whale was lost, the focal follow was dismissed and restarted once the whale was relocated again.

During a dedicated focal follow, the time (in minutes) was recorded from the first surface event and noted between each subsequent surface or blow (exhalation). The bearing and distance (in metres) from the whale and direction of travel after each surface event (in cardinal direction) was noted. The time between successive blows was used to determine the stage of the dive cycle (Figure 2), and direction of travel after each surface event was used to determine the behaviour of the individual (Table 1).

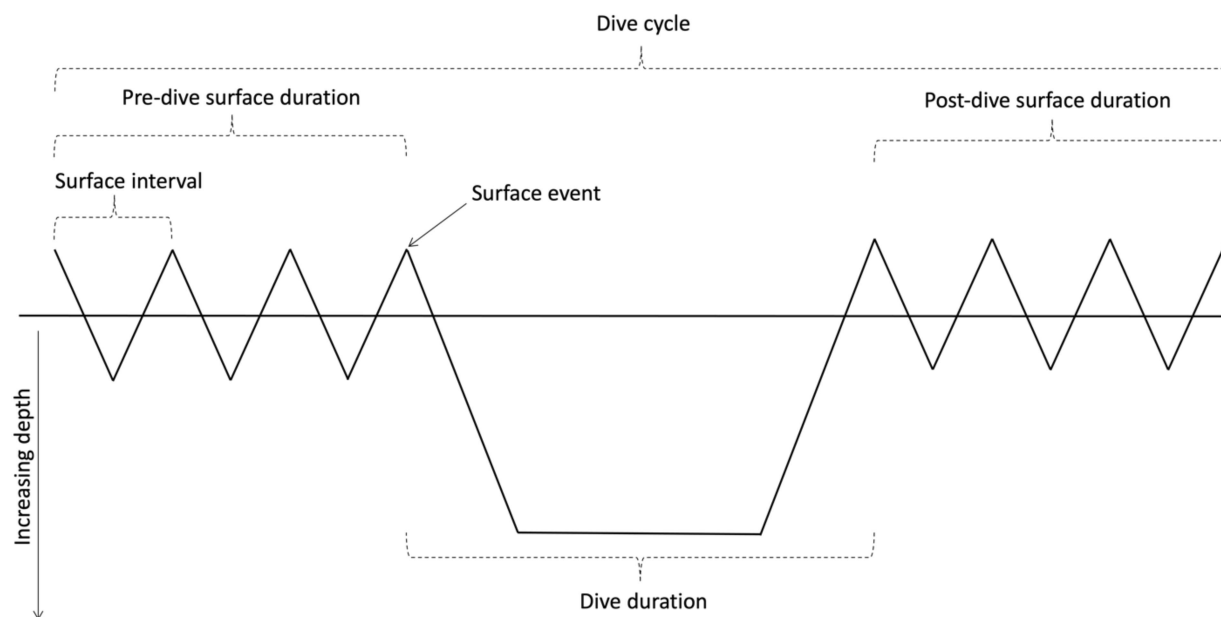


Figure 2. The dive cycle of a minke whale - see Table 2 for descriptions of each stage.

2.2. Classification of age class and behaviour

Each focal whale was assigned to an age class and behaviour prior to the start of the focal follow, based on descriptions in Table 1.

Table 1. Descriptions of age class and behaviour.

Class	Description
Adult	Darker coloured individuals with a body length of more than 6.5m (Mitchell and Kozicki 1975, quoted from Robinson <i>et al.</i> (2023)).
Juvenile	Lighter coloured individuals with a body length of less than 6.5m (Mitchell and Kozicki 1975, quoted from Robinson <i>et al.</i> (2023)).
Travelling	Moving in a straight line, with the direction remaining constant throughout. Surface events were regular with short surfacing intervals.
Feeding	Moving in a circular or figure of eight like pattern. Typically, with long dives over 1 min long. Other feeding behaviours may have been observed such as feeding strikes or bird-associated feeding.

2.3. Data analysis

Only focal follows lasting more than 20 minutes were used in the analyses. 12 (< 20 mins) were excluded from the study leading to a total of 47 for the subsequent analyses.

Each focal follow was individually processed, and the stages of the dive cycle were determined based on the descriptions in Table 2. Each surface interval and dive time was converted from minutes into seconds. To measure surface duration, the sum of the surface intervals in between dives was calculated. The final dataset comprised of each dive duration (in secs) with a corresponding pre-dive and post-dive surface duration. If two or more dives were adjacent to each other with only a single surface event, and therefore no surface interval, the surface duration was assumed to be 1 second (the length of one exhalation and inhalation). The first and last dive cycles of each focal follow were removed as they could not be associated with a complete dive cycle with both pre-dive and post-dive surface durations.

The surfacing rate (mean number of surface events per hour) was calculated for each whale using the equation adapted from Weir *et al.* (2023):

$$\left(\frac{B}{D} \times 60\right)$$

Where B is the total number of surfacing events – 1 and D is the total duration of the focal follow (in decimal minutes).

Table 2. Descriptions of each stage of the dive cycle, as seen in Figure 2.

Stage	Description
Pre-dive surface duration	The sequence of successive, short, regular surface events before a dive.
Post-dive surface duration	The sequence of successive, short, regular surface events after a dive.
Surface event	The whale breaking the surface of the water, which usually included a blow but was also defined as a back or dorsal fin sighting (Weir <i>et al.</i> , 2023).
Surface interval	The time elapsed between two successive surface events (also known as inter-breath interval (Weir <i>et al.</i> , 2023)), lasting for less than 60 seconds (Lagerquist <i>et al.</i> , 2000).
Dive	A true dive lasted for more than 60 seconds (Lagerquist <i>et al.</i> , 2000).
Dive cycle	The full cycle of a pre-dive surface duration, followed by a true dive and a post-dive surface duration.

2.4. Statistical analysis

R (v 4.2.2) was used to analyse the data set. 'Variables' hereby refer to dive duration, pre-dive surface duration, post-dive surface duration, age class, and behaviour.

A one-way analysis of variance (ANOVA) was used to analyse the surfacing rates to determine any statistical difference in age class (adults *versus* juveniles) and behaviour (feeding *versus* travelling), and the results were visualised using the ggplot function (CRAN: ggplot2).

Three generalised linear models (GLM) (with Gamma distribution and log link function) were fitted to the data, using the glm function, with dive duration, pre-dive surface duration and post-dive surface duration each as the response variable. A GLM was chosen for its flexibility to cope with non-linear relationships and lack of normal distribution in the data. GLMs also included age class and behaviour as potential predictors, as well as interactions between them. The dredge function (CRAN: MuMin) was used to perform backwards model selection on all GLMs based on model weights derived from Akaike's Information Criterion (AIC) to determine which variables should be included in the final best fitting model. All models with AIC values within 2 points of each other were included for model averaging using the model.avg function (CRAN: MuMin). In the summary of the model averages, the conditional averages (rather than full averages) were used, as not all variables were included in every model. *P* values were used to determine which of the predictors included in the model had a significant influence on the response variable. The predicted relationships and their 95% confidence intervals were visualised using the predict and ggplot functions (CRAN: ggplot2).

