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Dive behaviour and respiration rates of humpback whales (*Megaptera Novaeangliae*) during foraging off Northern Norway, with implications for metabolic rate estimates

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Master's thesis in Biology, BIO-3950, May 2022

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Acknowledgements

First and foremost, I want to express my gratitude to my incredible supervisors, Lars Folkow, Martin Biuw, and Lisa Elena Kettemer, for the time they have invested in helping me from start to finish. Special thanks to Lars who have provided insightful physiological knowledge. I want to thank Martin Biuw in particular with regards to helping me perform, but also understand, the statistical analyses in R, it would have been a real struggle without your help. Lisa, thank you for helpful feedback, proofreading and regularly checking in on me. Throughout my thesis, all of you have given me constructive feedback but also encouraged me and been excited about my project. This has given me motivation and a much-needed 'boost' when times got frustrating. I would also like to thank Audun Rikardsen for providing and allowing the use of the data collection. Next, I would like to thank my family, especially my beloved mom and dad. A thank you to my friends and fellow students for good laughs thought our time studying together. Finally, a special thanks to my better half, Benjamin, for listening to me ramble on about whales as well as helping me de-stress and feeding me when times got a bit intense.

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Abstract

Knowing the metabolic rate of marine mammals is often important as baseline knowledge of their biology and physiology, e.g., to allow ecosystem assessments and estimation of their resource needs and use, and prey requirements. However, our current knowledge of energetics of large cetaceans is limited compared to many smaller cetaceans. Determining the energy expenditure of large free-ranging whales is logistically extremely difficult and we must therefore often rely on various indirect methods such as modelling heat loss, using hydrodynamic models and respiration rate as proxies for metabolic rate.

In this thesis, I used pre-existing time-depth data of tagged humpback whales on their foraging ground in Northern Norway to investigate how the respiration rate is linked to different dive behaviour variables. I furthermore made some quantitative estimates of humpback whale metabolic rates based on own data on respiration rate and other available respiratory variables. Finally, I discuss and compare different approaches for estimation of energy costs of living in these mammals.

I present data covering 388 h, 4721 dive cycles, collected from altogether 21 out of 36 whales. The humpback whales mainly conducted short (4.6 ± 3.1 min) and shallow dives (41 ± 32 m) with a mean respiration rate of 1.25 ± 0.62 breaths min^{-1}. The results indicate that respiration rate is mostly affected by the degree of locomotor activity during foraging and non-foraging dives. The field metabolic rate of adult humpback whales, with an average size of 30 tonnes, was estimated to be 0.98 ± 0.29 W kg^{-1} which equals to 4.1 × BMR predicted by Kleiber's equation (1975). Similar estimations were seen for other rorquals and animal groups, indicating that the humpback whales have an energy expenditure within the magnitude as seen in other animals.

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1 Introduction

One of the few lineages of mammals that became fully aquatic is the cetaceans, which today, includes the world's largest organism, the blue whale (*Balaenoptera musculus*). During their evolution (Early Eocene to late Oligocene, ~50–23 million years ago), the five primitive cetacean families known as archaeoceti underwent changes such as regression of the hind limbs, enhanced spine flexibility, propulsion by vertical tail oscillation and streamlined bodies (Fish, 1996; Gingerich, 2003; Thewissen et al., 1994; Uhen, 2004). This promoted higher speed, efficiency, and thrust output while lowering drag and locomotion costs (Fish, 1996, 1998; T. M. Williams, 1999). Today, the modern whales contains the suborders mysticeti (baleen whales) and odontoceti (toothed whales) (Perrin et al., 2009; Uhen, 2004).

During the Eocene, the availability of rich and diverse food supplies, offered by increased primary productivity associated with upwelling, enabled the rapid evolution of novel marine vertebrates to exploit newly available ecological niches (Gingerich et al., 1983; Lipps & Mitchell, 1976). Today’s modern baleen whales are particularly distinguished from the other suborder toothed whales due to their lack of teeth. Instead of teeth, baleen whales use a specialized filter-feeding mechanism with bilaterally symmetric baleen plates attached to their upper jaw (Bannister, 2009; Pivorunas, 1979). This allows them to feed on lower trophic levels with smaller prey species, such as schooling fish and euphausiids (Bannister, 2009). Due to the tendency of these organisms to aggregate into dense schools, and the efficiency gained from skipping several trophic levels, filter feeding enables an evolutionary path towards extreme body sizes, as it allows for efficient consumption of large quantities of energy rich prey (Goldbogen, Cade, Wisniewska, et al., 2019).

1.1 Humpback whale

Humpback whales (*Megaptera Novaeangliae*; Figure 1) are a baleen whale that are found in all the world's oceans and known for their long migrations, their charismatic song, their playfulness, and often trusty behaviour towards humans, making them popular both for truism and science (Clapham, 2009; Hoyt, 2009). They can reach a length of 15-17 m, where females are about 1-1.5 m longer than males (Chittleborough, 1965; Nishiwaki, 1959), and can weigh up to 40 tonnes (Nishiwaki, 1959; Quiring, 1943), although around 30 tonnes is more common (Lockyer, 1976). When initiating diving, humpback whales lift and display their underside tail fluke pattern. This pattern can be used for individual identification (Katona et al., 1979), and has been employed in different scientific scenarios to increase knowledge about e.g., distribution and migration/movement (Baker et al., 1986; Katona & Beard, 1990; Stone et al., 1990), social interactions (Darling & Bérubé, 2001; Tyack, 1981; Tyack & Whitehead, 1982; Weinrich & Kuhlberg, 1991; Whitehead, 1983), feeding strategies (Jurasz & Jurasz, 1979) and population size through capture-recapture estimates (Katona & Beard, 1990).

Figure 1 Humpback whale mother with calf. *Photograph: "Humpback Whales" by Christopher Michel under CC BY 2.0.*

1.1.1 Distribution

Humpback whales are long-range migratory animals that exploit seasonally productive and energy rich high latitudes as feeding grounds during summer, and warmer tropical waters as breeding grounds during winter. They can undertake annual migration routes up to 19.000 km, giving them the record for all mammals (Palsbøll et al., 1997; Robbins et al., 2011). Based on genetic data there are three main populations with little exchange between them: North Atlantic, North Pacific and Southern Hemisphere (Baker et al., 1993; Jackson et al., 2014). Most North Atlantic humpback whales appear to use breeding areas in a subregion of North America (Dominican Republic, Puerto Rico and Virgin Islands area) called the West Indies (Katona & Beard, 1990; Martin et al., 1984), with a smaller number breeding off Africa around the Cape Verde Islands (Wenzel et al., 2009) (Figure 2). As summer comes, the whales breeding in the West Indies segregate into several feeding grounds at mid or high latitudes: Gulf of Maine, Gulf of St. Lawrence, Newfoundland, western Greenland, Iceland and northern Norway/Barents sea (Katona & Beard, 1990; Stevick et al., 1998). However, some humpback whales from the West Indies and Cape Verde Islands mix on the higher latitude feeding ground such as the Barents Sea (Hamilton et al., 2021; Wenzel et al., 2009). Genetic and photo-identification studies suggest that humpback whales display a strong site-fidelity to their feeding ground and philopatry to their breeding ground (Wenzel et al., 2009), likely maternally driven (Clapham, 1993; Larsen et al., 1996; Martin et al., 1984; Palsbøll et al., 1995).

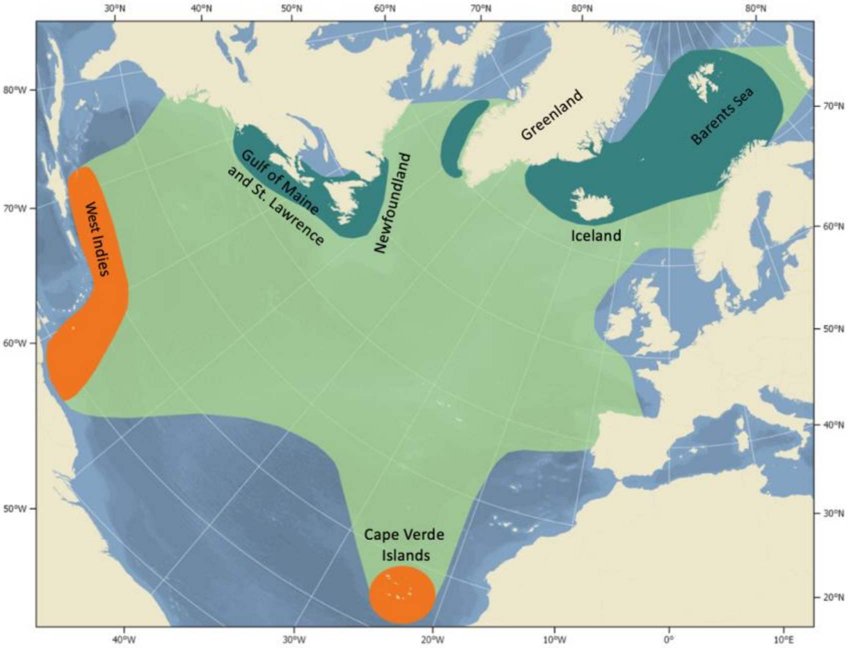

Figure 2 Annual distribution of North Atlantic humpback whales. *Light green area is the general distribution in the North Atlantic Ocean, whereas orange is breeding areas during winter and dark green is feeding areas during summer. Credit to Jill Prewitt/NAMMCO. Permission to use image and insert location names given by NAMMCO. Image taken from: https://nammco.no/humpback-whale/#1475843212917-9abc9066-967.*

1.1.2 Feeding strategy

As capital breeders, humpback whales mostly rely on energy stores deposited during foraging as an energy source for migrating and breeding. They are opportunistic feeders and prey upon different groups such as euphausiids and schooling fish (Baker et al., 1985; Clapham, 2009; Clapham et al., 1997; Friedlaender et al., 2009; Hain et al., 1982; Payne et al., 1986), where krill (such as *Meganyctiphanes norvegica*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*) are common prey for northeast Atlantic humpback whales (Løviknes et al., 2021). All rorquals (Family *Balaenopteridae*) use predominantly a lunge feeding strategy consisting of repetitive increases in acceleration, in contrast to the bowhead (*Balaena Mysticetus*) and right whales (Genus *Eubalaena*) that forage at a slow and steady pace (less than 1 m s^{-1}; Simon et al., 2009) using a continuous ram filter feeding strategy (Pivorunas, 1979). Lunge feeding (Figure 3) is characterized by accelerating towards the prey patch (Goldbogen et al., 2006, 2008) and lowering the lower mandible to achieve a mouth opening angle close to 80° (Brodie, 1993), causing large volumes of water and prey to be engulfed (Goldbogen et al., 2007). Rorquals have ventral grooves (Figure 3) extending from the mouth to the umbilicus (ca. 1/3 of body length) that, together with muscle contractions, allow the mouth cavity to expand in circumference up to ~160 % of its resting state (Shadwick et al., 2013). This causes the drag to increase and as the ventral grooves expand, and the animal's speed decreases. Rorquals can perform at least 15 lunges in one dive, but before each lunge, they must accelerate by increasing their fluke stroke frequency and amplitude (Goldbogen et al., 2008). This feeding strategy has therefore been labelled as energetically costly (Acevedo-Gutiérrez et al., 2002; Croll et al., 2001; Goldbogen et al., 2007, 2008, 2012; Potvin et al., 2012). Regardless of the high lunge cost, it is considered an efficient feeding method due to the ingestion of large quantities of energy-rich prey per lunge. However, for the strategy to be efficient, rorquals are dependent on aggregated and high densities of prey (Goldbogen et al., 2011). This could indicate that rorquals might be particularly affected by prey abundance perturbations (Acevedo-Gutiérrez et al., 2002).

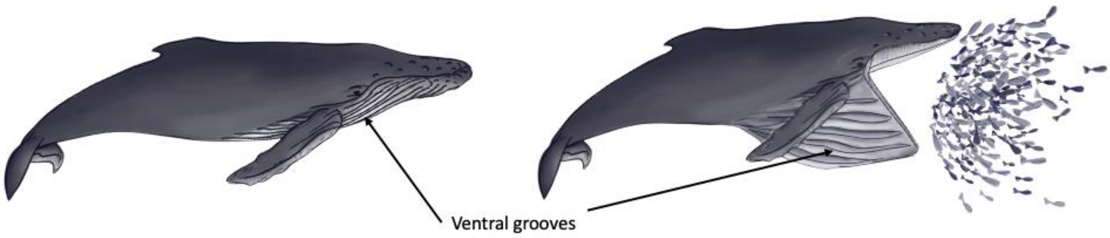

Figure 3 Illustration of a humpback whale before (left) and during (right) a lunge. *View text for more detailed description.*

Several different types of lunges have been identified: approaching a prey patch from beneath (horizontal lunge) or from the sides (vertical lunge). A third lunge type called bubble-net feeding is seen explicitly in humpback whales (and occasionally in Bryde's whale). During bubble-net feeding humpback whales collaborate to concentrate a prey patch by blowing a curtain of bubbles around it and then engulfing prey from below (Hain et al., 1982; Jurasz & Jurasz, 1979).

1.2 Energy metabolism

All organisms exploit their habitat to obtain food/energy and use it to fuel energy dependent processes throughout their body such as maintenance, muscular activity, biosynthesis, and thermoregulation. Heterotrophic animals extract energy from food substrates such as carbohydrates, fat, and protein. Energy must be converted to the "currency" of adenosine triphosphate (ATP) through cellular respiration, where oxygen is needed, and carbon dioxide is produced as a by-product. The production of ATP, like all other chemical reactions, is inefficient in the way that it produces heat, e.g., when ATP is produced and used, as stated by the second law of thermodynamics ('every energy transformation will cause an increased entropy, thus heat'). Energy in the form of heat cannot be used for any physiological work but still contributes to thermoregulation in homeotherms. Energy metabolism includes all the chemical reactions included in converting food to energy. The rate of this conversion is called the metabolic rate (energy used per unit time). The SI unit for energy is Joule (J), whereas the energy conversion rate is Watt (W) where $1 \text{ J s}^{-1} = 1 \text{ W}$. Another commonly used unit is calories (1 cal = 4.186 J) (Hill et al., 2018).

Several concepts are used for describing metabolic rate in relation to activity status of the organism: basal metabolic rate (BMR), resting metabolic rate (RMR) and field metabolic rate (FMR). The BMR refers to the energy needed to support vital processes in the body of an adult animal while in its thermoneutral zone, resting, fasting as well as not sleeping, stressed, reproductive or growing (Kleiber, 1975). Thus, BMR gives an indication of the energy required to fuel the basic functions when no extra work is performed. However, resting requires a small amount of energy, which can be difficult to account for (e.g., with experimental animals). Therefore, RMR is often used as an approximate BMR at rest as the conditions for BMR are difficult to fulfil, especially in wild animals. In contrast FMR takes into account all the activities of an animal throughout a certain period of time and thus represent an average cost of living (Hill et al., 2018).

1.3 Estimating metabolic rate of cetaceans and its importance

Knowledge of the metabolic rate of mammals is often important as baseline knowledge of their biology and physiology, e.g., to allow ecosystem assessments and estimation of their resource needs and use, and prey requirements. The energy requirement of an animal can give us information of its role in the ecosystem and food web. Estimating for example, the daily food consumption of a species gives an indication of what energy input is needed to support its daily life. By knowing how animals allocate their energy for different activities, we can get a better understanding of how they survive and accumulate sufficient resources to cover life history needs (Watanabe & Goldbogen, 2021).

Air-breathing marine mammals, such as cetaceans, are dependent on an adequate oxygen supply from air inhaled while at the surface. However, a large proportion of their time and activities such as reproduction, feeding, communication, etc., takes place under water. They must optimise their time in order to find a balance between their energetically costly feeding behaviour and avoiding depletion of ATP and acquiring a large oxygen debt while diving. Physiological adaptations have evolved in diving specialists to maximize the oxygen stores and minimize the oxygen depletion while diving (Scholander, 1940; Scholander et al., 1942; Scholander & Irving, 1941), promoting longer dive durations and lower oxygen consumption per unit time. By obtaining more detailed data on energetic requirements of different species, we can compare energetic data to get a better understanding of how these physiological adaptations differ between individuals, populations, or species. In addition, human-induced disturbance is increasing. This can cause, e.g., increased energy expenditure and reduced time for foraging (Jahoda et al., 2003), which can affect an individual's fitness, which can ultimately translate into population level consequences (Rode et al., 2010; Wiedenmann et al., 2011). Therefore, energetics is an important factor to account for when investigating individual physiological responses in relation to animal's environment.

There are two main ways to measure the metabolic rate of an animal: direct and indirect calorimetry. Direct calorimetry measures the rate at which heat leaves an individual's body, whereas indirect calorimetry refers to any method measuring more accessible proxies for energy conversion. Even though direct calorimetry is the most accurate, as the results unambiguously reflect the metabolic rate (provided no mechanical work is conducted inside the calorimeter), it is expensive to use and often requires large equipment. Consequently, indirect calorimetry is usually preferred as it is possible to employ in, for example, natural environments and with large animals as subjects (Hill et al., 2018). Despite some limitations, indirect calorimetry can still provide information and new knowledge about energy requirements and is the only method feasible for cetaceans. Several indirect calorimetry approaches exist although respirometry, as described in section 1.3.2.4, is the most widespread due to its relative simplicity and accuracy.

