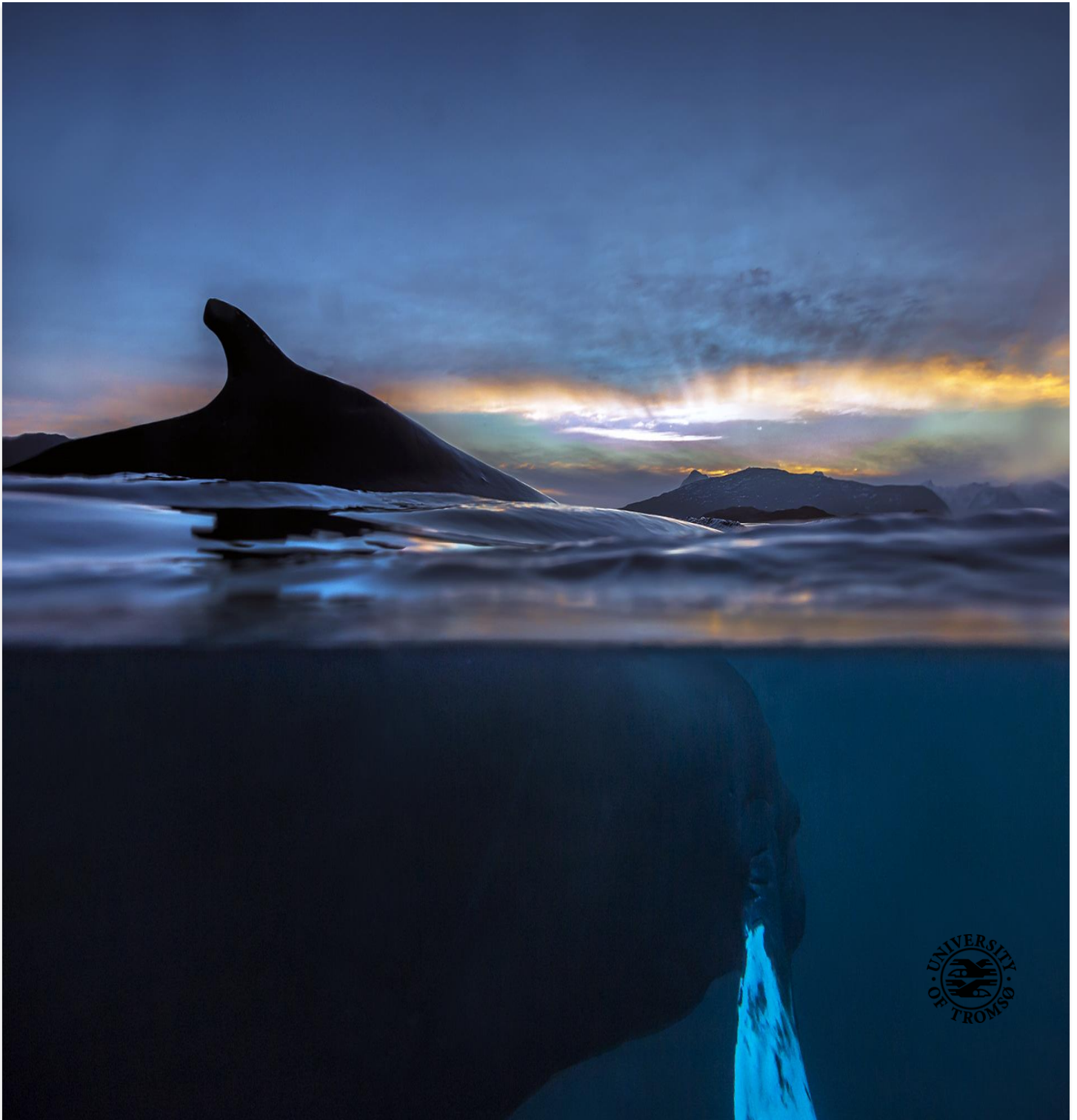Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Diving behaviour of humpback whales feeding on overwintering herring in North-Norwegian fjords
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Kevin Ochoa Zubiri