Additionally, a linear model (LM) was used to analyse the relationship between the number of pre-dive/post-dive breaths and pre-dive/post-dive surface durations. The relationships and their 95% confidence intervals were once again visualised using ggplot (CRAN: ggplot2). Model assumptions were checked.

3. Results

47 focal follows were collected between June and September 2006 to 2023, resulting in approximately 24.5 hours of focal follow data and a total of 1,243 surfacing events.

3.1. Surfacing Rates

The surfacing rates ranged from 20.58 to 85.95 hr^{-1} , with an overall mean surfacing rate of 52.44 hr^{-1} ($\text{SD} \pm 15.44$). Adult minke whales and feeding minke whales showed a significantly higher surfacing rate than juveniles and travelling minke whales (one-way ANOVA: $F_{1,42} = 7.11$, $P = 0.01$ and $F_{1,44} = 7.09$, $P = 0.01$, respectively).

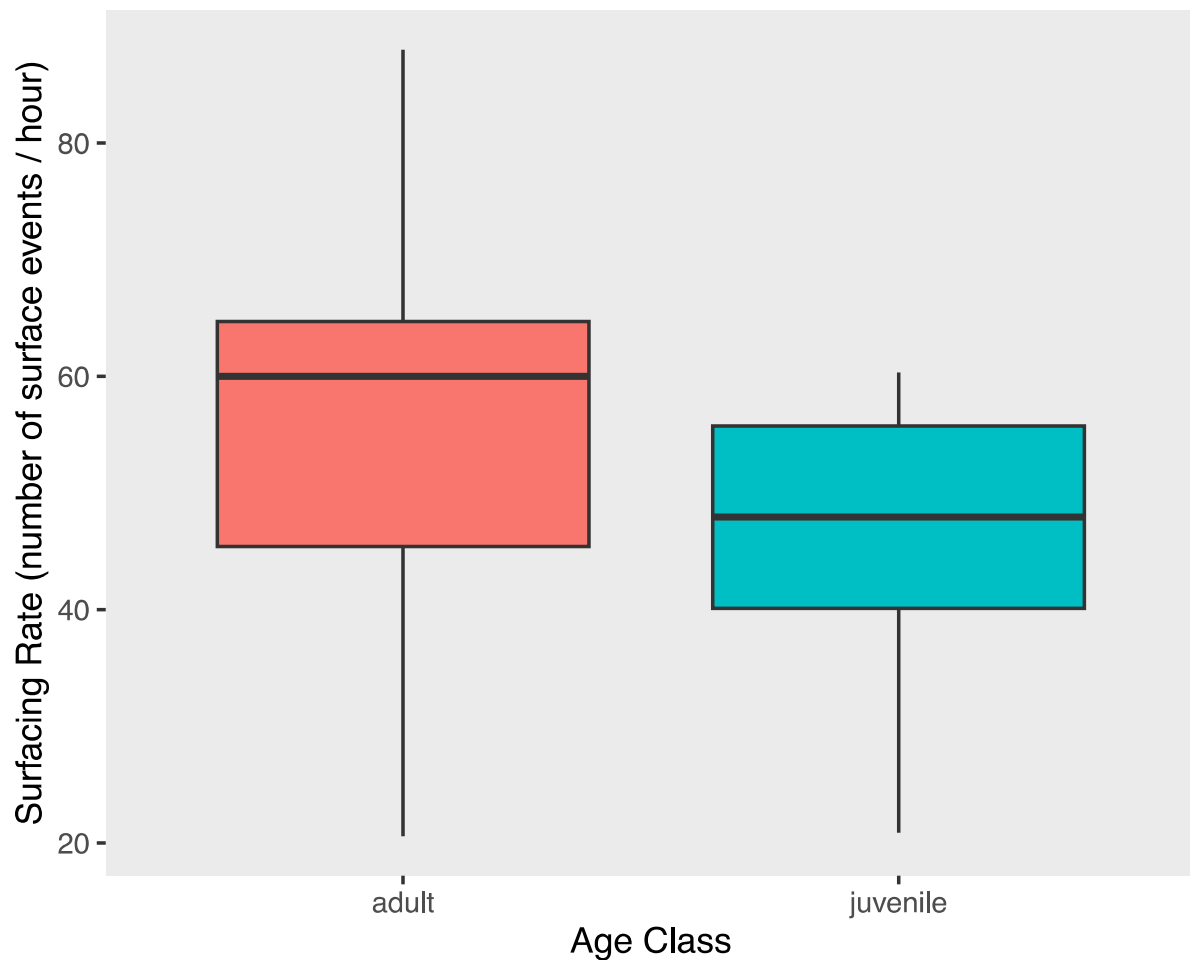


Figure 3. A comparison of the number of surfacing events per hour for adult and juvenile minke whales. (adults $N = 27$, juveniles $N = 20$). Boxplot presents maximum and minimum values (Adults: $\text{max} = 88.0 \text{ hr}^{-1}$, $\text{min} = 20.58 \text{ hr}^{-1}$. Juveniles: $\text{max} = 60.35 \text{ hr}^{-1}$, $\text{min} = 20.90 \text{ hr}^{-1}$) and median values (adults = 60 hr^{-1} , juveniles = 47.93 hr^{-1}).