1.3.1 Metabolic rates of small cetaceans

A convenient way to estimate an animal's metabolic rate is by indirect calorimetry based on oxygen consumption and or carbon dioxide production. It is considered to be a 'gold standard' method and commonly used for indirect estimates as the exchange of these two gasses between an animal and its environment has a direct relationship to its metabolic rate, provided no anaerobic metabolic processes are taking place (Lighton, 2019). When using this method, one must account for what type of substrate is being oxidized, as the amount of energy produced differs depending on the energy substrate (Table 1). As seen from Table 1, the difference in O_2 conversion factors (21.1 – 18.7 = 2.4) are smaller compared to CO_2 conversion factors (27.9 – 21.1 = 6.8). Thus, using CO_2 can cause a larger potential margin of error than O_2 if the wrong conversion factor was chosen. Furthermore, in some settings, it is common to simply assume a conversion factor of 20.1 J $mL_{O_2}^{-1}$, reflecting a mixture carbohydrates, lipids and proteins (Kleiber, 1965).

Table 1 Conversion factors used for calculating the energy produced pr mL O2 or CO2 for oxidation of carbohydrates, lipids and proteins *(Brown & Brengelmann, 1965; Hill et al., 2018).*

Substrate	**Conversion factors**	
	J $mL_{O_2}^{-1}$	**J $mL_{CO_2}^{-1}$**
Carbohydrates	21.1	21.1
Lipids	19.8	27.9
Proteins	18.7	23.3

Smaller cetaceans are good candidates for indirect calorimetry as they can be handled in captivity. This enables researchers to measure e.g., RMR under conditions met by Kleiber (1975), although stress and complete rest might be a challenging factor. In addition, it is possible to train smaller cetaceans, allowing researchers to train them to perform certain exercises (Fahlman et al., 2016; Ridgway et al., 1969; T. M. Williams et al., 1993).

It has been suggested that marine mammals have elevated BMR compared to terrestrial mammals of similar body size (Hennemann III, 1983; Kasting et al., 1989; T. M. Williams et al., 2001) predicted by Kleiber's equation (1975):

Eq. 1: $BMR = 3.4\ BM^{0.75}$

Where BMR is the basal metabolic rate in W and BM is the body mass in kg. However, the belief of elevated BMR has been rejected on multiple occasions (Innes & Lavigne, 1991; Lavigne et al., 1986; Reed et al., 2000; Watts et al., 1993; Worthy et al., 2013). For example, the oxygen consumption of bottlenose dolphin (*Tursiops truncatus*; 258 kg) has been measured, e.g., by Fahlman (2018), to be 0.72 l_{O_2} min^{-1} at rest. The RMR then equals 241 W or 3.7 W $kg^{-0.75}$ when assuming a conversion factor of 20.1 kJ $l_{O_2}{}^{-1}$, only 1.1 × BMR estimated by Eq. 1.

1.3.2 Metabolic rates of large cetaceans

Larger cetaceans are rarely or never held in captivity, and therefore training them to execute certain exercises is not possible, as it is with smaller cetaceans. There have only been few cases where the opportunity for physiological measurements of grey whale calves (*Eschrichtius robustus*) in captivity occurred (Sumich, 2001; Wahrenbrock et al., 1974). One of them being Gigi, where Wahrenbrock et al., (1974) conducted respiratory and oxygen consumption measurements. At a weight of approximately 3500 kg, the oxygen consumption was 16.8 l_{O_2} min^{-1}, giving a RMR of 5656 W or 8.8 W $kg^{-0.75}$ which equals to 2.6 × BMR. However, immature animals (including terrestrial) typically have metabolic rates of 1.2–2 × BMR (Kleiber, 1961). Because of limited studies, due to the inherent difficulties in maintaining, handling and conduction experiments with these large animals, our energetic and general physiological knowledge is very limited compared to many other animals. Therefore, a variety of indirect methods have been used to try gain new insight to the energy requirements of large whales.

1.3.2.1 Modelling heat loss rates

As stated in section 1.2, chemical reactions are inefficient because some energy is always released as heat. In fact, under many conditions, all energy turnover in animals will result in heat. The intensity of the activity, among other things, will affect the rate of heat loss and hence the metabolic rate. Calculation of conductive heat loss (HL: W) across the blubber layer of marine mammals can be used as an estimate of minimum heat loss rates under prevailing conditions, according to equation 2 (e.g., Folkow & Blix, 1992):

Eq. 2. $HL = \frac{k \times SA \times \Delta T}{d}$

Where k (W m^{-1} °C^{-1}) is thermal conductivity of blubber, SA (m^2) is surface area, ΔT (°C) is temperature difference across the blubber and d (m) is blubber thickness. This has been the baseline for several estimates of metabolic rate (Brodie, 1975; Kshatriya & Blake, 1988; Lockyer, 1981; Parry, 1949; Watts et al., 1993), but this approach is incomplete unless nonsensible (respiratory) heat loss is also accounted for, as done in some studies (Folkow & Blix, 1992; Sumich, 2021). However, measurements should be conducted while the animal is at its lower range of its thermoneutral zone (TNZ; range of ambient temperatures where there is no additional increase in metabolic rate, above BMR) assuming minimal blood flow in the cutaneous and blubber layer, providing a k comparable to dead blubber (e.g., Folkow & Blix, 1992). As a result, this approach cannot correctly reflect metabolic/heat loss rates for animals during, e.g., foraging or migration.

1.3.2.2 Hydrodynamic models – overcoming drag forces

Some energetic models are based on estimating the hydrodynamic drag and thereby predicting the metabolic cost required to swim through water. Marine mammals have a streamlined body as well as appendages adapted for locomotion in water, which provides a hydrodynamic advantage by reducing drag and thus reducing energetic cost associated with locomotion (Fish et al., 2008). Since drag resistance forces increase approximately equal to the square of swim speed, the O_2 consumption is expected to increase quadratically with increased speed (Hill et al., 2018), as seen in Figure 4.

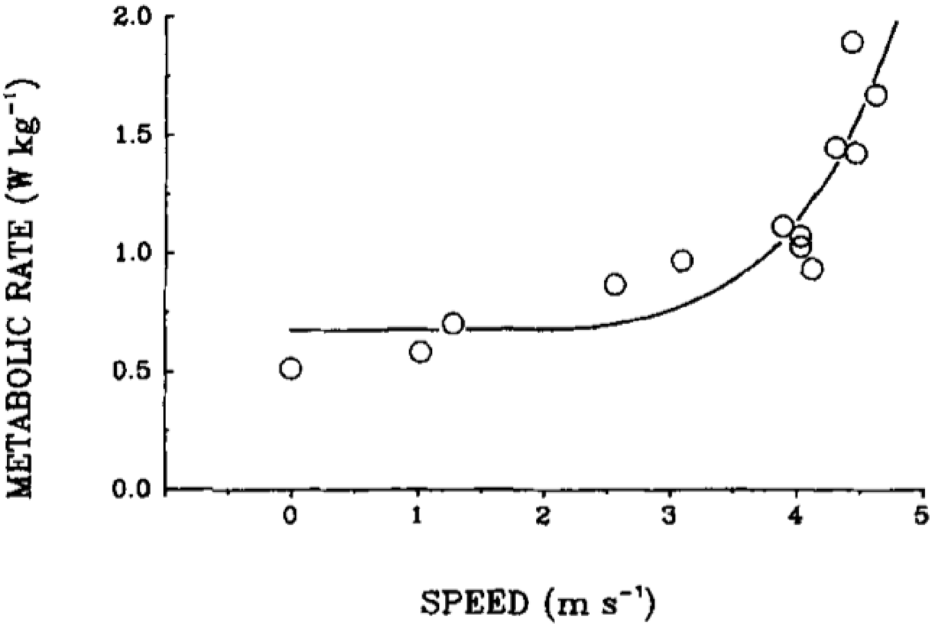

Figure 4 Changes in metabolic rate (MR: W kg-1) as speed (v: m s-1) increase. *The MR data are based on respiration rates of minke whales swimming at different speeds as estimated by Blix & Folkow* (1995)*. Relationship described by the equation: MR = 0.67 + 1.4 × 10^{-4} $v^{5.83}$. Figure taken from Blix & Folkow (1995).*

There are two main types of hydrodynamic models: steady (relatively constant speed) and unsteady (rapid changes in speed) swimming (Watanabe & Goldbogen, 2021). In the former, mechanical work (M: W) is the energy required to overcome drag forces (D: N) at a certain speed (V: m s^{-1}) for an actively swimming animal (e.g., Hind & Gurney, 1997):

Eq. 3*:* $M = D \times V$

Eq. 4 $M = 0.5\rho\lambda S C_d V^2 \times V = 0.5\rho\lambda S C_d V^3$

Where ρ is the density of water (kg m^{-3}), λ is the ratio of drag between an active and passive swimmer at equal speeds, S is surface area (m^3), C_d is the drag coefficient and V is speed (m s^{-1}). In order to convert the estimated mechanical work to metabolic power, additional dimensionless efficiency terms, such as aerobic (ε_a) and propulsive efficiency (ε_p), must be accounted for. These two terms indicate the animal's swimming performance, such as proportion of muscular work converted from chemical energy (aerobic efficiency) and proportion of muscular movements translates to forward thrust (propulsive efficiency) (e.g., Fish, 1993, 1996; Hind & Gurney, 1997; Watanabe & Goldbogen, 2021). However, these efficiency terms are unknown in large aquatic animals. Therefore, studies on hydrodynamic models have assumed similar efficiency terms as smaller related species (Braithwaite et al., 2015; Goldbogen et al., 2007; Gough et al., 2019; Hind & Gurney, 1997; Roos et al., 2016; Sumich, 1986; Watanabe et al., 2011).

Unsteady models are typically used for distinctive cases with sudden changes in speed and different maneuvers that can have large impacts on the energy budget, as for example during lunge feeding (Goldbogen et al., 2011; Potvin et al., 2009, 2012). These are more complex models that also account for changing drag forces during different phases of engulfment (Goldbogen et al., 2017; Potvin et al., 2009).

1.3.2.3 Respiration rate

Respiration increases with oxygen consumption, and this has been documented in marine mammals. Early respirometry (measurements of O_2 and CO_2 exchange) experiments showed that respiration rate in bottlenose dolphins (*T. truncatus*) and Florida manatees (*Trichechus latriostris*) increased predictably with the rate of oxygen consumption (Hampton et al., 1971; Scholander & Irving, 1941), which is also a well-known fact from studies of any animal. Obviously, an increase in oxygen consumption/metabolic rate would require an increase in ventilation, which implies that this relationship may be exploited for metabolic rate estimations in large whales. Being diving mammals, they presumably aim to spend little time at the surface and more time underwater. Cetaceans have an irregular breathing pattern, meaning their breath is followed by a respiratory pause (Wartzok, 2009). When they do breathe there must be a highly efficient respiratory exchange of oxygen (Kooyman, 1973; Olsen et al., 1969; Scholander, 1940; Scholander & Irving, 1941). Thus, an active marine mammal, e.g., during foraging, would be expected to present relatively constant respiratory features for optimalization of oxygen uptake, e.g., via high tidal volume and oxygen extraction (i.e., difference between oxygen in inhaled and exhaled air; %) (Fahlman et al., 2016). This indicates that respiration rate may be a reasonable proxy for metabolic rate estimates. The estimation of oxygen consumption (V_{O_2}: $\mathrm{l}_{\mathrm{O}_2}$ min^{-1}) from respiratory rate is based on the following equation (e.g., Folkow & Blix, 1992):

Eq.5: $V_{O_2} = V_T \times \Delta O_2 \times f$

where V_T (l) is the tidal volume, ΔO_2 (%) is oxygen extraction in the lungs and f (breaths min^{-1}) is the respiration rate. This principle has been used for multiple species under different activities (Blix & Folkow, 1995; Christiansen et al., 2014; Dolphin, 1987a; Krogh, 1934; Rodríguez de La Gala-Hernández et al., 2008; Roos et al., 2016; Sumich, 1986; Villagra et al., 2021; Villegas-Amtmann et al., 2015; R. Williams & Noren, 2009). However, V_T and ΔO_2 are logistically difficult to measure in large cetaceans which causes a lack of validation (constant V_T and ΔO_2) for the method. For large whales, the estimation of V_{O_2} must therefore rely on measurements of relevant variables from the few available studies on captive grey whale calves (Sumich, 2001; Wahrenbrock et al., 1974) as well as from smaller cetaceans, assuming that they display similar respiratory characteristics.

1.4 Aim of study

In this thesis, I used pre-existing time-depth data of humpback whales on their foraging grounds in northern Norway, to investigate their dive behaviour and assess factors (behaviours) that affect their respiration rate. I aim to link dive variables (*dive duration, bottom time*, *lunge rate, total vertical distance*, and *max depth)* to the respiration rate and their effects on energetic costs. Moreover, since direct measurements of energy expenditure of large free-ranging whales are extremely difficult and may never be possible, estimations of energy expenditure must rely on various indirect methods. Based on the respiration rate and other key respiratory variables such as total lung capacity, tidal volume and oxygen extraction, I estimated the field metabolic rate of these animals during foraging events. Furthermore, I discuss previous methodologies for estimating metabolic rates in large cetaceans and compared to the findings presented in this thesis.

2 Method

2.1 Study site

The data were collected in the Kaldfjord/Vengsøyfjord fjord system (hereafter referred to as Kaldforden) near Tromsø city in northern Norway (Figure 5) with an approximately length of 26 km and a max depth of 270 m. A total of 36 whales were tagged (2013–2016), all of which took place during the winter months (November until February). In the months of November until December in 2013 and 2014, a total of 17 whales were tagged. Additional 17 whales were tagged from November through February of 2015, as well as two whales in January 2016. Humpback whales congregate near-shore and in fjords while foraging on Norwegian spring spawning herring during winter (Jourdain & Vongraven, 2017), hence Kaldfjorden was chosen as a study site.

Figure 5 Map of study site, Kaldfjorden. *The main map is a zoomed version of the red square shown in the smaller map (top-right). Picture taken from Google maps.*

2.2 Tag description, attachment, and retrieval

36 whales were tagged (Figure 6) with time-depth recorders (TDR10-F-297C, Wildlife Computers, Redmond, WA, United States). These tags record the depth (± 0.5 resolution) registered from pressure sensors logged at a 1 s interval, as well as dry-sensor registering when the tag was in air. The TDR tags were placed in a custom-made rigid plastic housing that also contained a GPS component (SPLASH-F, Wildlife Computers) for geolocation and a VHF transmitter (model MM110 or MM120, Advanced Telemetry Systems. Isanti, Minnesota, USA) to enable localization during retrieval. The housing was equipped with four suction cups for attachment to the animal, allowing for a recording time up to approximately two days depending on the tag location, how well it was attached, the activity of the whale etc. The entire unit is called an HVTag (for Horizontal/Vertical tag, LKARTS, Skutvik, Norway) and altogether, including housing, weighs around 200 g. For short-term investigations, this is a frequently used tag attachment method. Suction cup tags are considered a non-invasive procedure because the device is merely attached to the skin's surface, though slight disruption and behaviour changes/reactions to the tagging encounter have been documented (Williamson et al., 2016). A steel cabin cruiser boat (30 ft) or a rigid inflatable boat (26 ft; 300 hk) was operated to approach the whale from behind, on either side, at an angle of 120-160 degrees relative to the head, during the attachment. The tag was attached to the left or right side of the dorsal hump using a hand-held carbon fibre pole (6 m) or the air-pressure system ARTS whale tagger (LKARTS-Norway, Skutvik, Norway) attached by Lars Kleivane (A. Rikardsen, personal communication).

Figure 6 Two humpback whales tagged with time-depth recorders. *Photo by Audun Rikardsen/UiT*

TDR tags must be located and retrieved as recorded data are locally saved in the tags. The retrieval process was done using an AF Antronics F150-3FB 3-element folding yagi antenna (Communication Specialists Inc, USA) connected to a digital radio direction finder DDF2011 (ASJ Electronic Design, Norway) and an R-1000 telemetry receiver (Communication specialists, Inc., USA) to locate the signal from the VHF (148–149 Hz). If a signal could not be found from the tag at sea level, it was tracked from high areas from land by use of a ATS R410 VHS Reciver. When the tag has been retrieved, the data could be downloaded and thereafter, the tags could be revised for any adjustments before redeployment.

The animal welfare aspect of the research protocol was approved in accordance with the regulations by the Norwegian Food Health Authority (Permit number FOTS-8165).

2.3 Data processing

In this thesis, all data handling and statistical analysis was performed in R Software version 4.1.2 (R Core Team, 2021).