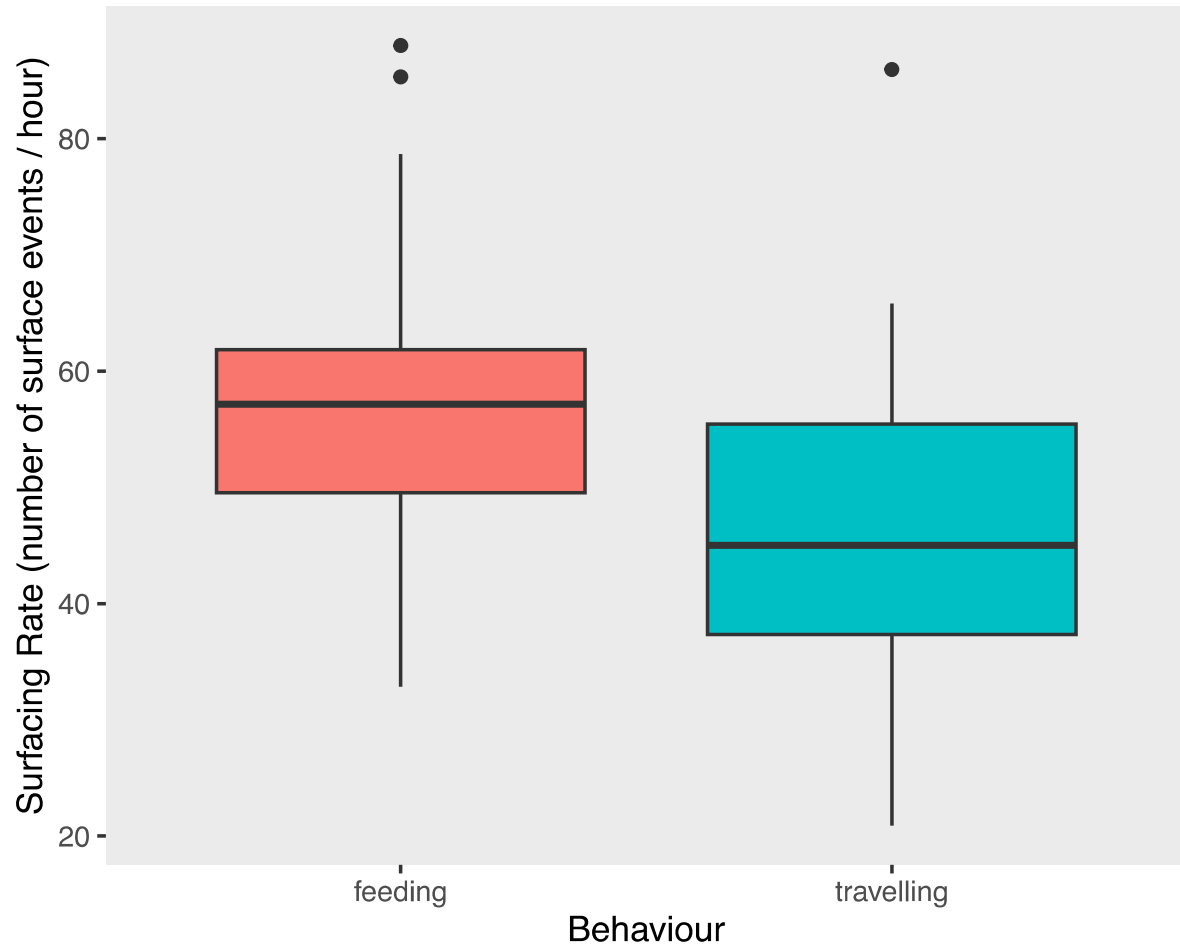


Figure 4. A comparison of the number of surfacing events for feeding and travelling minke whales. (Feeding $N = 29$, travelling $N = 18$). Boxplot presents maximum and minimum values (Feeding: $\max = 88.01 \text{ hr}^{-1}$, $\min = 20.58 \text{ hr}^{-1}$. Travelling: $\max = 85.95 \text{ hr}^{-1}$, $\min = 20.90 \text{ hr}^{-1}$) and median values (Feeding = 57.05 hr^{-1} , juveniles = 45.01 hr^{-1}).

3.2. Generalised Linear Models

3.2.1. Dive duration

The durations of true dives ranged from 60 to 731 seconds. Model averaging of the best fitting models showed that no variable in the model had a significant effect on dive duration. No significant relationship was detected between dive duration and pre-dive or post-dive surface duration ($Z = 0.93$, $P = 0.35$ and $Z = 1.17$, $P = 0.24$, respectively).

Table 3. 'Dredge' model selection results of GLM to explain dive duration: age = age class, beh = behaviour, pre = pre-dive surface duration, post = post-dive surface duration, + = additive.

Fixed effects	df	LogLik	AICc	delta	weight
age	3	-2198.85	4403.76	0.00	0.08
age+post	4	-2198.05	4404.20	0.43	0.07
post	3	-2199.20	4404.47	0.70	0.06
beh	3	-2199.33	4404.73	0.96	0.05
age+beh	4	-2198.33	4404.77	1.01	0.05
beh+post	2	-2200.38	4404.79	1.03	0.05
age+pre	4	-2198.40	4404.89	1.13	0.05
age+beh+post	4	-2198.56	4405.22	1.46	0.04
post+pre	5	-2197.63	4405.40	1.64	0.04
pre	4	-2198.75	4405.61	1.85	0.03
age+beh+pre	3	-2199.81	4405.68	1.91	0.03
beh+pre	6	-2196.74	4405.68	1.92	0.03
age+post+pre	5	-2197.79	4405.72	1.96	0.03
beh+post+pre	5	-2197.80	4405.76	2.00	0.03

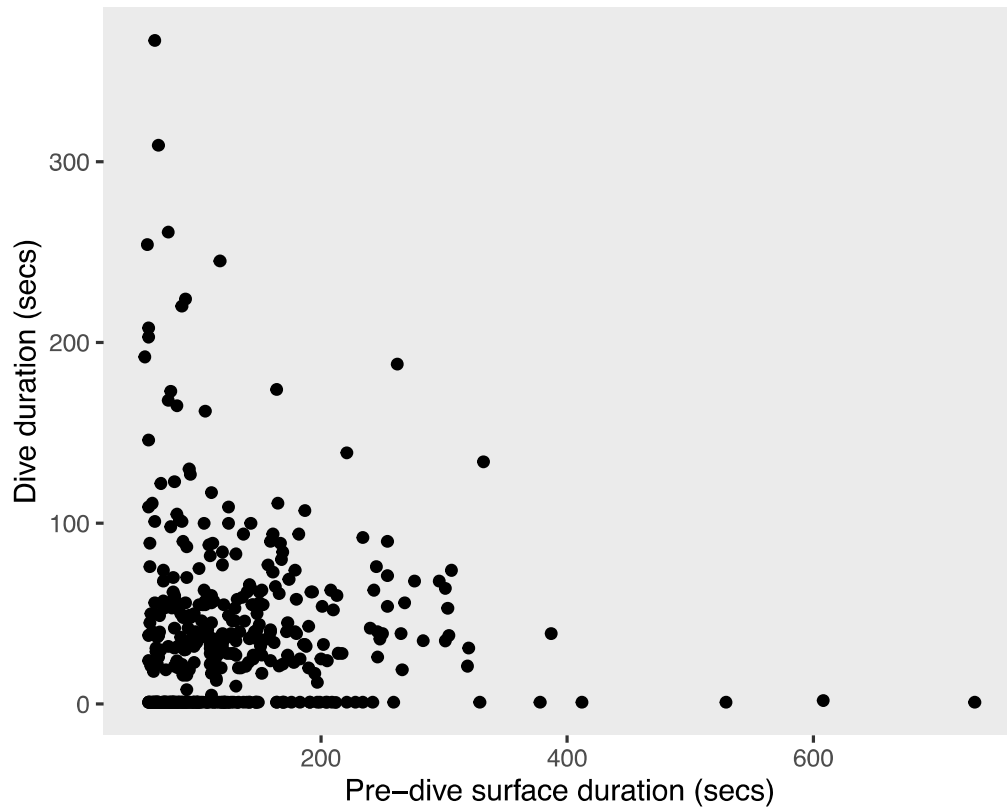


Figure 5. Lack of relationship between dive duration (secs) and pre-dive surface duration (secs).

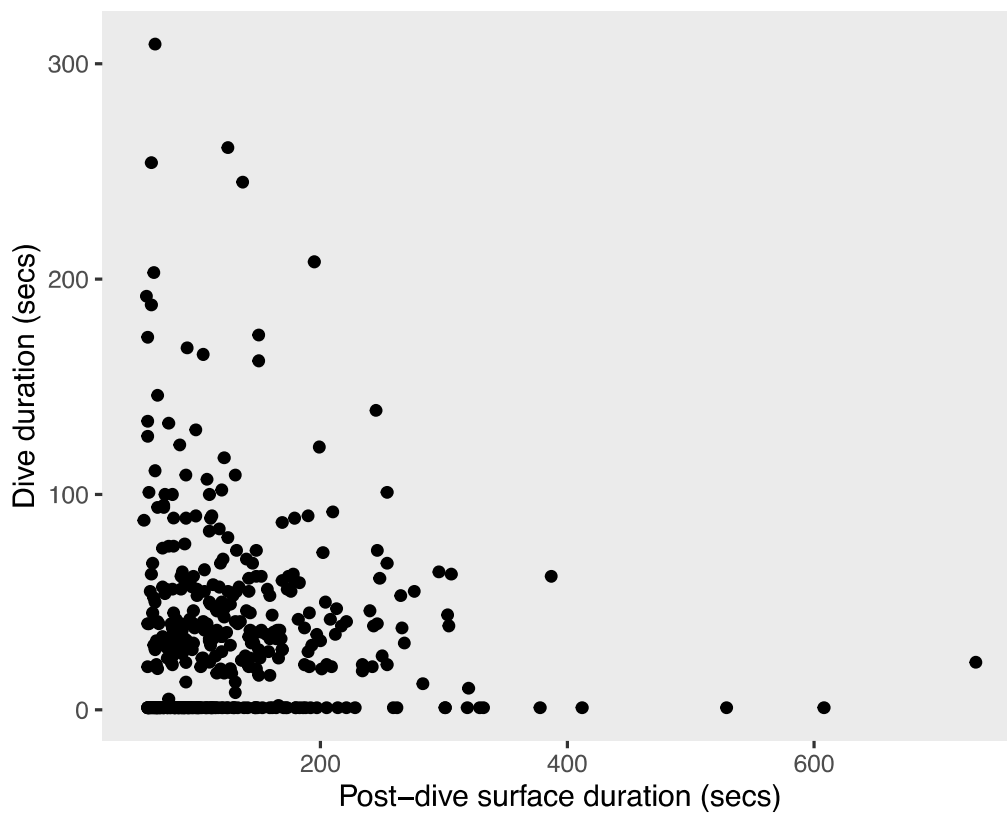


Figure 6. Lack of relationship between dive duration (secs) and post-dive surface duration (secs).

3.2.2. Pre-dive surface duration

Pre-dive surface durations ranged from 1 to 367 seconds. Both age class and behaviour were found to significantly influence the pre-dive surface duration averaged model ($Z = 2.83$, $P < 0.01$ and $Z = 2.61$, $P < 0.01$, respectively). Juvenile and travelling minke whales had shorter pre-dive surface durations. One interaction between age class and post-dive surface duration was detected but it was not found to be significant ($Z = 1.77$, $P = 0.08$). Overall, a non-significant negative relationship was detected between dive duration and pre-dive surface duration.

*Table 4. 'Dredge' model selection results of GLM to explain dive duration: age = age class, beh = behaviour, post = post-dive surface duration, dive = dive duration, + = additive, * = interaction.*

Fixed effects	df	LogLik	AICc	delta	weight
age+beh	4	-1814.35	3636.80	0.00	0.18
age+beh+post	5	-1813.81	3637.78	0.98	0.11
age+beh+post+age*post	6	-1812.90	3638.01	1.21	0.10
age+beh+dive	5	-1814.32	3638.79	1.99	0.07

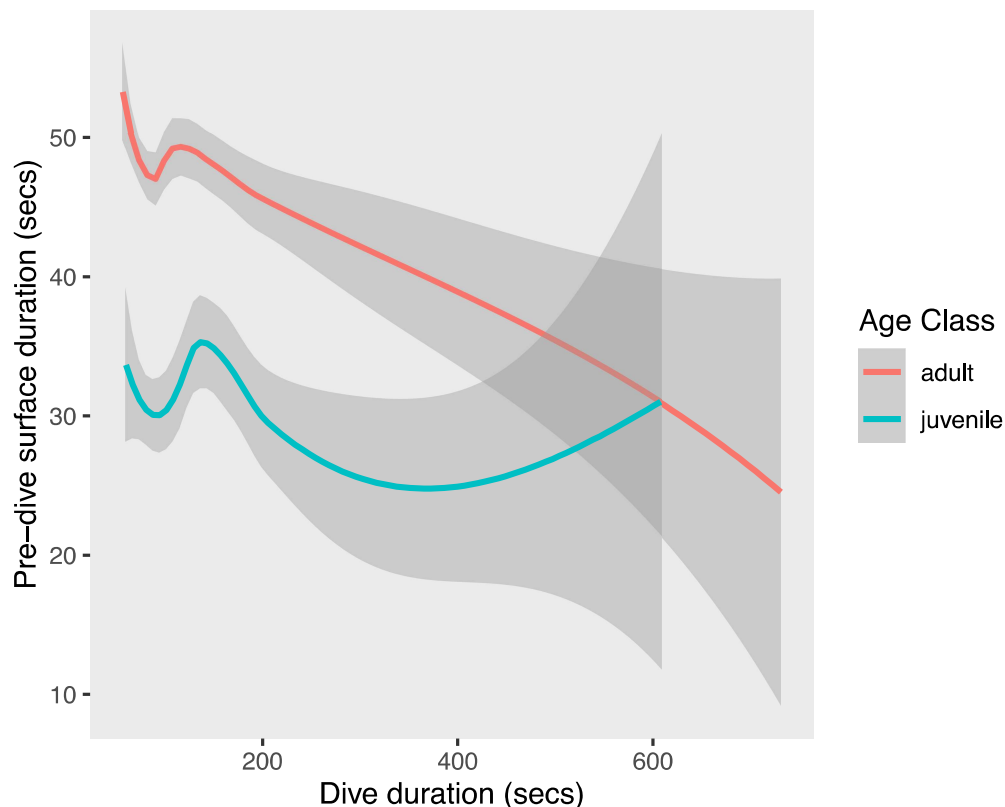


Figure 7. Predicted outputs of the GLM using a gamma regression analysis (response = pre-dive surface duration (secs), predictors = dive duration (secs) and age class) with 95% confidence intervals.