The original raw data was prepared by Lars Kleivan, and further pre-processed by Kevin Ochoa Zubiri (2017). The calculations of dive variables were generated with a custom-made function created by Martin Biuw at the institute of Marine Research. The dive variables, presented in Table 2 and visually shown in Figure 7, were calculated for all dives. A dive was defined as a submersion deeper than 10 m as it approximately equals one body length (Goldbogen et al., 2008; Narazaki et al., 2018), with the dive duration (D_D; s) being the time from submerging until its return to the surface and the maximum depth (*MD*; m) as the deepest point. The bottom time (*BT*; s) was the time between two inflection points based on a broken stick method (Fedak et al., 2002; Heerah et al., 2014; Photopoulou et al., 2015). The first inflection point reflected a significant behavioural change during the end of the descending phase, while the second inflection point was in the start of the ascending phase (Zubiri, 2017). The vertical movement (*VM*; m) in the water column was calculated by summing the absolute different between pair-depths throughout a dive. The post-dive, hereafter called surface period and its duration as D_S (s), consists of dives shallower than 10 m and surfacing's (*SB*; breaths). All the dive variables were arranged into dive cycles consisting of the dive and its surface period. It was assumed that each (approximate) instantaneous surfacing represents one breath (Figure 7) which is common for many cetaceans, included humpback whales. However, when depth readings remain close to zero for an extended period (e.g., resting at the surface), this assumption no longer holds.

The respiration rate (f: breaths min^{-1}) was calculated for each dive cycle where f is equal to SB divided by the cycle duration ($D_C = D_D + D_S$). A change in BT, MD or VD would all cause a change in the D_C, and therefore also f.

An additional variable included in the dive cycles was the number of lunges (*nLunges*) provided in Maren Andrea Pedersen's (2020) master's thesis. She used a lunge detection for three-dimensional acceleration data to optimise an algorithm that allows the detection of lunges in time-depth data.

Table 2 All dive variables present in a dive cycle.

Variable name	Unit	Explanation
D_D	s	Duration of a dive
D_S	s	Duration of surface period
D_C	s	Cycle duration ($D_D + D_S$)
BT	s	Bottom time
VD	m	Total vertical distance: the absolute sum of difference between pair-depths throughout a dive.
MD	m	Maximum depth of a dive
SB		Number of breaths during D_S
nLunges		Number of lunges during D_D
f	Breaths min^{-1}	Respiration rate of a dive cycle (*nBreaths*/D_C)
f_S	Breaths min^{-1}	Surface respiration rate (*nBreaths*/D_S)
LR	Lunges min^{-1}	Lunge rate of a dive cycle (*nLunges*/D_D)

When two dives are separated by a single instantaneous surfacing, the two dives were combined and considered as belonging to the same dive cycle (see Dive cycle 1 in Figure 7). This was decided because the oxygen debt of, say, a longer dive followed by one breath would not be sufficient to meet the oxygen requirement.

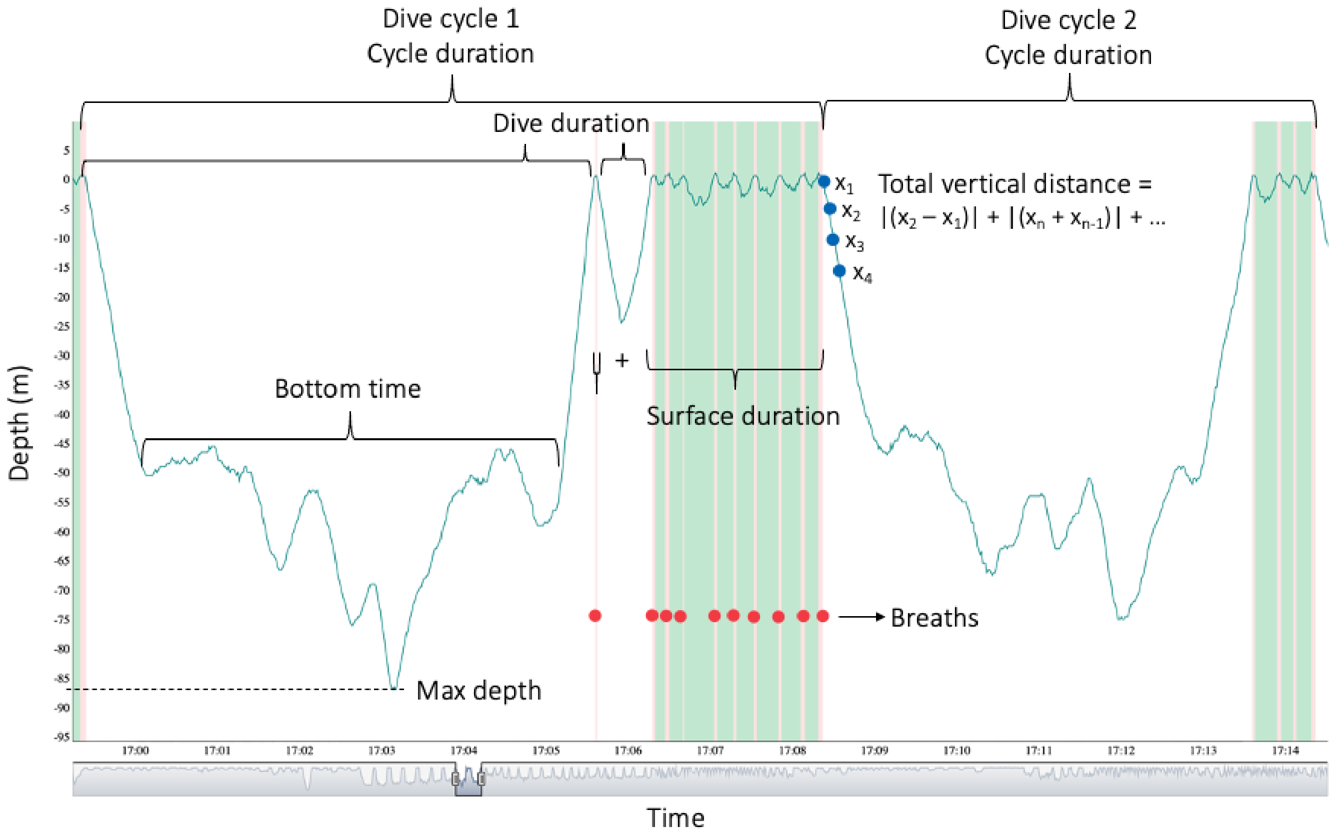

Figure 7 Example trace from Whale2013Dec02, for visualization of dive variables within a dive cycle. *White areas (Dive duration) indicate dives deeper than 10 m where the deepest point is defined as the max depth. Whereas dives shallower than 10 m are surface dives (green vertical lines), and each red line/dot is one breath. These two combined are the surface period. Overall, the cycles' duration equals to the sum of the dive and surface duration. The bottom time consists of the time spend at the bottom of a dive. The absolute sum of the difference between pair-depths (x1 and x2, x2 and x3, etc.) throughout the dive is the total vertical distance (surface periods not included).*

The first dive cycle was excluded since its characteristics being too heavily influenced by disturbance from the tagging event (Williamson et al., 2016). The last dive was also removed because it is often incomplete, as the tag usually falls off while the whale is in the middle of the dive. It therefore does not have a subsequent surface period and hence no dive cycle variables can be calculated.

In this thesis 21 out of 36 datasets were included. The 15 datasets were excluded due to one or a combination of the following reasons:

1. Respiration rate could not be determined. Datasets in which dive variables were not correctly calculated throughout the dataset.
2. Less than 20 dive cycles. Small datasets were removed as they would not be expected to show a representative long term respiration rate of that individual.

2.4 Relationship between estimated respiration rate and dive variables

Surfacings are the only periods where the humpback whales can perform any respirations to restore O_2 and eliminate CO_2. The respiration rate is linked to the oxygen consumption of an animal, but different dive behaviours, as indicated by dive variables, may affect the respiration rate, and hence oxygen consumption, in different ways or magnitudes. A linear mixed-effect model (lmer) with the R package *lme4* version 1.1-28 (Bates et al., 2015) was used to evaluate the relationship between estimated *respiration rate* and dive variables. The response variable and the predictor variable are the two main components of a lmer model. Unlike a standard linear model, however, fixed and random effects can be included in mixed models. Firstly, focusing on the former, which are variables that are the same across individuals (as in a regular linear model), and hence ‘fixed’. In this thesis, *lunge rate, total vertical distance, dive duration, max depth*, and *bottom time* were all fixed effects on the response variable *respiration rate*. In addition, interaction terms between *lunge rate* and *dive duration*, as well as *total vertical distance* were included. This was done to test how the *respiration rate* was affected by lunges performed for (1) different dive durations and (2) the degree of vertical movement which can be translated to the amount of locomotion activity. Both of these would require an increased oxygen demand due to longer breath holds or increased activity (Scholander, 1940; Scholander & Irving, 1941). Secondly, as dive cycles were collected from different individual whales, data points within individuals are not independent of each other. Therefore, *WhaleID* was treated as a random effect by allowing individual variations in intercept.

Two models (A and B) were fitted to the dive data. Model A contained all dive cycles to describe the overall effect on *respiration rate*. However, in 2652 out of 4721 dive cycles, the whales did not perform any lunges (*lunge rate* = 0), causing the *lunge rate* data to be zero-inflated and dramatically changing its relationship with *respiration rate* (Figure 8). Therefore, the *lunge rate* estimate would not be a realistic representative for its effect on the *respiration rate* when using all dive cycles. Therefore, to assess *lunge rates* effect, Model B was constructed only using dives that contained lunges (‘lunge dive cycle’). In addition, interaction terms were only used in Model B for the same reason.

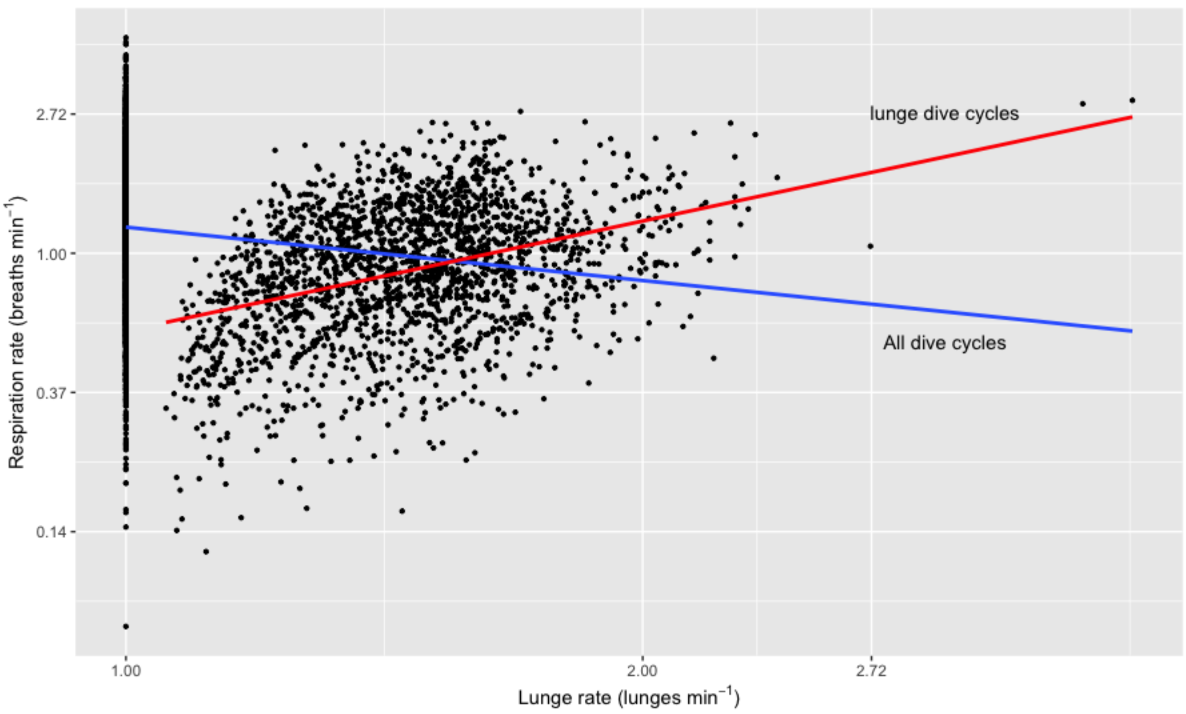

Figure 8 Relationship between respiration rate (breaths min^{-1}) and lunge rate (lunges min^{-1}) for all whales. *Blue line is all cycles (including zero-inflated lunge rates) and red line is cycles where lunge rate is above 0. Legends are given on a log scale.*

The R package *LmerTest* version 3.1-3 (Kuznetsova et al., 2017) was used for a backward step elimination on both models. The input model of a backward step elimination should consist of all additive and interactive terms as well as random effects of interest. The elimination process conducts a step-wise removal of fixed and random effects with high p-values to then return an adequate model (Kuznetsova et al., 2014), which was used in this thesis.

To predict the effects of different dive variables on the respiration rate, the random effect and all dive variables should be controlled and accounted for, this can be done using marginal predictions. Marginal predictions between respiration rate and dive variables were generated from Model A and Model B by the use of the *predictInterval* function from the R package *merTools* version 0.5.2 (Knowles & Frederick, 2020).

2.5 Changepoint analysis and categorization of respiration rate

In this thesis, I have aimed to investigate changes in the respiratory rate of humpback whales during various types and levels of activity to try to assess their energy expenditure. Since respiration rate and metabolic rate are intimately related (Hampton & Whittow, 1976; Scholander & Irving, 1941; Yazdi et al., 1999), it should be possible to do a reverse analysis. Hence, a change in the animal's respiration rate should correspond to a change in its behaviour. I did so by performing a changepoint analysis and then categorising the segments that emerged as a result of the analysis in an attempt to objectively define dive behaviours.

I first performed a changepoint analysis with a change in mean and variance using the R package *changepoint* (Killick et al., 2012; Killick & Eckley, 2014) on all datasets. A changepoint analysis detects when and where there are changes in a variable, here respiration rate, of a time-series. The framework of a changepoint analysis is illustrated by Figure 9 from simulated normally distributed data. The figure shows when there is a statistical change in the mean and/or variance of a variable. In this case there are two changepoints creating the three segments seen as red, green and blue in the scatterplot. Each segment has its own distribution and hence its own mean and standard deviation (right side in Figure 9).

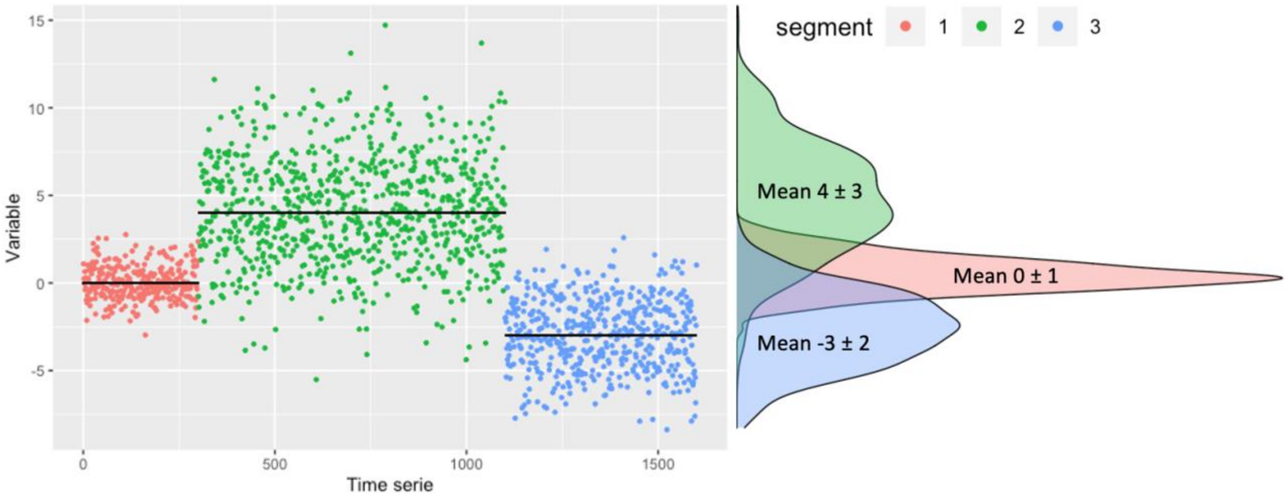

Figure 9 A typical example illustrating the concept of a changepoint analysis. *To the left is a scatterplot of how an imaginable variable changes over time. There are three segments (red, green and blue), separated by two changepoints (300 and 1100), where the black line represents the segments mean. The distribution of each segment can be seen to the right with its respective mean ± sd.*

There are multiple available algorithms for detecting changepoints for the respiration rate. In this thesis, the pruned exact linear time (PELT) algorithm method was chosen, as it is considered an accurate method for multiple changepoints (Killick et al., 2012), together with the modified Bayes Information Criterion (mBIC) as model selection (Zhang & Siegmund, 2007).

For the categorization of respiration rate segments, I decided to divide the segments into three categories: *High*, *low*, and *variable* respiration rate segments. The threshold for a segment to be defined as high or low was a mean segment value above or below 1 breaths min^{-1} (Bejder et al., 2019; Dolphin, 1987a). If the segment's variance was above 70 % of the total variance of the dataset, it would be categorized as *variable*. This threshold was set subjectively based on visual inspection of the data, leading to potential subjectivity issues with using this threshold for classification.