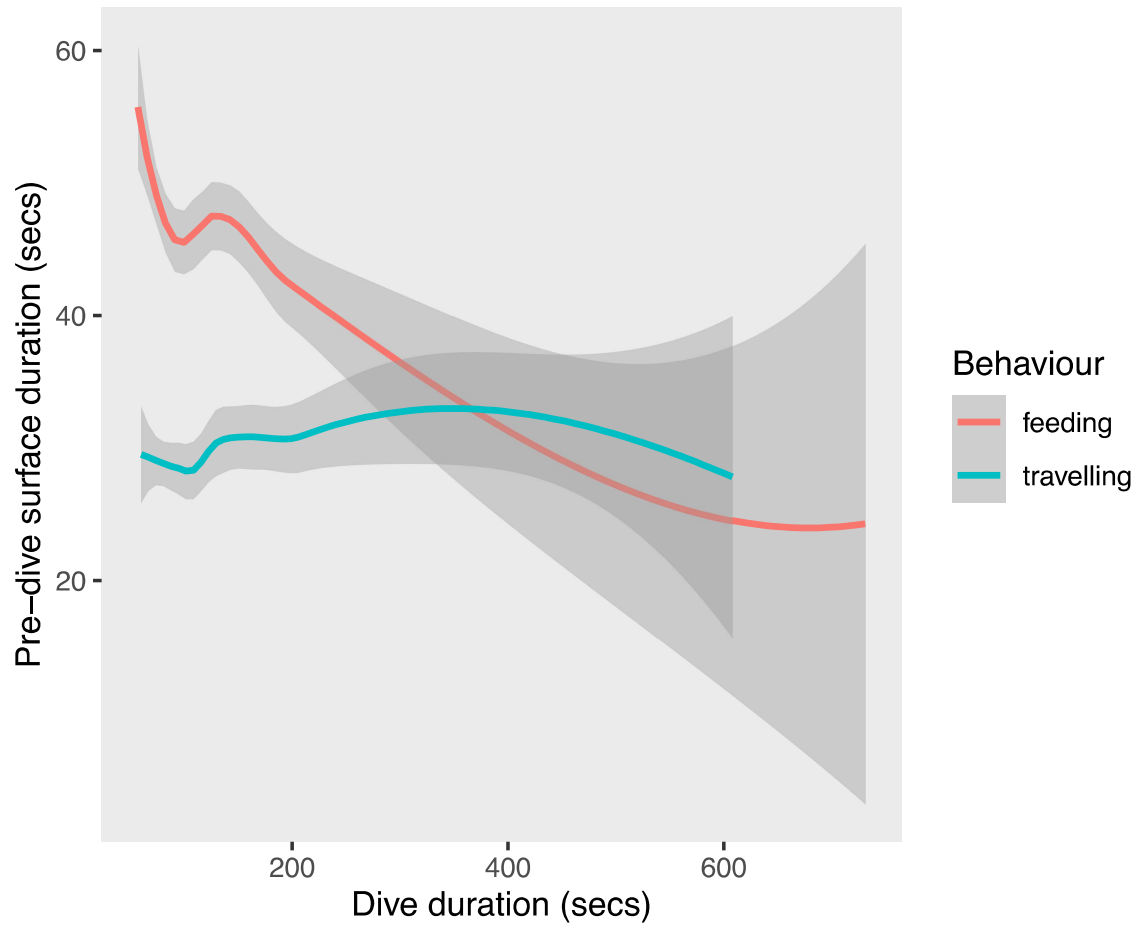


Figure 8. Predicted outputs of the GLM using a gamma regression analysis (response = pre-dive surface duration (secs), predictors = dive duration (secs) and behaviour) with 95% confidence intervals.

3.2.3. Post-dive surface duration

Post-dive surface durations ranged from 1 to 309 seconds. All variables were found to influence the post-dive surface duration model and were included in the final averaged model (Table 4), however only age class was found to have a significant effect ($Z = 3.07$, $P < 0.01$). Juveniles had a shorter post-dive surface duration than adults (Figure 9). Overall, a non-significant negative relationship was detected between dive duration and post-dive surface duration.

Table 5. 'Dredge' model selection results of GLM to explain post-dive surface duration: age = age class, beh = behaviour, pre = pre-dive surface duration, dive = dive duration, + = additive.

Fixed effects	df	LogLik	AICc	delta	weight
age+beh	4	-1798.91	3605.93	0.00	0.12
age	3	-1800.06	3606.18	0.25	0.11
age+pre	4	-1799.46	3607.01	1.08	0.07
age+beh+dive	5	-1798.46	3607.07	1.15	0.07
age+beh+pre	5	-1798.49	3607.13	1.20	0.07
age+dive	4	-1799.56	3607.21	1.29	0.06

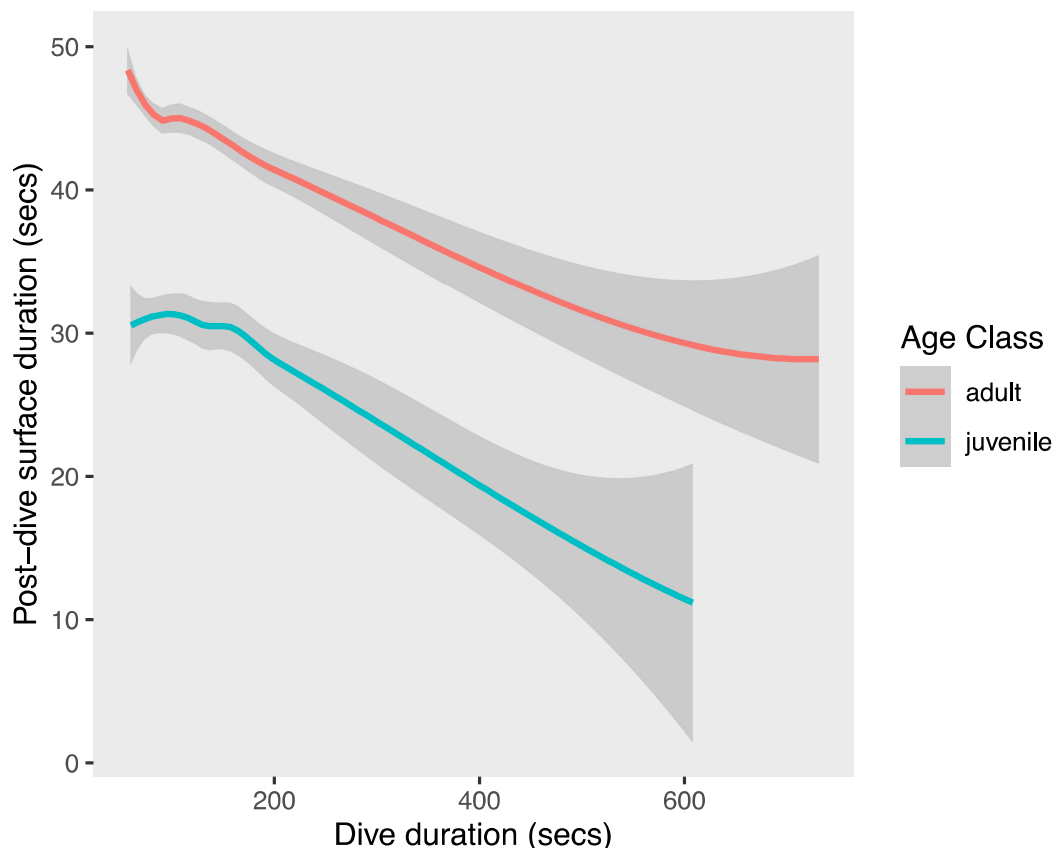


Figure 9. Predicted outputs of the GLM using a gamma regression analysis (response = post-dive surface duration (secs), predictors = dive duration (secs) and age class), with 95% confidence intervals.