3 Results

3.1 Data and dive variables

The present thesis covered data of 388 hours, 4721 dive cycles, collected from 21 out of 36 whales (Table 3). The data duration ranged from 2 hours to 62 hours, thus covering all hours of the day. Of all dive cycles (n = 4721) approximately half represented lunge dive cycles (i.e., foraging dives, n = 2069). The dive variables mean values for all datasets used are presented in Table 4. The overall mean respiration rate was 1.25 ± 0.62 breaths min^{-1} (n = 4721), whereas dive cycle with (n = 2069) and without lunges (n = 2652) were 0.98 ± 0.43 and 1.47 ± 0.66 breaths min^{-1} (Table S1), respectively. The maximum dive depth was 265 m with a mean depth of 41 ± 32 m and longest dive duration was about 22 min with a mean of 4.6 ± 3.1 min.

Table 3 WhaleID, tagging date and time, data duration (hours), number of dive cycles and number of lunge dive cycles for each dataset.

Whale ID	**Tagging date and time**		**Data duration**	**Nr. Of cycles**	**Cycles with lunges**
	Start	**End**			
Whale2013Dec02	01.12.13, 12:21	02.12.13, 00:34	12	172	69
Whale2013Nov27	28.11.13, 13:02	28.11.13, 17:27	4	71	29
Whale2013Nov29	30.11.13, 10:46	30.11.13, 19:03	8	83	59
Whale2014Dec05	06.12.14, 09:56	06.12.14, 14:55	5	46	44
Whale2014Nov26	27.11.14, 10:35	27.11.14, 14:50	2	26	16
Whale2014Nov27	28.11.14, 10:35	28.11.14, 14:14	4	31	24
Whale2014Nov30	01.12.14, 12:30	01.12.14, 16:26	4	21	13
Whale2015Dec29	30.12.15, 09:44	31.12.15, 18:35	33	460	235
Whale2015Dec29C	31.12.15, 13:29	01.01.16, 04:43	15	402	37
Whale2015Dec30	31.12.15, 12:22	01.01.16, 07:43	19	379	128
Whale2015Feb20	21.02.15, 10:32	21.02.15, 22:08	12	159	71
Whale2015Feb23	23.02.15, 13:25	25.02.15, 08:19	43	358	201
Whale2015Jan31	01.02.15, 10:21	02.02.15, 21:00	35	625	153
Whale2015Nov14	15.11.15, 09:57	16.11.15, 00:49	15	176	43
Whale2015Nov21	20.11.15, 14:37	20.11.15, 23:41	9	174	43
Whale2015Nov21B	22.11.15, 11:54	22.11.15, 14:23	2	42	13
Whale2015Nov22	23.11.15, 13:06	26.11.15, 03:32	62	412	284
Whale2015Nov30	01.12.15, 10:18	02.12.15, 23:50	38	350	157
Whale2015Nov30B	01.12.15, 10:47	02.12.15, 09:32	23	241	165
Whale2016Jan20	21.01.16, 11:48	22.01.16, 06:11	18	185	137
Whale2016Jan26	26.01.16, 13:47	27.01.16, 14:33	25	308	148
Total			**388**	**4721**	**2069**

Table 4 Dive variables are represented as mean ± sd for individual whales. *f = respiration rate (breaths min^{-1}), f_S = surface respiration rate (breaths min^{-1}), SB = number of breaths, LR = lunge rate (lunges min^{-1}), D_C = cycle duration (s), D_D = Dive duration (s), D_S = Surface duration (s), BT = Bottom time (s), VD = Total vertical distance (m), MD = max depth (m). Dive variables total mean is based on all dive cycles.*

Whale ID	f	f_S	***LR***	D_C	D_D	D_S	***BT***	***VD***	***MD***	***SB***
Whale2013Dec02	1.36± 0.55	4.51± 1.76	0.19± 0.26	243± 158	209± 124	85± 115	100± 88	115± 66	31± 18	4.64± 2.54
Whale2013Nov27	1.39± 0.54	3.36± 0.95	0.20± 0.28	221± 88	214± 87	94± 54	51± 35	108± 45	28± 12	4.73± 2.12
Whale2013Nov29	0.91± 0.43	4.58± 1.70	0.25± 0.22	353± 150	329± 141	70± 37	155± 89	182± 85	53± 30	4.65± 1.91
Whale2014Dec05	1.08± 0.54	4.42± 1.19	0.68± 0.33	383± 164	359± 154	90± 45	186± 109	318± 133	99± 43	6.28± 3.10
Whale2014Nov26	1.37± 0.60	4.10± 2.02	0.51± 0.77	311± 217	280± 194	124± 123	118± 93	152± 98	39± 25	6.38± 4.66
Whale2014Nov27	0.81± 0.52	4.69± 2.28	0.33± 0.27	420± 214	397± 202	72± 48	182± 136	272± 136	84± 46	4.55± 2.05
Whale2014Nov30	0.48± 0.19	3.69± 1.67	0.15± 0.18	662± 233	631± 223	87± 43	358± 196	298± 146	77± 55	4.81± 2.02
Whale2015Dec29	1.18± 0.52	4.86± 1.74	0.26± 0.30	253± 157	241± 151	67± 61	114± 90	132± 84	33± 26	4.24± 2.05
Whale2015Dec29C	1.59± 0.39	7.78± 2.78	0.06± 0.21	131± 79	122± 72	32± 44	48± 30	98± 52	30± 6	3.25± 1.74
Whale2015Dec30	1.41± 0.45	6.82± 2.49	0.22± 0.35	179± 104	167± 93	43± 47	69± 50	146± 79	39± 14	3.79± 1.76
Whale2015Feb20	1.18± 0.55	4.23± 1.42	0.20± 0.26	257± 118	243± 111	72± 41	107± 66	122± 78	33± 25	4.58± 2.25
Whale2015Feb23	0.90± 0.33	3.96± 1.15	0.30± 0.30	427± 205	408± 194	97± 56	237± 145	241± 151	58± 39	5.95± 3.15
Whale2015Jan31	1.87± 0.69	5.75± 2.97	0.13± 0.36	198± 116	192± 113	80± 83	80± 53	112± 66	26± 17	5.75± 3.59
Whale2015Nov14	0.95± 0.35	4.36± 1.01	0.09± 0.17	300± 139	290± 134	63± 30	141± 83	120± 81	27± 27	4.34± 1.82
Whale2015Nov21	1.73± 0.55	4.72± 1.68	0.13± 0.25	182± 145	164± 134	80± 115	57± 60	86± 53	22± 11	4.74± 2.75
Whale2015Nov21B	1.62± 0.74	5.42± 2.51	0.15± 0.25	210± 158	200± 149	62± 50	82± 99	117± 71	29± 19	4.45± 1.90
Whale2015Nov22	0.69± 0.48	4.19± 1.71	0.25± 0.23	537± 292	498± 241	95± 137	304± 198	266± 127	61± 34	4.81± 1.95
Whale2015Nov30	0.90± 0.40	4.05± 1.40	0.18± 0.25	382± 264	351± 204	94± 162	160± 126	162± 121	42± 42	4.92± 3.17
Whale2015Nov30B	0.99± 0.51	5.01± 3.20	0.33± 0.29	336± 216	325± 212	83± 97	149± 131	192± 120	46± 30	4.69± 3.84
Whale2016Jan20	1.26± 0.43	4.24± 1.19	0.37± 0.26	353± 123	316± 109	103± 37	191± 87	211± 85	68± 29	6.89± 2.40
Whale2016Jan26	1.23± 0.56	4.64± 1.50	0.18± 0.22	285± 133	267± 122	76± 44	156± 94	171± 94	55± 41	5.31± 2.59
Total mean	**1.25± 0.62**	**5.07± 2.39**	**0.21± 0.28**	**291± 209**	**273± 188**	**76± 88**	**138± 129**	**159± 112**	**41± 32**	**4.85± 2.80**

As seen in Figure 10, there was a shift in distribution for the dive variables *respiration rate*, *lunge rate*, *dive duration*, *bottom time*, *total vertical distance*, and *max depth* when comparing dive cycles with (n = 2652) to those without lunges (n = 2069). In this regard, the *respiration rate* had a decreasing shift in mean from 0.98 to 1.47 breaths min^{-1}, whereas the remaining dive variables had an increase in mean of 2 – 2.5-fold (Table S1).

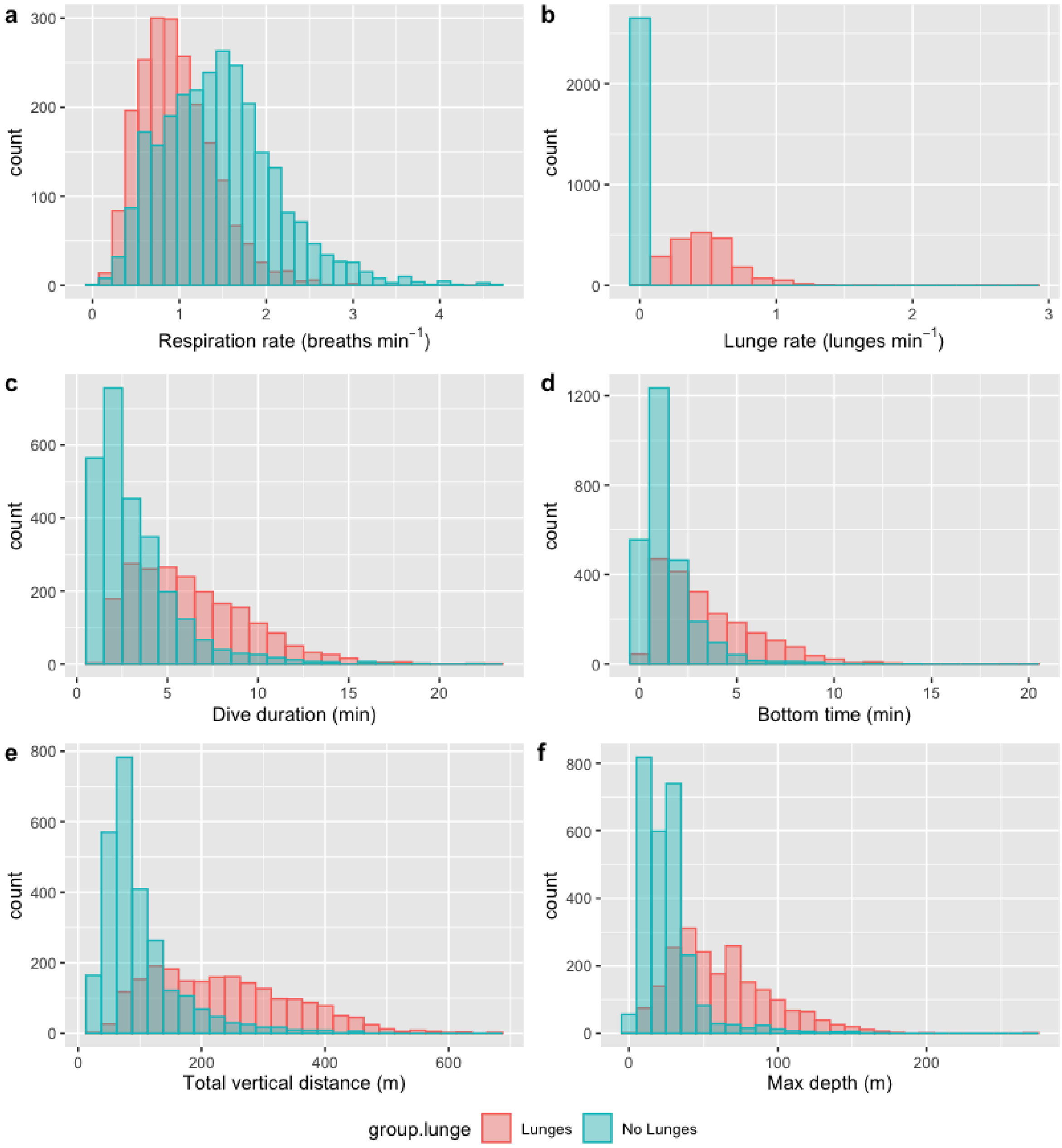

Figure 10 Frequency of (a) respiration rate, (b) lunge rate, (c) dive duration, (d) bottom time, (e) total vertical distance and (f) max depth for dive cycles with (pink) and without (blue) lunges. *Distributions derives from all whales.*

3.2 Relationship between estimated respiration rate and dive variables

The relationship between the dive variables *lunge rate*, *total vertical distance*, *max depth*, *bottom time* and *dive duration*, and *respiration rate* as raw data are displayed in Figure 11. When separating Figure 11b into plots for each whale, the variations between individuals becomes apparent (Figure 12).

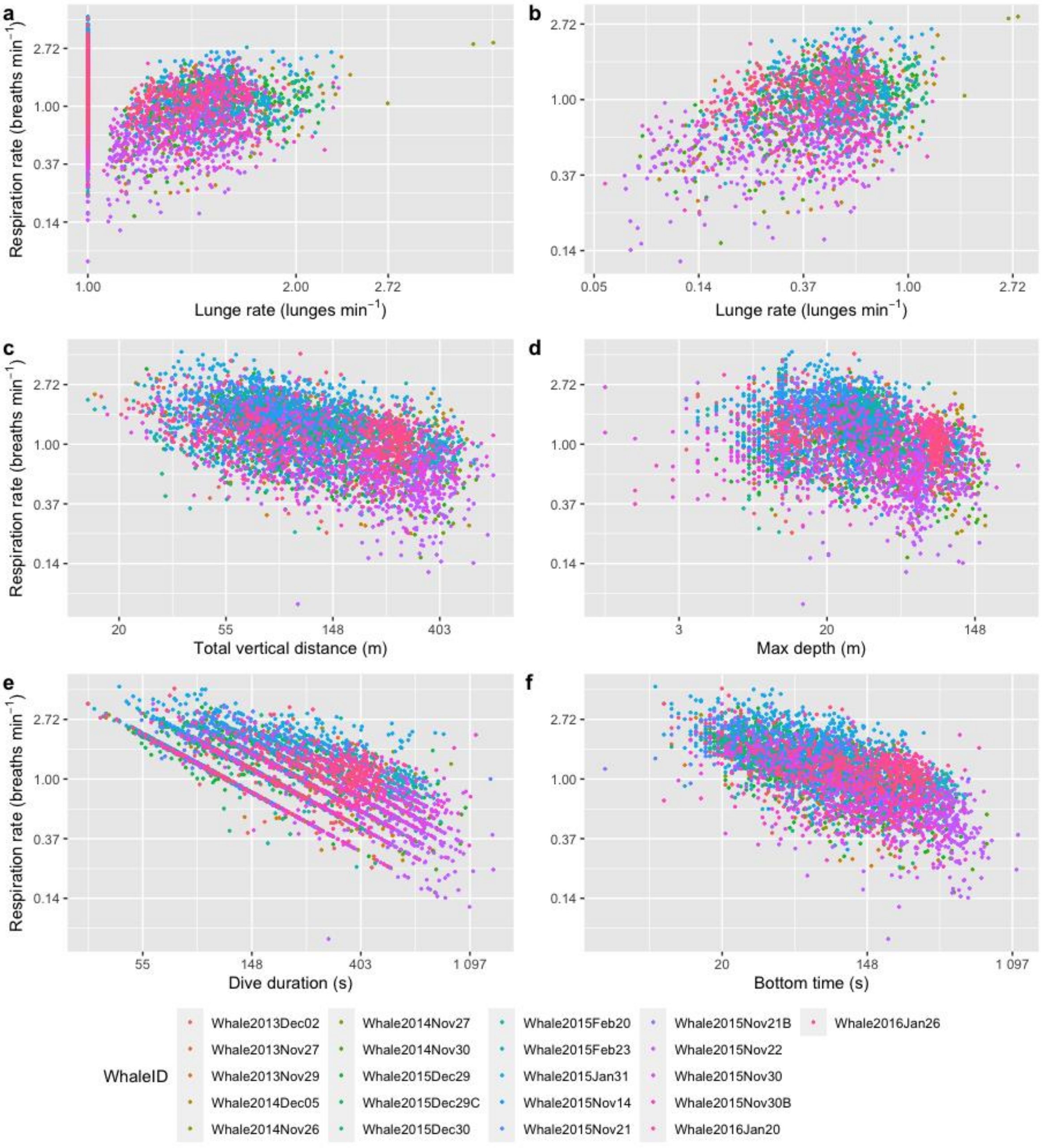

Figure 11 Relationship between (a) lunge rate (all dive cycles), (b) lunge rate (cycles where lunge rate > 0), (c) total vertical distance, (d) max depth, (e) dive duration and (f) bottom time, and respiration rate. *Colours represent different individuals. All legends are given on a log scale*

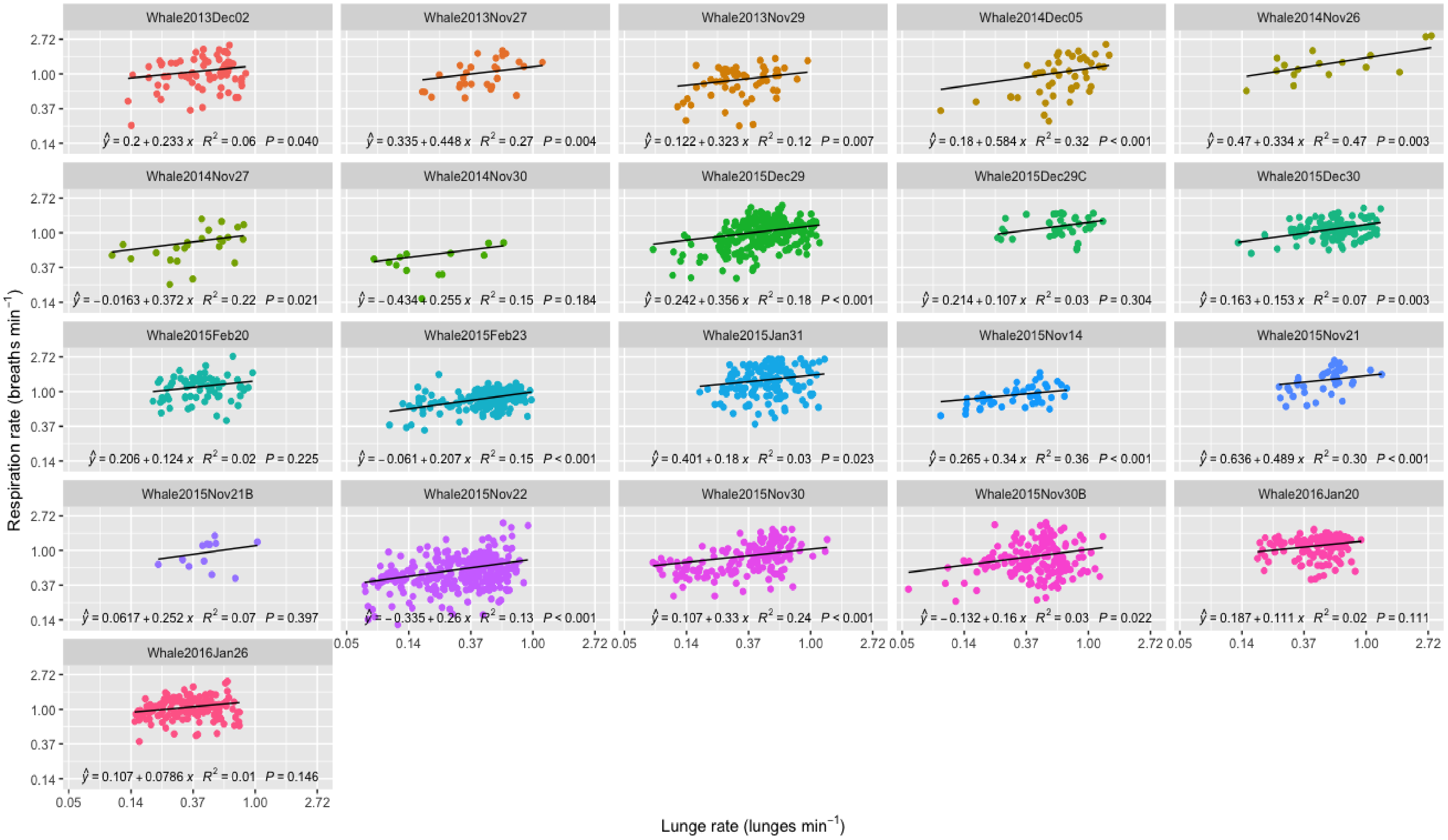

Figure 12 The effect of Lunge rate (lunge min^{-1}) on the respiration rate (breaths min^{-1}) for each of the 21 whales. *Note shift in regression line between the individuals. The legends are given on a log scale.*

Estimates from lmer models are presented in Table 5, with Model A derived from all dive cycles and Model B from lunge dive cycles (*lunge rate* > 0). All fixed and random effects were included by the backward step elimination. For both models, the estimated *dive duration, max depth* and *bottom time* had a negative effect on the *respiration rate* whereas *vertical distance* had a positive effect on the *respiration rate*. The only insignificant estimate was *lunge rate*, but both its interaction terms with *dive duration* and *total vertical distance* were significant. However, *lunge rate* was significant before interaction terms were included, indicating take *lunge rate* itself may not be the most important effect on the *respiration rate* but rather its effect together with *dive duration* and *total vertical distance.*

I will focus on Model A's random effects in the following section as the two model outputs are very similar, with some minor differences in their estimates. When only accounting for variance explained by the fixed effects (marginal R^2), the R^2 was 45.5 %. However, when including the random effect, and hence variance explained by fixed and random effects (conditional R^2), the R^2 improved and increased to 57.8 %. Thus, there was an improvement in the model due to the inclusion of individual whales as a random effect. The *Between-whale variance* describes how different whales' intercepts vary from the estimated grand mean intercept of 2.30 breaths min^{-1} (95 % CI: 2.17–2.43), whereas the *within-whale variance* is the remaining variance within each individual that is not explained by the random effect (Figure S1).

Table 5 Estimated effects of dive variables on respiration rate. *Model A: all dive cycles (n = 4677). Model B: dive cycles where lunge rate > 0 (n = 2052).*

	Model A Respiration rate [log]			**Model B Respiration rate [log]**		
Predictors	***Estimates***	***CI***	***p***	***Estimates***	***CI***	***p***
(Intercept)	2.30	2.17 – 2.43	**<0.001**	1.62	1.28 – 1.96	**<0.001**
1 + Lunge rate [log]	-0.06	-0.12 – -0.01	**0.025**			
Total vertical distance [log]	0.53	0.48 – 0.59	**<0.001**	0.40	0.27 – 0.52	**<0.001**
Dive duration [log]	-0.72	-0.77 – -0.67	**<0.001**	-0.49	-0.61 – -0.37	**<0.001**
Max depth [log]	-0.18	-0.20 – -0.15	**<0.001**	-0.16	-0.21 – -0.10	**<0.001**
Bottom time [log]	-0.07	-0.10 – -0.04	**<0.001**	-0.06	-0.10 – -0.02	**0.007**
Lunge rate [log]				-0.08	-0.40 – 0.25	0.649
Lunge rate [log] * Dive duration [log]				0.12	0.03 – 0.21	**0.007**
Lunge rate [log] * Total vertical distance [log]				-0.10	-0.20 – -0.00	**0.050**
Random Effects						
Within-whale variance	0.11			0.11		
Between-whale variance	0.03 $_{\text{WhaleID}}$			0.03 $_{\text{WhaleID}}$		
N	21 $_{\text{WhaleID}}$			21 $_{\text{WhaleID}}$		
Observations	4677			2052		
Marginal R^2 / Conditional R^2	0.455 / 0.578			0.278 / 0.432		

Model A and B was used to create marginal predictions (hence, all dive variables and random effects controlled for) for interpretations of individual dive variables effect on the *respiration rate*. It should be emphasised that these are not raw data points as seen in Figure 11, but rather a visualization of the estimates made by the lmer models (Table 5). Predictions derived from Model A, seen in Figure 13, had a steady increase in the *respiration rate* as the *total vertical distance* increased (Figure 13a), whereas the remaining dive variables showed a steeper change in the beginning before slowly decreasing (Figure 13b-d).

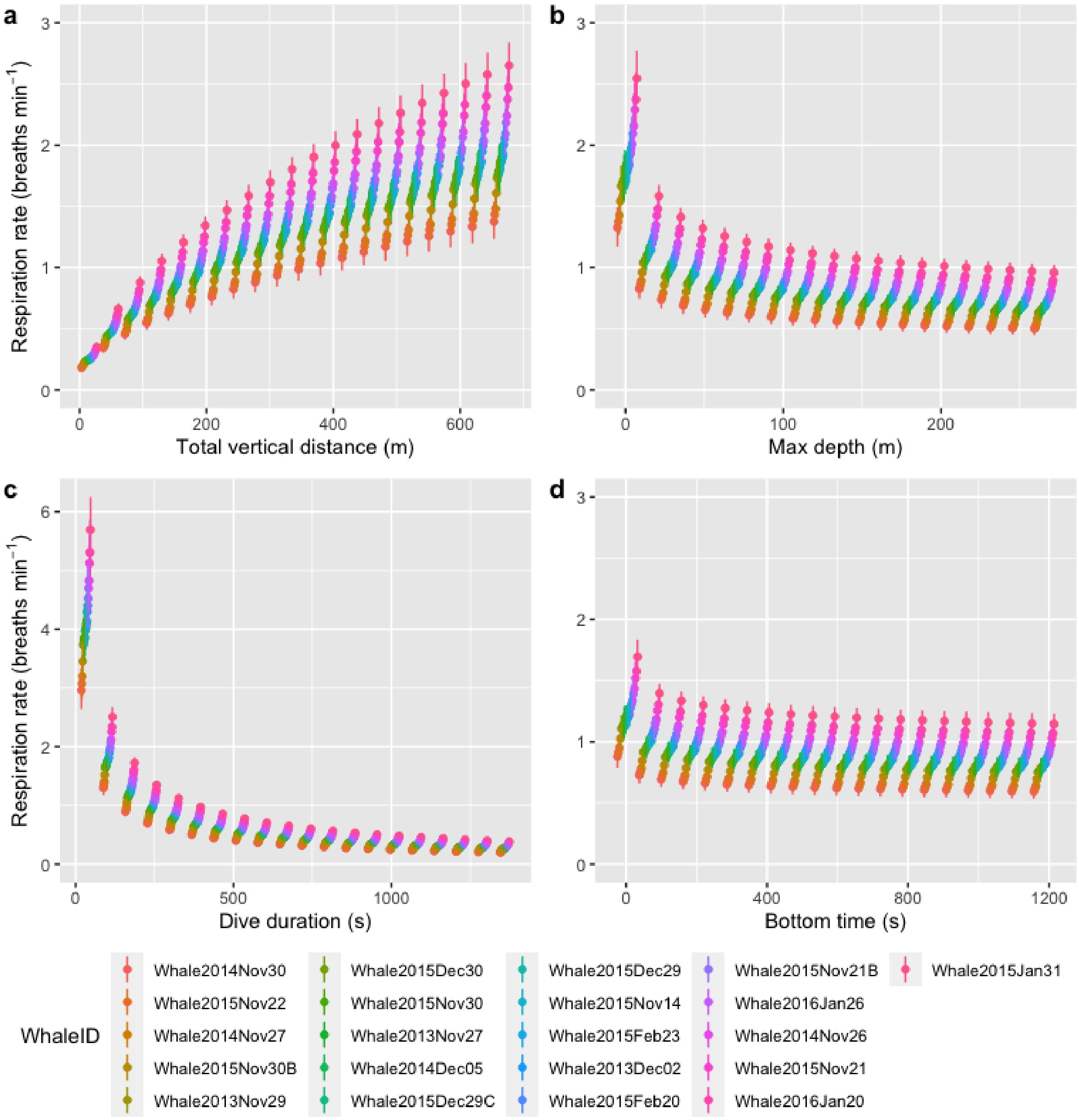

Figure 13 Predicted relationship between (a) total vertical distance, (b) max depth, (c) dive duration and (d) bottom time, and respiration rate. *All predictions derive from Model A. Vertical lines represents 95 % CI for the different colour coded individual whales (WhaleID). Note differences y-axis scale for plot c and the rest.*

Model B was used to assess how the predicted relationship between *respiration rate* and *lunge rate* changed as *dive duration* and *total vertical distance* increased (Figure 14). The former (Figure 14a) had a positive change of 0.12 in slope whereas the latter (Figure 14b) had a negative change of -0.10 in slope as *lunge rate* increases (see interactions table 5). The *dive duration* and *total vertical distance* were both controlled for and kept constant at three increasing intervals (quantiles: 0.1, 0.5 and 0.9) to clearer see the effect of *lunge rate* on the *respiration rate*.

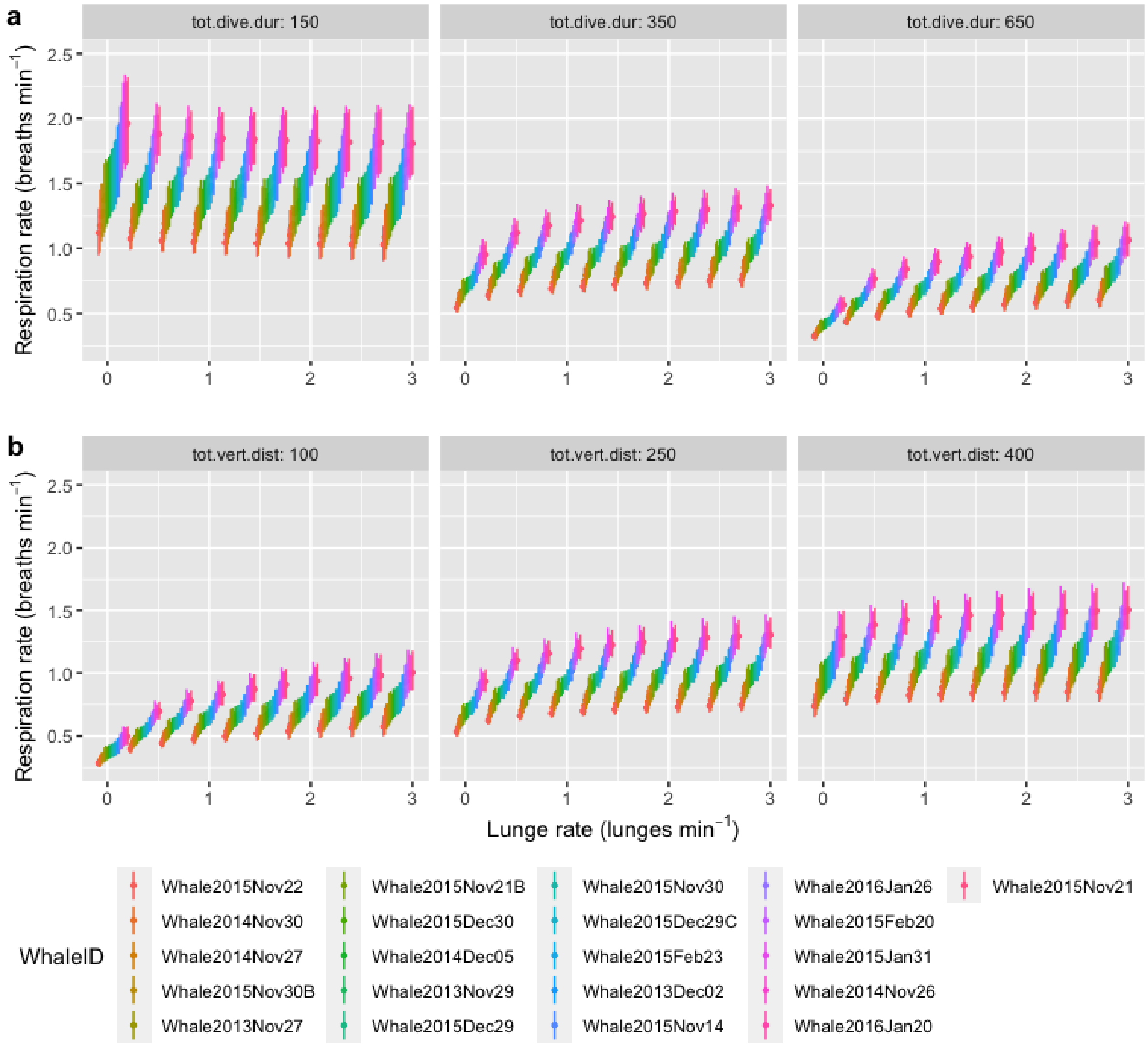

Figure 14 Predicted relationship between respiration rate and lunge rate at three different dive durations (150, 350 and 650 s) and total vertical distances (100, 250 and 400 m). *Vertical lines for each colour coded individual represent 95 % CI. Each prediction was done by using the same lunge rates (n = 20) ranging from lowest (0.6 lunges min^{-1}) to highest (2.9 lunges min^{-1}). Note that all the 20 lunge rates' are the same for all individuals, but slightly shifted in position.*

3.3 Changepoint analysis and categorization of respiration rate

Segmentation of the respiration rate was created by a changepoint analysis. Unfortunately, I was unable to complete the analysis because there were no clear distinctions between the behavioural categories. Therefore, the results are addressed and discussed in this section.

For each whale, the respiration rate segments were aligned with time-depth data for comparison (Figure 15), in addition to categorizing the segments into classes of high, low or variable (Figure 16). However, there was no consistent pattern, as some segments with or without lunges were found in all categories. Despite these irregularities, periods of foraging events, which usually occur at night, appear to have periods of high-intensity with respiration rates up to ~2.5 – 3 breath min^{-1}. In addition, others have observed humpback whales following the diel vertical migration of sand lance (Friedlaender et al., 2009), which is not unlikely to be the case for humpback whales foraging on Norwegian spring spawning herring (Jourdain & Vongraven, 2017). This indicates that there is more to investigate, but a more sophisticated analytical method would be needed.

For further investigation I would recommend starting the analysis simpler by having two categories (e.g., low, and high) and slowly increasing its complexity, by including more categorize if fitting but also accounting for individual variation and other relevant parameters (e.g., solar amplitude). Alternatively, it would be helpful to use data containing speed, accelerometer, body orientation and location as parameters for defining categories. It could be possible to apply such data to e.g., a behavioural changepoint analysis that detects significant changes in the behavioural movements for a more complex model (Gurarie et al., 2009), to thereafter correlate the behavioural changes with respiration rate.