3.3. Pre-dive and post-dive breaths

The number of pre-dive and post-dive breaths ranged between 1 and 12 and showed strong, positive correlations with their corresponding surface durations (Adjusted $R^2 = 0.83$, $P < 0.001$, and adjusted $R^2 = 0.80$, $P < 0.001$, respectively).

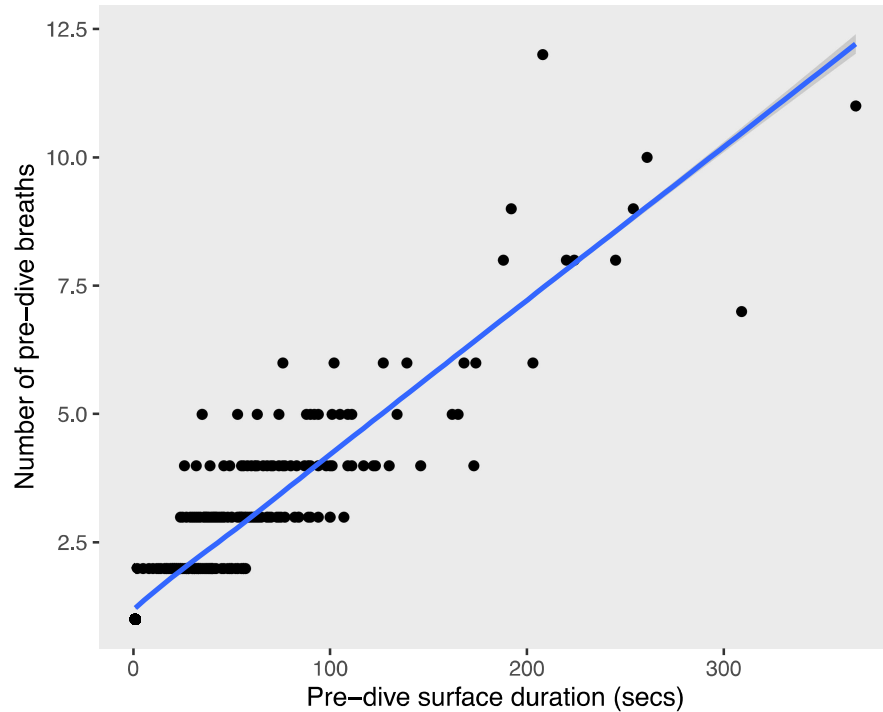


Figure 10. Predicted outputs of the LM (response = number of pre-dive breaths, predictors = pre-dive surface duration (secs)), with 95% confidence intervals.

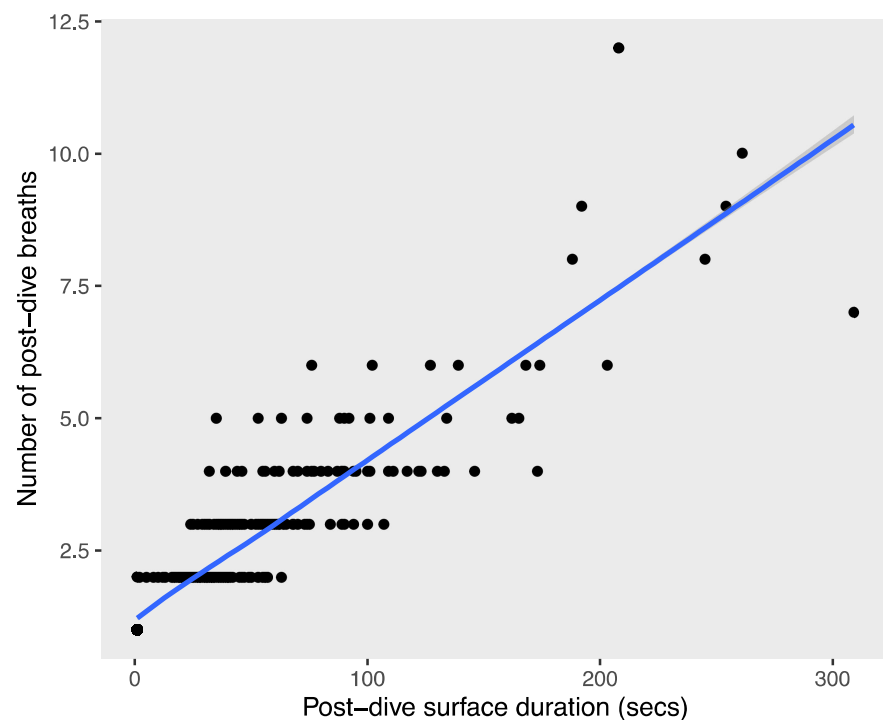


Figure 11. Predicted outputs of the LM (response = number of post-dive breaths, predictors = post-dive surface duration (secs)) with 95% confidence intervals.

4. Discussion

The aim of this study was to better understand the intraspecific variation in the diving and surfacing behaviours of coastal minke whales in the Moray Firth, and to understand how and why these differences occur.

The hypotheses for the study are re-stated as follows: firstly, adult minke whales dive for longer durations than juveniles, due to their larger oxygen stores, therefore requiring a longer surface duration to recover, and leading to a higher surfacing rate per hour. Secondly, feeding minke whales dive for longer than travelling minke whales, due to their need to access their prey, therefore they require a longer surface duration to recover, and have a higher surfacing rate per hour. Thirdly, there is a strong correlation between dive duration and surface duration.

4.1. Surfacing rates

As predicted in the first and second hypotheses, significantly higher surfacing rates were found in adult and feeding minke whales (Figures 3 & 4). The overall mean surfacing rate was 52.44 hr^{-1} (SD ± 15.44), notably similar to other studies on minke whale surfacing behaviour that found surfacing rates of 46.1 and 52.4 hr^{-1} (Weir *et al.*, 2018; Joyce *et al.*, 1989, respectively). Surfacing rates were found to be higher than recorded for sei whales (*Balaenoptera borealis*) at 31.5 hr^{-1} (Weir *et al.*, 2018), lower than humpback whales (*Megaptera novaeangliae*) at 71 hr^{-1} , and very similar to fin whales (*Balaenoptera physalus*) at 52 hr^{-1} (Joyce *et al.*, 1989). The consistency between studies on minke whale surfacing patterns suggests that surfacing rates are a reliable parameter to correct for availability bias in cue count surveys (Heide-Jørgensen and Simon, 2023).