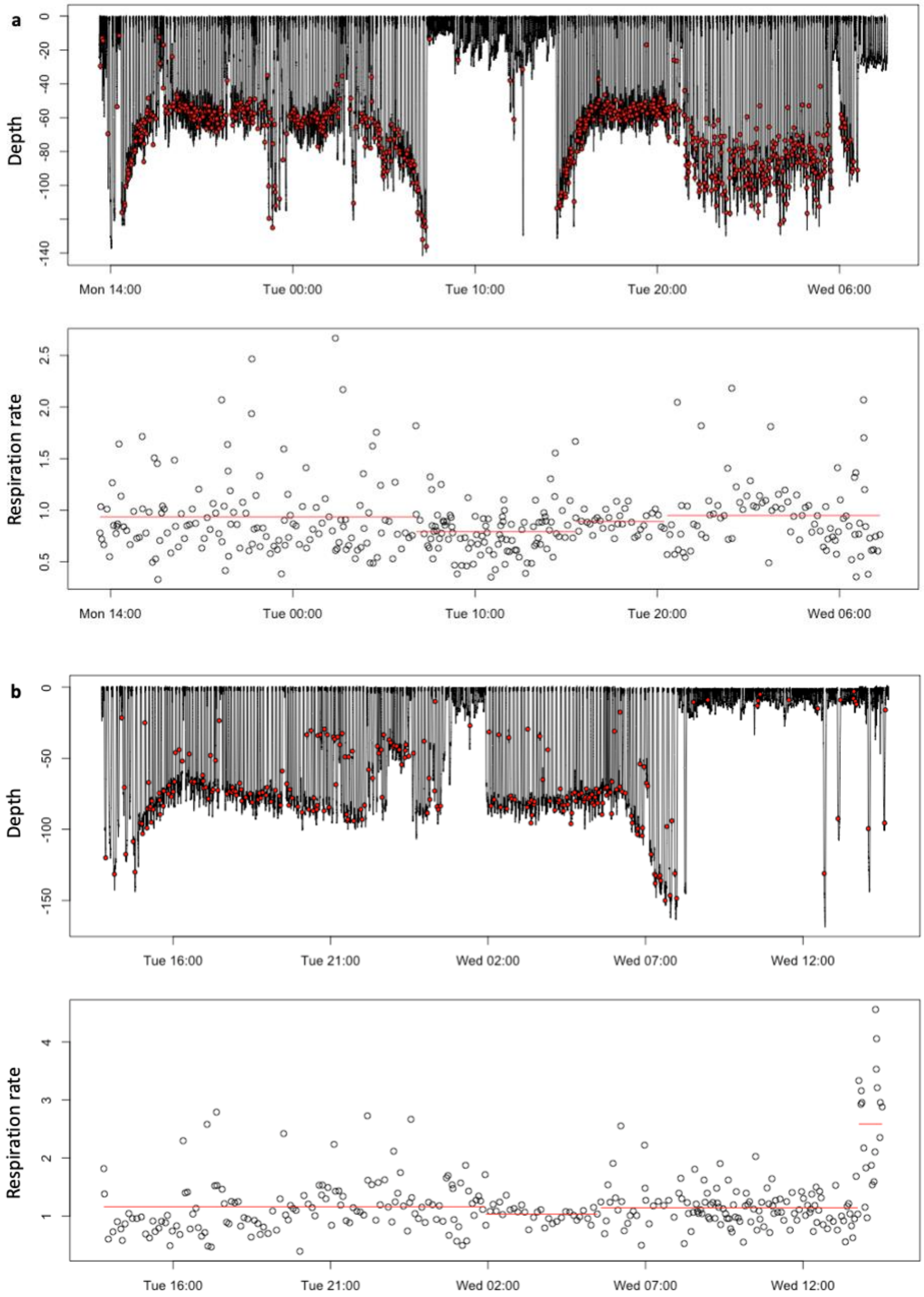

Figure 15 Segmentation of respiration rate (breaths min^{-1}) for two whales (a and b) created from changepoint analysis (bottom panel) aligned with the depth (m) data (top panel) during the same time period (x-axis). *Red dots are represented as detected lunges while each red line represent one respiration segment.*

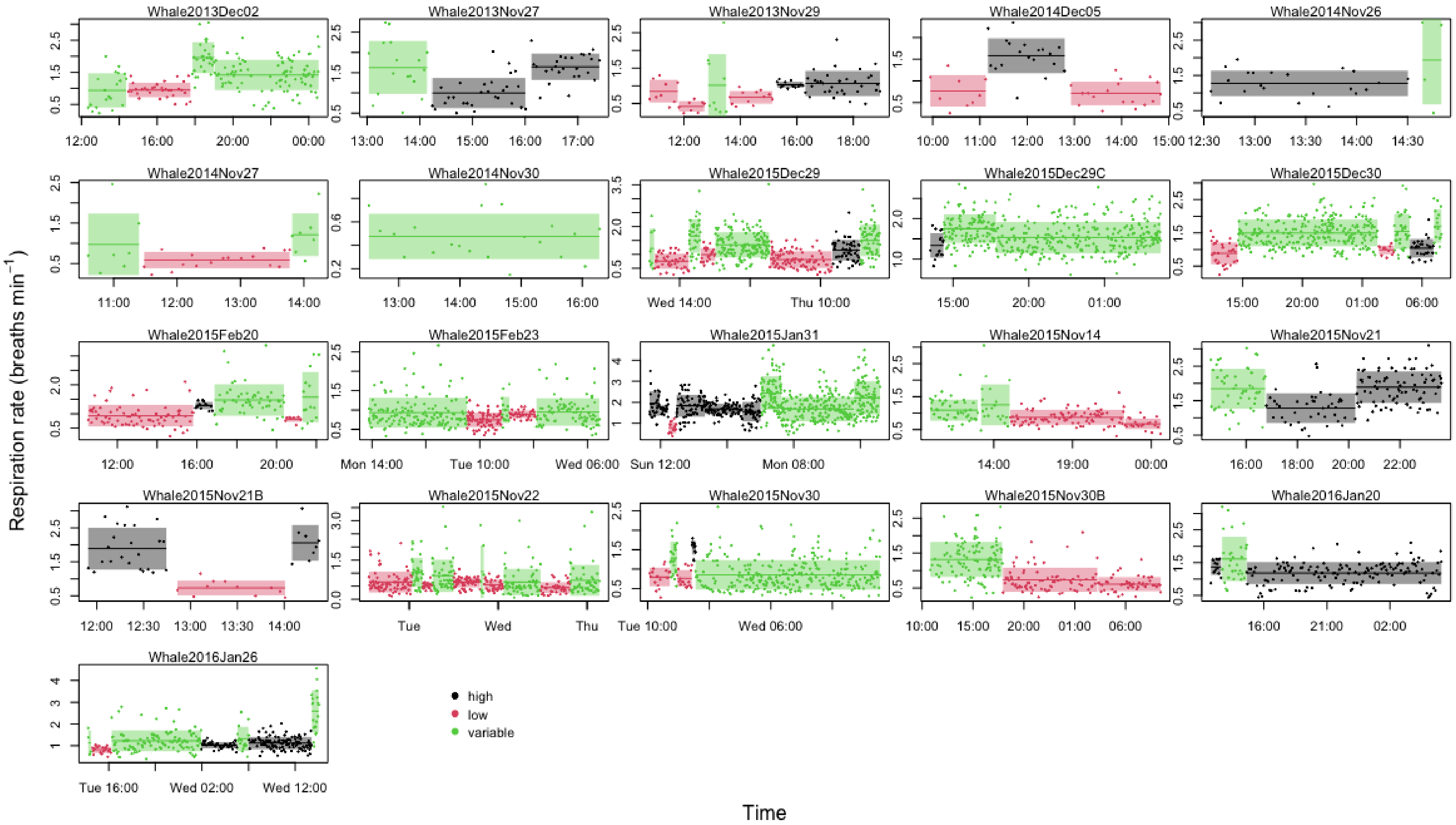

Figure 16 Categorization of respiration rate segments for each individual whale. *Note that the x-axis (Time of day) and y-axis (respiration rate) are different for each whale.*

4 Discussion

In this thesis I aimed to link the behaviour of humpback whales, as reflected by the dive variables *dive duration*, *bottom time, total vertical distance*, *max depth* and *lunge rate*, to their *respiration rate*. This was done in an attempt to assess to what extent and how, different behaviours were associated with different energetic costs, assuming that *respiratory rate* is a reasonable proxy for oxygen consumption (metabolic) rates in these animals. I furthermore made some quantitative estimates of humpback whale metabolic rates based on available data on *respiration rate*, and literature values and physiological reasoning around the other required variables. Finally, I discuss different approaches for estimation of energy costs of living in these mammals.

4.1 Dive behaviour

Most dives performed by humpback whales presented in this thesis were shallow and short dives, with a mean depth of 41 ± 32 m (n = 4721) and duration of 4.6 ± 3.1 min (n = 4721), respectively (Table 4). This is in accordance with previous findings, showing between depths of 28 – 66 m and dive duration of 1.4 – 4.7 min (Akiyama et al., 2019; Dolphin, 1987a; Friedlaender et al., 2009; Keen & Qualls, 2018; Narazaki et al., 2018; Tyson et al., 2016), whereas others have found a drastically deeper dive depth of 100 – 189 m and longer dive duration of 6.5 – 9.6 min (Burrows et al., 2016; Goldbogen et al., 2008, 2012; Witteveen et al., 2008). This is likely due to humpback whales' adjustments to the ocean floor topography as well as prey's diel vertical migration (Friedlaender et al., 2009; Hazen et al., 2009).

As humpback whales shifted from non-foraging to foraging, the dives became 2 – 2.5-fold longer and deeper (Table S1). The same shift has been observed in fin, blue and other humpback whales with a slightly lower but similar increase of 1.5 – 2 fold (Croll et al., 2001; Witteveen et al., 2008). The whales in this present thesis increased their vertical distance as well as bottom time during foraging. This is not unexpected from a foraging rorqual, as a series of lunges consists of repetitive cycles of approaching a prey patch (Hain et al., 1982). Hence, larger distances accumulate by swimming up and down in the water column and longer time spent around the prey. Dolphin (1987b) used sonar to trace the depth of humpback whale dives and krill density patches in southeast Alaska. Of the recorded dives (n = 284), less than 3 % exceeded 120 m and no dives were made beyond 200 m. I find similar results for the north Atlantic humpback whales of this thesis, however, one whale was recorded to reach a depth of

265 m (Whale2015Nov30), and similar depths have also been described by others (Goldbogen et al., 2012; Narazaki et al., 2018; Simon et al., 2012). For humpback whales foraging on the schooling fish capelin, Simon et al. (2012) reported a mean and maximum number of lunges (3.4 and 9, respectively) similar to what I report in this thesis (2.2 ± 1.4 and 10, n = 2069, Table 4) during foraging on Norwegian spring spawning herring (Jourdain & Vongraven, 2017). Other reports substantially more lunges with a mean of 6 – 9 lunges per dive while feeding on krill (*E. pacifica*) (Goldbogen et al., 2008, 2012). When foraging on rich, dense prey patches, they try to maximise foraging efficiency in that patch, by cutting down on the number of transits between the surface and the prey patch (Gallon et al., 2007; Sparling et al., 2007; Thompson & Fedak, 2001), and adjusts the number of lunges per dive (Akiyama et al., 2019).

4.2 Energetics of dive behaviours, as assessed from variations in respiration rate

The energy expenditure of a dive will depend on the whale's activity as well as the activity's intensity. By investigation different dive variables as a reflection of the whale's dive behaviour, we can form a picture of its energetic costs, assuming the respiration rate is a proxy for oxygen consumption. In this thesis, when accounting for all dive cycles and thus the overall dive behaviour (i.e., foraging and non-foraging; Model A in Table 5; Figure 13), the respiration rate decreased with max depth, dive duration and bottom time while it increased with total vertical distance. The respiration rate was higher when a dive was of short duration (Figure 13c), shallow max depth (Figure 13b) or a short bottom time (Figure 13d), compared to a lower, but relatively stable respiration rate during longer dive durations, deeper max depths, or longer bottom times. Furthermore, for low dive durations (~1 min), the respiration rate was predicted to be up to almost 6 breaths min^{-1}. However, this is likely to be a result of the simple fact that dive duration automatically affects the calculation of respiration rate (breaths per cycle duration). The results indicated that the max depth and bottom time are not the main drivers of changes in respiration rate, as indicated by their small effects (Table 5). This makes sense as these three dive variables (dive duration, max depth and bottom time) do not necessarily relate to high activity. For example, a whale could dive down to 50 m and stay there calmly before returning to the surface. The only predicted positive correlation in Model A was between respiration rate and total vertical distance (Figure 13a). As lunges consist of repetitive up and down movements in the water column, it is reasonable to assume that an increased total vertical distance is associated with lunge events (Goldbogen et al., 2006). This is shown in the results from Model B (i.e., lunge dive cycles), where an increased total vertical distance during lunge dive cycles caused an increase in respiration rate (Table 5; Figure 14b). Basic physiology implies that exercise would result in an increased ventilation (i.e., V_T and respiration rate) by initiating stronger contraction of diaphragm and intercostal muscles, indirectly stimulated by central and peripheral chemoreceptors detecting changes in arterial partial pressure of O_2 and CO_2 as well as H^+ concentrations (Hill et al., 2018). A lunge event consists of short bursts of high tail oscillations, and thus rapid increase in speed, resulting in high muscle activity as well as metabolic output (Potvin et al., 2012; Rivero, 2018). This would imply an increased locomotor activity and thus increased respiration rate (Hill et al., 2018). The respiration rate during a lunge dive cycle was also affected by the dive duration, with lower respiration rates as the dive duration rate increased (Figure 14a).

It might seem paradoxical that dive with a longer breath-hold period (increased dive duration, max depth or bottom time) causes lower respiration rates. There are two main aspects that could explain a decreased respiration rate: (1) the decrease may be partly due to longer intervals between surfacing's which will give increased ΔO_2. When venous O_2 levels have a large drop, as with longer dives, the diffusion gradient of alveoli-lung capillaries becomes steeper. A decreased respiration rate may be compensated for by increased V_T and/or ΔO_2 (Hill et al., 2018). (2) Marine mammals reduce the bodies oxygen consumption by slowing down the heart rate (bradycardia) and restricting blood flow to pump between heart and brain (peripheral vasoconstriction), called the diving response (Scholander, 1940). Extreme bradycardia has been measured in grey seals (*Halichoerus grypus*) where there was a reduction from 120 beaths min^{-1}(bpm) all the way down to only 4 bpm in voluntary dives down to 70 – 80 m (Thompson & Fedak, 1993). Recently, Goldbogen et al. (2019), measured the heart rates in blue whale with an electrogram-depth recorder tag and saw a reduction from 25 – 37 bpm to 4 – 8 bpm almost irrespectively of maximum depth and dive duration. The diving response ultimately decreases the oxygen consumption in peripheral tissue, giving an overall lowering in total oxygen consumption. When initiating a dive with longer duration and/or higher activity, the diving response would be expected to be more profound (Thompson & Fedak, 1993).

4.3 Estimating metabolic rate from respiration rate

In this section I will attempt to quantify energy costs of humpback whales based their estimated respiration rate, to illustrate how indirect estimates of the metabolic rate of these large mammals may be made. This approach is based on the following relations: When an animal breathes, its oxygen uptake rate will depend on the tidal volume (V_T : l), how often it breathes (f: breaths min^{-1}) and the percentage of oxygen that is taken up from lung air and into their blood (lung oxygen extraction; ΔO_2: %) (Eq.7; e.g., Folkow & Blix, 1992):

Eq. 6 $V_{O_2} = V_T \times \Delta O_2 \times f$

In estimating the oxygen consumption for larger cetaceans based on eq.7, most studies have used, or assumed, mean V_T and ΔO_2 values (Armstrong & Siegfried, 1991; Christiansen et al., 2014; Dolphin, 1987a; Folkow & Blix, 1992; Sumich, 1983; R. Williams & Noren, 2009). On a shorter time scale, there will, of course, be quite substantial breath-by-breath variations in both these variables. For example, breath-by-breath V_T in cetacean has been measured to vary by as much as 50 % in grey whale calves (Wahrenbrock et al., 1974) and ΔO_2 in bottlenose dolphins was found to range between 1.5 – 17.0 % and 1.2 – 11.8 % during pre- and post-exercise (Fahlman et al., 2016), respectively. Due to the high variability of V_T and ΔO_2 measurements and lack of validation in large cetaceans, it is extremely difficult to make accurate estimations of short-term changes in metabolic rate, while predictions that aim to average energy expenditure over time, e.g., as with estimates of field metabolic rate (FMR), are likely to be more realistic.

4.3.1 Respiratory variables: V_T, ΔO_2 and f

Cetaceans are ‘fast’ breathers, in which large quantitates of lung air are typically exchanged in each respiratory cycle. Each breath consists of short surfacings with little time available for respiratory exchanges. During these short periods, marine mammals must have efficient exchange of air in order to replenish their O_2 stores and eliminate built-up CO_2 levels before performing a new dive (Boutilier et al., 2001).