The significant difference in surfacing rates for both age class and behaviour highlights the need to understand the intraspecific differences in diving and surfacing behaviour, in order to provide age and behaviour-specific surfacing parameters. This would allow for availability bias to be corrected in areas known to be highly associated with certain age groups or activity. The reasons for these differences are further investigated in this study.

4.2. Dive duration

The present findings showed that no significant relationship occurred between dive duration and surface duration (Figures 5 & 6), regardless of age or behavioural status. A study by Hooker and Baird 1999 on the deep-diving behaviour of the northern bottlenose whales (*Hyperoodon ampullatus*) also found a lack of correlation between these two variables indicating that these whales are not reaching their aerobic dive limit (ADL). In the case of minke whales in the Moray Firth, this could be a result of the bathymetry of the study area,

or the depth of the prey layer, such that prey may be distributed deeper in the water column resulting in longer dives to access it. Little data exists on the maximum dive depths of the common minke whale. However, studies have logged the maximum dive depth for the Antarctic minke whale (*Balaenoptera bonaerensis*) as $105 \pm 1\text{m}$ (Friedlaender *et al.*, 2014). In the Moray Firth, the minke whale has a strong preference for the lesser sandeel (*Ammodytes marinus*) (Robinson *et al.*, 2023), commonly found between 30-70 metres in the North Sea (Wright *et al.*, 2000). This suggests that the minke whales in the study area are not reaching their maximum dive depth when accessing the prey layer and are therefore not exceeding their ADL. A study by Kooyman *et al.* (1980) on Weddell seals stated that when the maximum ADL threshold was exceeded, the post-dive surface duration increased disproportionately faster than dive duration. Diving below the ADL would therefore maximise time for foraging without the need for a longer recovery time and which would explain why our data show little correlation between dive and surface duration.

4.3. Pre-dive surface duration

The pre-dive surface duration model supported both hypotheses that adult and feeding minke whales spend an increased amount of time at the surface since both age and behaviour had a significant influence on the pre-dive surface duration (Figures 7 & 8). Similarly, to the post-dive surface duration model, the effect of age is most likely a result of the costs of energetically expensive foraging strategies, in view of the active feeding mechanisms more commonly used by adults (Robinson *et al.*, 2023).

Travelling minke whales are simply moving from one patch to another and so are not attempting to maximise their time underwater (Acevedo-Gutiérrez *et al.*, 2002). Therefore, they have no need to prepare for a dive with a long surface duration beforehand, which would require maximising their oxygen uptake. Travelling minke whales are believed to perform short dives to just a few metres depth to avoid the drag created by the surface turbulence (Christiansen *et al.*, 2015), expending less energy and requiring a lower respiration rate to surface less frequently between dives. Baleen whales have also been found to use gliding as a way to reduce energy expenditure (Christiansen *et al.*, 2015) and this strategy may be utilised by minke whales in order to minimise recovery time at the surface post-dive. According to Christiansen *et al.* (2015) minke whales adjust their surfacing patterns with respect to their activities, supporting why higher surfacing rates are inevitably observed in feeding whales.

4.4. Post-dive surface duration

Model averaging showed that age had a significant influence on post-dive surface duration and supported the hypothesis that adults would display a longer surface duration than juveniles (Figure 9). The size of a minke whale increases with age which therefore suggests

there would be differences in both lung capacity and oxygen stores between adults and juveniles which would alter their respective ADLs. Watwood *et al.* (2006) stated that oxygen stores scale linearly and so the larger an animal, the longer it can dive, but the longer it then needs to subsequently recover.

In the Moray Firth, Robinson *et al.* (2023) found that juveniles showed a strong preference for shallow, inshore waters compared to adults, which respectively favoured deeper, offshore waters. Adults also showed greater dietary plasticity than their juvenile counterparts, as well as a greater preference for active feeding strategies such as corralling that expend significantly higher amounts of energy in contrast to the passive feeding strategies more commonly utilised by juveniles. This would suggest that the adults are using more specialised foraging strategies that require increased recovery time post-dive. Thus, showing an increased surfacing rate as a result of their more energetically costly dives.

4.5. Pre-dive and post-dive breaths

Both linear models showed equally strong correlations between pre-dive breaths and pre-dive surface duration, and post-dive breaths and post-dive surface duration, with neither model indicating any preference for preparing for or recovering from a dive (Figures 10 & 11). Longer surface durations will inevitably result in whales taking more breaths to replenish their oxygen reserves; however, the results of the present study suggest a non-significant, negative correlation between surface duration and dive duration with the whales unexpectedly taking fewer breaths when diving longer. This outcome implies that minke whales restore their oxygen levels over multiple dive cycles, rather than single dives, regardless of their activity. Thus, it is difficult to determine if minke whales specifically prepare for or recover from a single dive as they rebalance their oxygen stores over multiple surface durations. Future studies should consider longer focal follows times to account for this, to capture longer periods of oxygen debt to understand the behaviours involved in replenishing oxygen stores.

4.6. Limitations of the study and further research

The present study relied on visual observations of minke whale behaviour at the surface, but further research would benefit from the ability to observe depth and underwater behaviours in relation to dive and surface durations. Since, minke whale behaviour may also vary with other factors, such as human disturbance from whale watching boats (Christiansen *et al.*, 2014; Sprogis *et al.*, 2020), prey type and availability (Anderwald *et al.*, 2012) and time of day/year (Stockin *et al.*, 2001), it would be useful to investigate these in order to provide additional criteria to correct population estimates year-round. The methodology was restricted to favourable conditions during the summer months and, therefore, may not be representative of the behaviour of the species at other times of the year.

Studies such as Christiansen *et al.* (2015), for example, subdivided feeding into specific activities, allowing for deep foraging, near-surface foraging, and surface feeding to be individually analysed for differences in dive durations and recovery times. However, this would also require additional data collection from dedicated tagging studies. Since adults and juveniles evidently show habitat partitioning by age class, further studies into the specific location of sightings would prove useful to consider the differences in diving and surfacing characteristics between habitats. As suggested previously, longer focal follows would prove useful to investigate how oxygen levels are restored over multiple dive cycles.

5. Conclusion

The present study provides accurate information on the varying diving behaviour and surfacing characteristics of minke whales in the Moray Firth, in NE Scotland. Both age and behaviour were found to significantly influence the time spent at the surface and would therefore influence the probability of detection during cue count surveys which should be accounted for when estimating population sizes. The lack of correlation between surface duration and dive duration is ultimately a result of the minke whales not reaching their aerobic dive limit, however surface time is clearly influenced by the specific learned strategies being undertaken by different age classes of whales within the Moray Firth. This study was unable to resolve the fundamental question of whether minke whales prepare for or recover from a dive, but it did suggest that oxygen store management may occur over several dive cycles and therefore should be considered when analysing variations in the surfacing patterns of these ecologically important baleen whales.

Acknowledgements

Firstly, I wish to thank Dr Joanna Kershaw, for her expert guidance and teaching throughout this project.