4.3.1.1 Tidal volume

Most respiratory data regarding V_T in marine mammals derives from small cetaceans (as well as pinnipeds), whereas it has on rare occasion been measured in large cetaceans due to logistical difficulties such as body size and maintenance. However, V_T measurements from small cetaceans may still be relevant for large cetaceans as they face the same challenge of maximizing their time under water, and thus may have similar solutions.

For cetaceans, a full respiratory cycle (exhale and inhale) have an approximate duration of only 1 – 3 s (Fahlman, Brodsky, et al., 2019; Fahlman, Epple, et al., 2019; Kooyman et al., 1975; Martins et al., 2020; Sumich, 2001). In addition, they have the ability to exchange V_T that are close to their total lung capacity (*TLC*), presumably in order to optimize oxygen uptake during short and intermittent surfacings. Several studies have reported that cetaceans maintain V_T that are much higher than achieved by terrestrial mammals (Denison et al., 1971; Fahlman et al., 2015, 2020; Fahlman, Epple, et al., 2019; Kooyman & Sinnett, 1979; Olsen et al., 1969), e.g., Scholander & Irving (1941) compared V_T as proportion of body mass (kg) for resting Florida manatee as 2.9 % as well as harbour porpoise as 5.3 % in comparison to 0.7 % in humans.

For all animals, the V_T maintained will depend on the activity (Hill et al., 2018), e.g., as seen by a significant increase from pre- to post-exercise measurements of bottlenose dolphins (Fahlman et al., 2016), and the same would be expected for a resting vs. active (e.g., foraging) humpback whale. Measurements of V_T in cetaceans are very limited to smaller cetaceans with a few derived from baleen whales (Kooyman et al., 1975; Sumich, 2001; Wahrenbrock et al., 1974). However, by knowing the TLC, it can provide an indication of where V_T might vary. Previous studies have reported that V_T may vary in proportion of *TLC* (Table 6) as 60 % in grey whale calves (Wahrenbrock et al., 1974), 32 – 95 % in harbour porpoise (Fahlman et al., 2015, 2016; Irving et al., 1941; Reed et al., 2000) and 20 – 88 % in pilot whale (Olsen et al., 1969). Whereas, in comparison, a typical terrestrial mammal exchanges only 10 – 15 % of *TLC* (Wartzok, 2009). Fahlman et al. (2016) argued that assuming that V_T represents 60 – 80 % of *TLC* would result in an overestimation compared to their own measurements (Fahlman et al., 2015) from bottlenose dolphins for voluntary breaths (25 – 45 % of *TLC*) and maximum effort (63 – 95 % of *TLC*) during rest at the surface, as only 8 breaths exceeded 80 % of TLC (n = 45). However, a cetacean conducting long and deep dives would be expected to minimize its surface period with rapid replenishment of oxygen stores (Boutilier et al., 2001) and have larger V_T compared to the resting dolphins in Fahlman et al. (2015) with no limitations to ventilation.

For this present thesis, the V_T was estimated as a fraction (%) of TLC of the freely-swimming humpback whales, where TLC was determined using an allometric relationship between TLC and body mass of baleen whales. However, body mass was not measured nor estimated for the tagged whales. Therefore, the average body mass of an adult humpback whale was assumed to be 30 tonnes (Lockyer, 1976). Figure 17 shows the logarithmic linear relationship between TLC and body mass (BM) for 22 adult baleen whales (12 minke whales, 3 sei whales and 5 fin whales), described by Eq. 8:

Eq. 7 $TLC = 0.34\ BM^{0.819}$

where TLC is given in litres and body mass in kg. Unfortunately, the TLC of humpback whales has not previously been quantified. It is therefore assumed that humpback whales follow the same allometric relationship as other baleen whales, resulting in a TLC of 1578 l for a 30 tonnes humpback whale as seen by dashed lines in Figure 17.

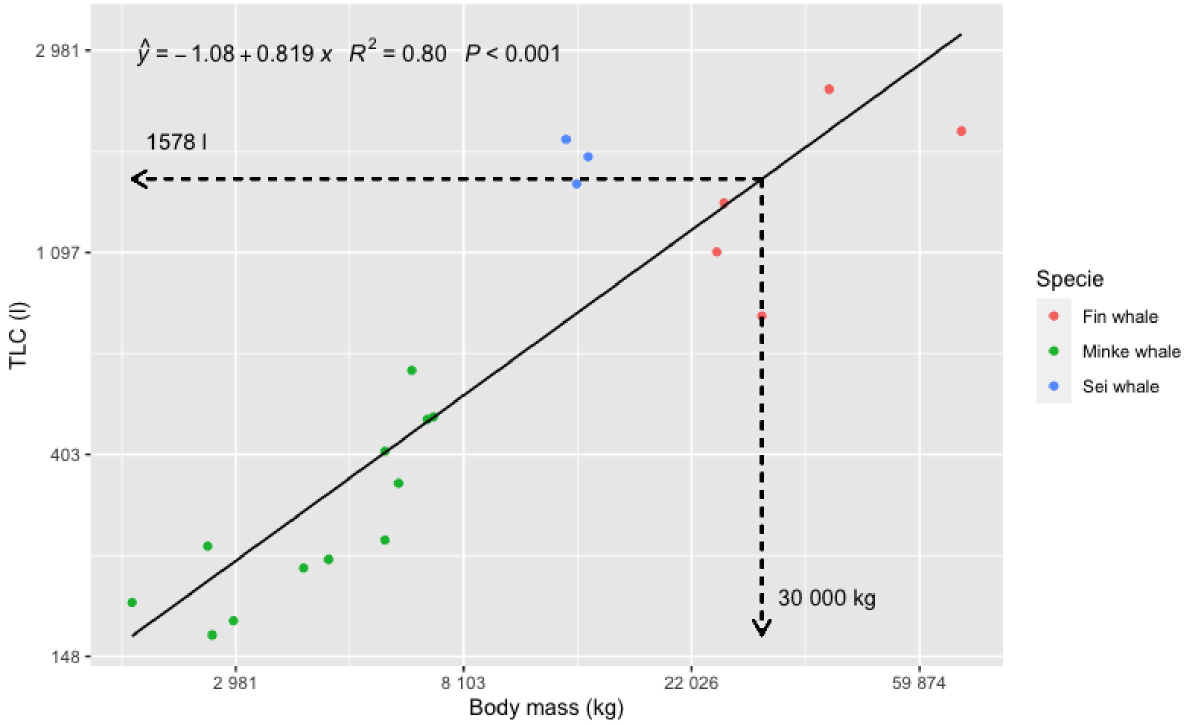

Figure 17 logarithmic relationship between total lung capacity (TLC: l) and body mass (BM: kg) of adult baleen whales. *Regression line can also be expressed as TLC = 0.34 × $BM^{0.819}$, dashed lines are based on this equation. Data from Folkow & Blix* (1992), *Leith & Lowe* (1972) *and Scholander* (1940).

The same allometric relationship between TLC (l) and body mass (BM; kg) has previously been postulated for mammals in general (Eq. 9 and 10) and for marine mammals (Eq. 11):

Eq. 8 $TLC = 0.0535\ BM^{1.06}$ (Stahl, 1967)

Eq. 9 $TLC = 0.056\ BM^{1.02}$ (Tenney & Remmers, 1963)

Eq. 10 $TLC = 0.135\ BM^{0.135}$ (Kooyman, 1973)

However, previous studies have shown that marine mammals tend to deviate from the respiratory allometric relationships of terrestrial mammals (Fahlman, Brodsky, et al., 2018; Kooyman, 1973; Kooyman & Sinnett, 1979; Kriete, 1995). Unsurprisingly, the TLC estimated by Eq. 11 was close to the estimated TLC in this thesis (1775 l vs. 1578 l), as Kooyman (1973) only used data from marine mammals. However, a TLC of 1578 l was still chosen as Eq. 8 explicitly accounts for baleen whales.

The V_T was assumed to be 50 % of TLC, slightly above the approximate mean from previous respiratory data (Table 6), as most of the reported percentages are dominated by resting individuals. As previously discussed, there are large variations in V_T and therefore also uncertainties. For example, Irving et al. (1941) proposed that all whales probably exchanged 80 % of their lung air for each breath, as seen in their study animal (bottlenose dolphin), but gave limited information on his process to this conclusion. Furthermore, it is not unlikely that the reported percentage of Irving et al. (1941) is towards the extreme of respiratory exchange in cetaceans, as Olsen et al. (1969) and Fahlman et al. (2015) have reported maximum percentages at 88 % and 95 %, respectively. However, a 50 % exchange was chosen as it is an intermediate percentage of the reported values, being mostly above what is seen in resting individuals, but lower than the maximum effort breaths (i.e., the percentage more likely to be expected during short-term intense exercise).

4.3.1.2 Oxygen extraction

The ΔO_2 is the difference between the percentage of oxygen in the inhaled (21 %) and in exhaled air and, hence, reflects how much oxygen is extracted (i.e., transferred to blood) in the lungs. Measurements from bottlenose dolphins and grey whale calves have revealed ΔO_2 -values as high as approximately 18.5 % (Ridgway et al., 1969; Sumich, 2001), reflecting that an uptake of as much as ~90 % of the inhaled oxygen is possible under some circumstances.

However, other ΔO_2 values have been measured to vary drastically in relation to diving history (Ridgway et al., 1969) with large overlaps between resting and active animals (Table 6). Despite this overlap, there is a significant increase in ΔO_2 with activity (Fahlman et al., 2015, 2016; Kriete, 1995; Ridgway et al., 1969) and breath hold duration (Fahlman, Brodsky, et al., 2019).

Table 6 Oxygen extraction (ΔO_2: %) and the tidal volume (V_T) proportion of total lung capacity (TLC) for cetacean species under different activities collected from the literature.

Specie	**ΔO_2 (%)**	**V_T as % of *TLC***	**Activity**	**Reference**
Grey whale (calf)	4.8 – 18.3		Freely swimming in pool	(Sumich, 2001)
Grey whale (calf)	9.2[1]		Freely swimming	(Sumich, 1994)
Grey whale (calf)	4.5 – 12.5		Freely swimming	(Sumich, 1986)
Grey whale (calf)	8.5 – 12.5	60 %	Resting	(Wahrenbrock et al., 1974)
Bottlenose dolphin	8.8	80 %	Resting	(Irving et al., 1941)
Bottlenose dolphin	8.7	~37 % [6]	Resting [2]	(Fahlman et al., 2015)
Bottlenose dolphin	7.3	~71 % [6]	Resting [3]	
Bottlenose dolphin	5[4]	32 % [6]	Pre-exercise	(Fahlman et al., 2016)
Bottlenose dolphin	5.8[5]	34 % [6]	Post-exercise	
Bottlenose dolphin	10.6		Resting	(Fahlman, Brodsky, et al., 2018)
Bottlenose dolphin	4.3	27 % [6]	Resting	(Fahlman, McHugh, et al., 2018)
Bottlenose dolphin	9.6	30 % [6]	Resting	(Fahlman, Brodsky, et al., 2019)
Bottlenose dolphin	7.8 – 18.8		Active	(Ridgway et al., 1969)
Harbour porpoise	~11	40 % [7]	Resting	(Reed et al., 2000)
Pilot whale	10.5 – 13.5	55 % [8]	Resting	(Olsen et al., 1969)
Killer whale	7.7		Resting	(Kriete, 1995)
Killer whale	9.7		Active	
Mean±sd All	~9.5±3.6	~46 %		

[1] For mean total respiratory cycle duration of 25.5 sec.
[2] Spontaneously breaths
[3] Maximal effort breaths
[4] Mean of estimated values, range: 1.5 – 17 %
[5] Mean of estimated values, range: 1.2 – 11.8 %
[6] From estimated TLC (= 0.135 $BM^{0.92}$; Kooyman, 1973)
[7] From estimated TLC (= 0.10 $BM^{0.96}$; Kooyman, 1989)
[8] Range: 20 – 88 %

Ridgway et al. (1969) measured the oxygen content of exhaled air after diving to different depths and for different breath-hold durations in a bottlenose porpoise (Figure 18). The porpoise was trained to execute three exercises: breath-hold close to the surface, rapid swimming at a depth of 20 m and deep dives down to approximately 300 m. Ridgeway and co-workers observed that the first breath after a deep dive had a greater O_2 content in exhaled air (hence, lower ΔO_2) compared to a dive at 20 m, despite having the same breath-hold duration and similar requirements in muscular activity. The authors concluded that this difference was a result of a lung collapse, seen from an underwater camera, restricting the extraction of oxygen during deeper dives. This underlines the fact that instantaneous ΔO_2 of lung air may vary not only depending on the activity of the animal, but also due to indirect effects of the dive depth – again underlining the importance of taking care and using physiological insight when selecting input values for use in Eq. 7.

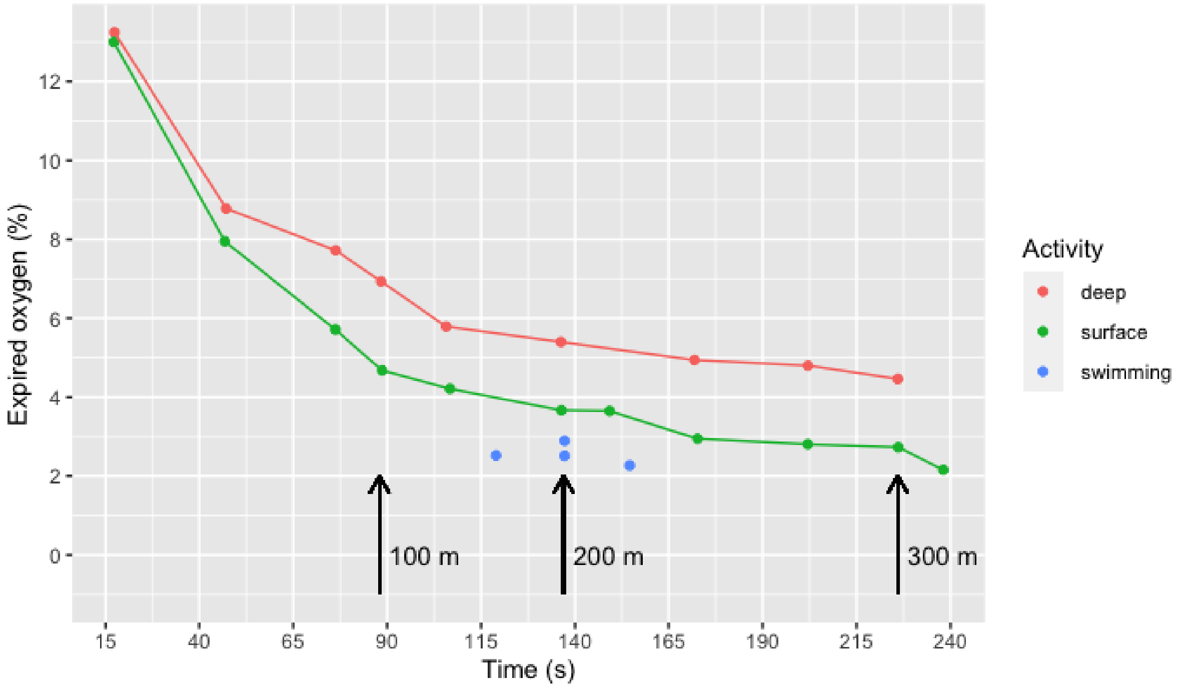

Figure 18 Changes in a bottlenose porpoises expired O_2 with breath-hold durations (time). *The bottle nose dolphin three different exercises: deep dives down to 300 m (red), breath-hold close to the surface (green) and rapid swimming at 20 m (blue). Black arrows indicate the respective depths for deep dives. Each point represents the mean value of randomly collected breaths for 7 – 20 dive/breath-holds. Figure modified from Rigdway et al.,1969.*

Irving et al. (1941) reported a mean ΔO_2 of 8.8 % in bottlenose dolphins resting in an experimental tank and suggested that whales are unlikely to exceed 10 %. Despite the variation of ΔO_2 from previous studies, an extraction of 10 % might be realistically sustainable for long-term scenarios, similar to an approximate mean of 9.5 % when accounting for various activities collected from previous studies (Table 6). Therefore, an ΔO_2 of 9.5 % was considered as an appropriate value, and hence used in this thesis.

4.3.1.3 Respiration rate

The mean respiration rate of humpback whales for all dive cycles in this thesis was 1.25 breaths min^{-1}. This fits well with previously reported respiratory rates of foraging humpback whales of 1.24 – 1.3 breaths min^{-1} (Bejder et al., 2019; Dolphin, 1987a; Keen & Qualls, 2018). In addition, Dolphin (1987a) observed the respiration rate at different depth intervals with an overall mean of 1.24 breath min^{-1}. He reported the highest respiration rate in connection with shallow diving (0 – 21 m; 1.33 breaths min^{-1}), while respiration was slower during deeper diving (21 - 120 m; ~0.88 breaths min^{-1}). A similar result was obtained in the present study, with a predicted negative relationship between respiration rate and maximum dive depth (Figure 13b). This is possibly because max depth does not necessarily translate to increased activity, as discussed in Section 4.2. Based on these considerations, I have used the mean value of 1.25 breaths min^{-1} to estimating FMR during foraging for these animals, by use of Eq. 7.

One should note that the respiration rate presented in this thesis is only representative for a limited period (i.e., foraging ground) of the humpback whales' annual life. The FMR estimation in this thesis only reflects the 'cost of living' on the feeding ground of the northern humpback whales. Their diving behaviour are quite different from breeding to feeding ground, with a much higher activity in the latter, and thus different respiration rates.

4.3.2 Estimating FMR

For the estimation of FMR, V_T was assumed to be 50 % of the estimated TLC of 1578 l from Eq. 8, a mean respiration rate of 1.25 breaths min^{-1} (Table 4), a ΔO_2 of 9.5 % (Table 6) was assumed to be a realistic value for estimation of FMR for the humpback whales to account for a mixture of foraging and non-foraging activity. These values were inserted into Eq. 7 (p. 38), to yield an estimate of oxygen consumption (V_{O_2}: l_{O_2} min^{-1}), as follows:

$$V_{O_2} = (0.5\ \times 1578\ l) \times 0.095 \times 1.25\ breaths\ min^{-1} = 94\ l_{O_2}\ min^{-1}$$

To estimate FMR (Eq. 13), a caloric equivalent for oxygen of 20.1 kJ ${l_{O_2}}^{-1}$ was assumed, reflecting catabolism of a mixture of carbohydrates, proteins, and lipids (Kleiber, 1965). By multiplying V_{O_2} and the caloric equivalent, the FMR (kJ min^{-1}) was estimated as follow:

Eq. 11 $FMR = \ V_{O_2}\ x\ caloric\ equivalent$

The FMR was calculated as kJ min^{-1} by Eq. 13 and then converted to W, W kg^{-1} or W kg$^{-0.75}$:

$$FMR = 94\ l_{O_2}\ min^{-1} \times 20.1\ kJ\ l_{O_2}{}^{-1} = \ 1889\ kJ\ min^{-1}$$

Converted to Watts (W = J s^{-1}):

$$FMR = 1889\ kJ\ min^{-1}\ \times \frac{1000}{60} = 31483\ W$$

Converted to W kg^{-1} and W kg$^{-0.75}$:

$$FMR = \frac{31483\ W}{30000\ kg} = 1.05\ W\ kg^{-1}$$

$$FMR = \frac{31483\ W}{(30000\ kg)^{0.75}} = 13.8\ W\ kg^{-0.75}$$

By following this example but using the mean respiration rate of each individual whale, assuming all whales were of equal size, the FMR estimate equals 0.98 ± 0.29 W kg^{-1} (12.9 ± 3.8 W kg$^{-0.75}$; n = 21; Figure S2). Kleiber's (1975) equation predicts a BMR of 3.4 W kg$^{-0.75}$ for all mammals. My estimate thus implies a FMR that corresponds to 4.1 × BMR predicted by Kleiber.

Dolphin (1987a) estimated the energy expenditure for different dive depth intervals based on respiration rate and respiratory allometric relationships of humpback whales on their foraging ground in southeast Alaska. In his paper, an average humpback whale (32 700 kg) had the highest energy expenditure 5.41×10^3 kJ min^{-1} (2.8 W kg^{-1}) during shallow dives while a lower range was seen for deeper dives 3.30 – 4.04×10^3 kJ min^{-1} (1.7 – 2.1 W kg^{-1}), with an overall mean of 5.05×10^3 kJ min^{-1} (2.6 W kg^{-1}). This results in a 2.5-fold higher FMR than estimated in this thesis. Dolphin estimated V_T as 80 % of the vital capacity (V_C; maximum volume that can be exchanged in one breath in litres) from Stahl's (1967) allometric relationship ($V_C = 0.0567 \times BM^{1.03}$) of mammals. By conducting the same procedure for a 30 tonnes humpback whale, this would equal a TLC of 2317 l, almost the same as the measured TLC of 2400 l from a 40 tonnes fin whale (Leith & Lowe, 1972). Allometric relationships between respiratory variables such as V_T and V_C with body mass of marine mammals have been shown to deviate from the allometric relationship of terrestrial mammals (Fahlman, Brodsky, et al., 2018; Kooyman & Sinnett, 1979; Kriete, 1995). This, in addition to a higher assumed V_T as % of TLC, might be a reason for the higher FMR estimations reported by Dolphin.

Model outputs from various indirect approaches could be compared, thereby enabling researchers to narrow down the possible range of metabolic cost data. For example, Folkow & Blix (1992) calculated the minimum total heat loss rates of minke whales (*Balaenoptera acutorostrata*) based on blubber thickness, body temperature and total lung capacity from harvested minke whales, and compared data to metabolic rate estimations based on respiratory rates, as recorded in freely swimming minke whales (Blix & Folkow, 1995). The total rate of heat loss was estimated to be at least 4.06 W $kg^{-0.75}$ on average (Folkow & Blix, 1992), while the estimated average metabolic rate based on respiratory rate and TLC recordings was 4.33 W $kg^{-0.75}$. Even though two different methods were employed, the results did not differ substantially, indicating that metabolic costs of minke whales are likely to be in the reported order of magnitude.

Multiple studies have suggested that rorqual whales have large energetic costs due to high drag forces during lunge feeding. Potvin et al. (2012) simulated that metabolic rate in a 27 m blue whale during lunge dive cycles could reach 50 × BMR, based on outputs of engulfment power from unsteady hydrodynamic models. However, this is based on their absolute maximum values. If maximum values were to be applied for the humpback whales of this thesis by e.g., using V_T as 95 %, ΔO_2 as 18.8 % (Table 6) and respiration rate of ~4 breath min^{-1}, it would equal 49 × BMR, which is not a sustainable FMR estimate. However, any increase in activity would result in an increased oxygen consumption, but whether lunges are more energetically costly than other animals' activities, might be questionable. Boyd & Croxall (1996) suggested that a diving animal conducting normal activities (including foraging) would have a FMR of 4 × BMR based on previous measurements from sea lions and diving birds. Furthermore, Koteja (1991) reviewed the FMR in comparison to BMR of terrestrial species (31 birds, 9 marsupials and 18 eutherians) where the FMR had a range of ~3 – 4 × BMR. Goldbogen et al. (2011) estimated the metabolic cost of lunge feeding dives and compared it to the energy gain from krill to assess the efficiency of blue whale foraging. He and co-workers used the estimated metabolic requirements during lunges based on an unsteady hydrodynamic model in combination with metabolic rates estimated from allometric relationships (Croll et al., 2006). An estimated cost of foraging for a ~96000 kg blue whale was 0.88 W kg^{-1} (15.5 W $kg^{-0.75}$; 4.6 × BMR). Furthermore, Goldbogen et al., (2012) used similar methods and estimated energetic requirements of 0.97 W kg^{-1} (12.8 W $kg^{-0.75}$; 3.8 × BMR) for a foraging humpback whale (assumed to be 30 tonnes). A similar FMR estimate is presented in this thesis, indicating that the FMR of northern humpback whales are within the expected margin as previously reported for rorqual whales as well as other animal groups.

4.3.3 Other energetic considerations

Estimations of energetic requirements have been used in different scenarios including changes in body composition due to ecosystem changes and to assess the impact of human disturbance. Blubber thickness and body condition has previously been used to assess cetacean energy stores, usually in relation to reproduction (Aoki et al., 2021; Christiansen et al., 2013, 2016; Lockyer, 1987; Miller et al., 2011; Vikingsson, 1990, 1995; R. Williams et al., 2013), but also for cetaceans entangled in fishing gear (van der Hoop et al., 2016). As baleen whales are capital breeders, they only spend limited time of the year on their feeding grounds. Hence, this period is essential for build-up of energy before returning to their breeding grounds to support migration, survival and reproduction. Furthermore, the energy needed can vary depending on the animal's sex, age and reproductive status. Thereby, investigating energetic costs associated with different life stages can provide valuable information about e.g., which life stage is the more vulnerable to variability in environmental changes, prey density and variation and anthropogenic disturbance. Drastic changes in energy budgets can cause fatal outcomes, as seen in entangled right whales where an additional cost of $3.95 \times 10^9 - 4.08 \times 10^{10}$ J was estimated, which can be critical for sensitive populations (van der Hoop et al., 2016).

New models are continuously developed to understand respiratory variation, often for smaller cetaceans which may be tested for larger cetaceans in the wild (Fahlman et al., 2016; Roos et al., 2016). However, all energetic methods applied for free-ranging cetaceans, as for other animals, require validation which is difficult logistically. However, biotelemetry has become a valuable contributor to increased knowledge on cetacean lifestyles, allowing for more extensive and complex data. This provides an opportunity to investigate alternative and new methods for understanding how marine mammals cope physiologically and ecologically with their environment and daily lives. For humpback whales, and other rorqual species, a large focus has been on their foraging behaviour. For example, swim speed and acceleration patterns have been measured and linked to lunges (Friedlaender et al., 2009; Goldbogen et al., 2008). One promising method to estimate respiration and/or tidal volume in cetaceans is the use of phonospirometry, or flow noise from tags. Flow noise from grey whale calves has previously been used to investigate the relationships between respiratory variables and the duration and amplitude of respiratory cycles (Sumich, 2001; Sumich & May, 2009). This could be implemented in more biotelemetry devices to enable flow noise recordings. However, the placement of the tag can cause large error if not accounted for. With more explorations and testing, this could result in a method for obtaining respiratory data from freely swimming cetaceans without any disturbance and minimized human induced errors.

4.4 Conclusion

Knowing the energetic requirement of an animal is essential for our understating on how animals allocate their energy as well as what energy input is needed to support their daily activities. However, due to logistical difficulties in obtaining measurements, little is known about the energetics of large cetaceans. As a result, various methods have been used to improve our knowledge regarding these animals' energetic costs and challenges. I have employed one particular method by assuming that changes in respiration rate reflect changes in oxygen consumption (hence, metabolic rate). From biotelemetry deployments, the respiration rate of northern humpback whales was estimated and linked to the whales’ dive behaviour. The respiration rate was only slighty influenced by dive depth and bottom time but increased with locomotor activity during foraging and non-foraging dives.

One limitation of the dive data used in this thesis is the inability to estimate RMR/BMR. Because, when the whale is resting at the surface, instantaneous surfacings on which I based the analysis will not be present. As a result, the whales resting respiration rate and energetic expenditure cannot be estimated with the present method. The lack of validation and detailed measurements of V_T and ΔO_2 from large cetaceans further causes uncertainties for metabolic rate estimations, especially in short-term circumstances. However, comparison between methods enables us to narrow down the possible range of variability of metabolic costs. The FMR of humpback whales I estimated in this thesis is similar to estimates for other foraging rorquals, as well as in close proximity to estimates for other animal groups. New technology is constantly developed and will allow us to collect more detailed data and produce models with higher complexity. We can increase our knowledge about the ecology and physiology of larger cetaceans by exploring new methods and testing them on smaller, more accessible relatives.

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Appendix

Table S1 Proportion between dive variable means for dive cycles with (n = 2069) and without lunges (n = 2652). *f = Respiration rate (breaths min^{-1}), D_D = dive duration (s), BT = bottom time (s), VD = vertical distance (m) and MD = Max depth (m). Proportion = mean with lunges / mean without lunges*

Dive cycle	*f*	D_D	*BT*	*VD*	*MD*
With lunges	0.98 ± 0.43	377 ± 191	205 ± 145	236 ± 114	62 ±34
Without lunges	1.47 ± 0.66	193 ± 140	85 ± 81	100 ± 64	25 ± 19
Proportion	0.67	1.95	2.41	2.36	2.48

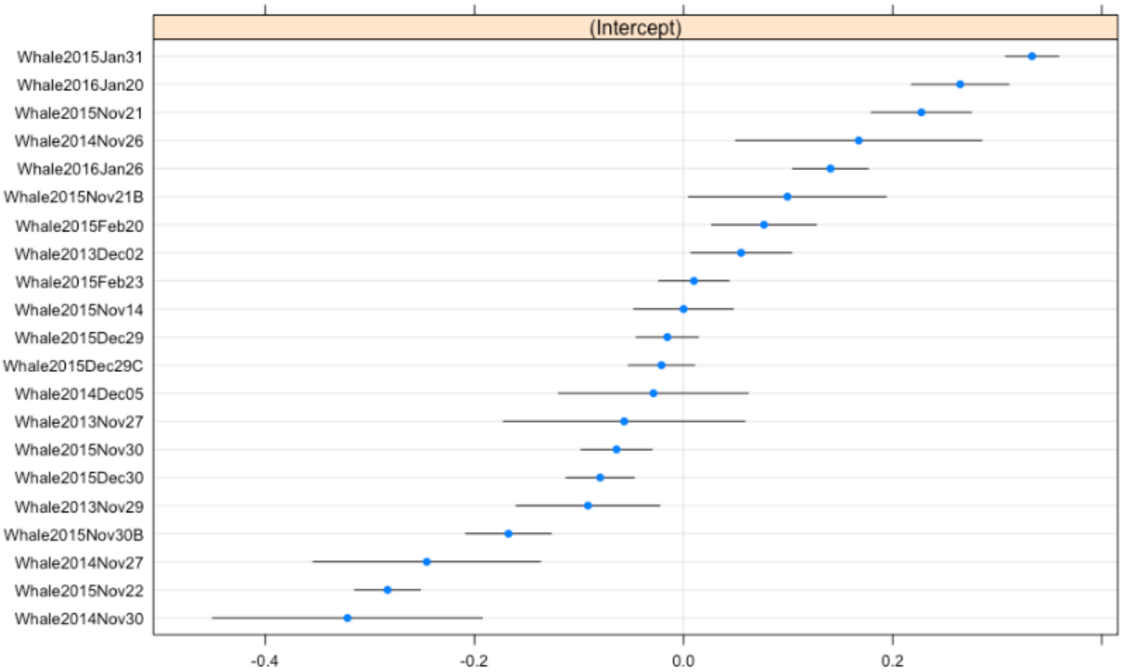

Figure S1 Show how the individual whales intercept differ (blue dots) from the estimated grand mean for respiration rate (0 on x-axis) for model A. *The variance of the individual whales intercepts represents the between-whale variance. The horizontal bars represent the 95 % confidence intervals for each of the 21 whales where its variance is the within-whale variance.*

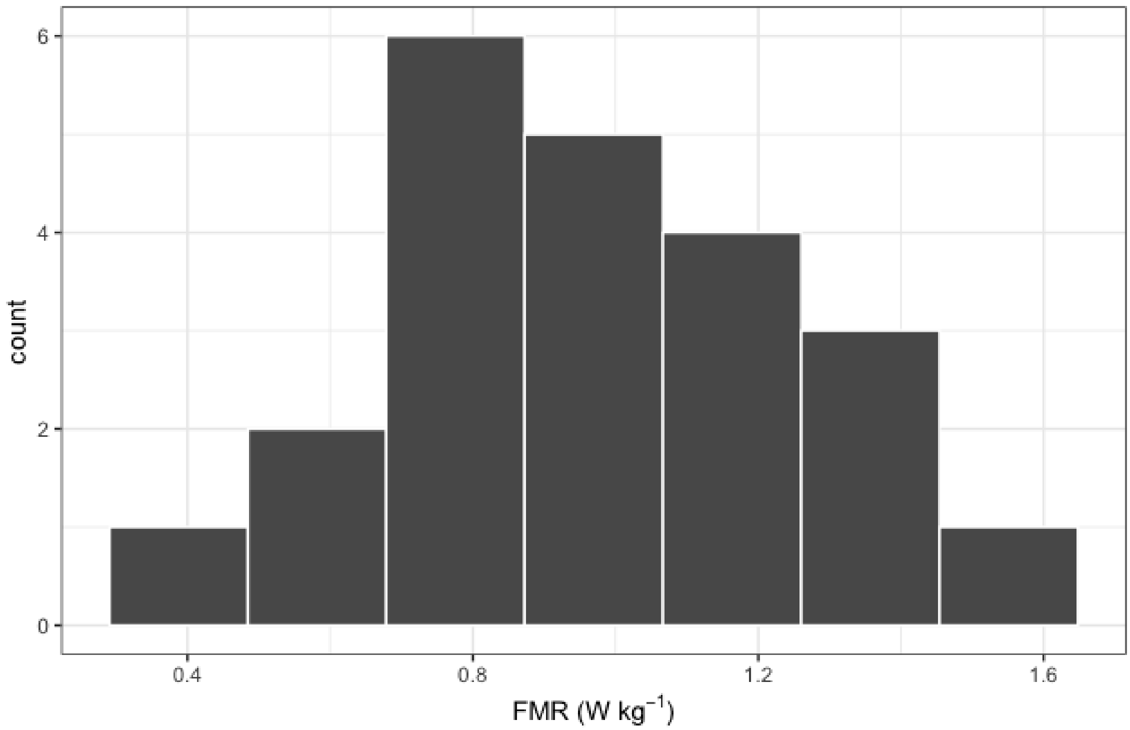

Figure S2 Distribution of FMR (W kg^{-1}) from 21 whales. *Mean ± sd: 0.98 ± 0.29 W kg^{-1}.*