Secondly, I would like to extend my gratitude to Dr Kevin Robinson, at the Cetacean Research & Rescue Unit, for giving me the opportunity to take on this project and inspiring me to pursue a career in marine mammal science.

References

- Acevedo-Gutiérrez, A., Croll, D. A., & Tershy, B. R. 2002. High feeding costs limit dive time in the largest whales. *The Journal of Experimental Biology*, 205(12), 1747–1753.
- Anderwald, P., Evans, P. G. H., Dyer, R., Dale, A., Wright, P. J., & Hoelzel, A. R. 2012. Spatial scale and environmental determinants in minke whale habitat use and foraging. *Marine Ecology Progress Series*, 450, 259–274.
- Barlow, J. 2015. Inferring trackline detection probabilities, $g(0)$, for cetaceans from apparent densities in different survey conditions. *Marine Mammal Science*, 31(3), 923–943.
- Butler, P. J. 2006. Aerobic dive limit. What is it and is it always used appropriately? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 145(1), 1–6.
- Christiansen, F., Rasmussen, M. H., & Lusseau, D. 2014. Inferring energy expenditure from respiration rates in minke whales to measure the effects of whale watching boat interactions. *Journal of Experimental Marine Biology and Ecology*, 459, 96–104.
- Christiansen, F., Lynas, N. M., Lusseau, D., & Tschertter, U. 2015. Structure and dynamics of minke whale surfacing patterns in the Gulf of St. Lawrence, Canada. *PLOS ONE*, 10(5), e0126396.
- Clapham, P. J., Young, S. B., & Brownell, R. L. 1999. Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Review*, 29(1), 37–62.
- Cooke, J.G. 2018. *Balaenoptera acutorostrata*. *The IUCN Red List of Threatened Species* 2018: e.T2474A50348265.
- Croll, D. A., Acevedo-Gutiérrez, A., Tershy, B. R., & Urbán-Ramírez, J. 2001. The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 129(4), 797–809.
- Friedlaender, A. S., Goldbogen, J. A., Nowacek, D. P., Read, A. J., Johnston, D. W., & Gales, N. J. 2014. Feeding rates and under-ice foraging strategies of the smallest lunge filter feeder, the Antarctic minke whale (*Balaenoptera bonaerensis*). *The Journal of Experimental Biology*, 217(16), 2851–2854.
- Hammond, PS, Lacey, C, Gilles, A, Viquerat, S, Boerjesson, P, Herr, H, Macleod, K, Ridoux, V, Santos, M, Scheidat, M, Teilmann, J, Vingada, J & Oeien, N. 2017. *Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys*. Wageningen Marine Research.

Heide-Jørgensen, M. P., & Simon, M. 2023. A note on cue rates for common minke, fin and humpback whales off West Greenland. *The Journal of Cetacean Research and Management*, 9(3), 211–214.

Hiby, L., Ward, A. and Lovell, P. 1989. Analysis of the North Atlantic sightings survey 1987: aerial survey results. Report of the International Whaling Commission, 39: 447-455.

Hoelzel, A. R., Dorsey, E. M., & Stern, S. J. 1989. The foraging specializations of individual minke whales. *Animal Behaviour*, 38(5), 786–794.

Hooker, S. K., & Baird, R. W. 1999. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings of the Royal Society B: Biological Sciences*, 266(1420), 671–676.

Horwood. 1989. *Biology and exploitation of the minke whale* [Google Books]. CRC Press.

IWC 2021. Total catches. [Available at: <https://iwc.int/total-catches>]

Joyce, G.G., Øien, N., Calambokidis, J. and Cubbage, J.C., 1989. Surfacing rates of minke whales in Norwegian waters. *Reports of the International Whaling Commission*, 39, pp.431-433.

Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W., & Sinnett, E. E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, 138(4), 335–346.

Lagerquist, B. A., Stafford, K. M., & Mate, B. R. 2000. Dive characteristics of satellite-monitored blue whales (*Balaenoptera musculus*) off the central california coast. *Marine Mammal Science*, 16(2), 375–391.

Lechwar, A., Rasmussen, M. H., Basran, C. J., & Collins, S. 2023. Habitat preference of common minke whale (*Balaenoptera acutorostrata*) in Skjálfandi Bay, Iceland. *The Journal of Cetacean Research and Management*, 24(1), 29–46.

Marine Scotland. 2020. *Southern Trench Marine Protected Area: business and regulatory impact assessment*.

Mitchell, E. D., & Kozicki, V. M. 1975. Supplementary Information on Minke Whale (*Balaenoptera acutorostrata*) from Newfoundland Fishery. *Journal of the Fisheries Research Board of Canada*, 32(7), 985–994.

Pike, D. G., Gunnlaugsson, Þ., Sigurjónsson, J., & Víkingsson, G. A. 2020. Distribution and Abundance of Cetaceans in Icelandic Waters over 30 Years of Aerial Surveys. *Nammco Scientific Publications*, 11.

Quick, N. J., Cioffi, W. R., Shearer, J. M., Fahlman, A., & Read, A. J. 2020. Extreme diving in mammals: first estimates of behavioural aerobic dive limits in Cuvier's beaked whales. *The Journal of Experimental Biology*, 223(18).

Ridgway, S.H., 1986. Diving by cetaceans. *Diving in animals and man*, pp.33-62.

Robinson, K. P., & Tetley, M. J. 2007. Behavioural observations of foraging minke whales (*Balaenoptera acutorostrata*) in the outer Moray Firth, north-east Scotland. *Journal of the Marine Biological Association of the United Kingdom*, 87(1), 85–86.

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

Robinson, K. P., Macdougall, D., Bamford, C. C. G., Brown, W. J., Dolan, C. J., Hall, R. M., ... Culloch, R. M. 2023. Ecological habitat partitioning and feeding specialisations of coastal minke whales (*Balaenoptera acutorostrata*) using a recently designated MPA in northeast Scotland. *PLOS ONE*, 18(7), e0246617.

Sprogis, K. R., Videsen, S. K. A., & Madsen, P. T. 2020. Vessel noise levels drive behavioural responses of humpback whales with implications for whale-watching. *eLife*, 9.

Stockin, K. A., Fairbairns, R., Parsons, E. C. M., & Sims, D. 2001. Effects of diel and seasonal cycles on the dive duration of the minke whale (*Balaenoptera acutorostrata*). *Journal of the Marine Biological Association of the United Kingdom*, 81(1), 189–190.

Thomsen, Ugarte, & Evans. 2004. Estimation of $g(0)$ in line-transect surveys of cetaceans. *European Cetacean Society*.

Weir, C. R., Taylor, M., Jelbes, P. a. Q., & Stanworth, A. 2023. Cue rates and surfacing characteristics of sei whales (*Balaenoptera borealis*) in the Falkland Islands. *The Journal of Cetacean Research and Management*, 19(1), 43–55.

Wong, L. 2023. Whaling in Norway: a brutal tradition that still exists today. *Earth.Org*.

Wright, P. J., Jensen, H., & Tuck, I. 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research*, 44(3–4), 243–256.