ACKNOWLEDGEMENTS

ABSTRACT

Since 2011, large numbers of humpback whales have aggregated to feed on Norwegian spring-spawning herring overwintering from late October to February within the fjords of the Troms county in Northern Norway. Whale aggregations are new in this region and little information on the whales' behaviour is available. How whales dive and forage and how they adjust to the extreme light regime at this latitude is largely unknown. To study this, high-resolution time-depth recorders were attached by suction cups during three winter seasons (2013-2016). A total of 42 tag deployments collected more than 450 hours of diving behaviour and almost 8500 dives. The whales spent a median of ~21% of the time at the surface and over 70% of dives were shallower than 50 m and shorter than 3 min. The deepest dive was recorded at 266 m and the longest dive lasted 21 min. Large behavioral differences were found among individuals. A foraging index was defined as the standardized residuals of a linear regression involving time spent at the bottom of a dive as a function of maximum depth and duration. No common diel pattern was found in the diving behaviour or in the presumed foraging activity of the whales but it was possible to group individuals into clusters. Approximately 2/3 of the whales were found to perform their deepest dives during the lightest hours of the day, while half of the whales seemed to intensify their foraging activity during the darkest hours of the day. These results are in accordance with herring diel vertical migration described in previous overwintering grounds, where fish was located at depth during the day and closer to the surface during the night. This study contributes to a better understanding of this predator-prey relationship and could help assessing the whales' impact on the herring stock within the fjords. Thus, these findings may play a part in the ecosystem based management of the herring fishery quota for Northern-Norway.

KEY WORDS: *Megaptera novaeangliae*, humpback whale, North Atlantic, Norway, diving behaviour, diel, herring.

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INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are known for their extensive migrations between feeding areas and breeding grounds in the different oceans around the globe (Winn & Reichley, 1985). Most populations feed in cold waters at high latitudes during the summer and migrate to warmer waters during winter, where they breed and calve, but do not feed (Winn & Reichley, 1985). However, some individuals have been found to overwinter on feeding grounds at high latitudes (Reilly *et al.*, 2008), which suggested that not all humpback whales migrate every year (Clapham, 2009).

In the North Atlantic Ocean**,** individual humpback whales show strong site-fidelity to their summer feeding grounds, which range from the Gulf of Maine to north up to the Arctic (Clapham, 2009). Some of these feeding grounds, such as the Gulf of Maine, are broadly studied (Baker *et al.*, 1994; Palsboll *et al.*, 1997). However, humpback whales feeding in northeastern Atlantic waters are less studied, and knowledge on their movements is limited.(Stevick *et al.*, 2003; Wenzel *et al.*, 2009).

Productive waters at high latitudes are known to attract large numbers of top predators such as humpback whales. Around 1450 individuals are found in the Barents Sea (Jakobsen & Ožigin, 2011) feeding mainly on capelin *(Mallotus villosus)* during late summer and autumn (Jakobsen & Ožigin, 2011). Every winter since 2011 large numbers of humpback whales have reiteratively visited the fjords around Tromsø to feed on Norwegian spring spawning herring (*Clupea harengus*) (hereafter referred as NSS herring) (Bakketeig *et al.*, 2016).

The NSS herring tends to form dense aggregations in defined areas during the winter (Huse & Korneliussen, 2000; Huse *et al.*, 2010), but the location of their overwintering grounds has changed over the last half century (Huse *et al.*, 2010). Since the winter of 2011-2012, a part of the total herring stock has been steadily overwintering in the North-Norwegian fjords of Troms (Bakketeig *et al.*, 2016). Large aggregations of top predators from whales to seabirds and fish follow this concentrated and lipid-rich resource (Lawson *et al.*, 1998). Herring is also a valuable resource for fisheries, so humans and all these predators may interact as they are all targeting the same prey (A. Rikardsen, pers. comm.).

During the winter feeding aggregation in North-Norwegian fjords, the humpback whales have been observed to use different feeding strategies, both surface oriented and underwater (A. Rikardsen, pers. comm. and personal observation). According to the optimal foraging theory, breath-hold divers should perform longer-lasting foraging dives when they feed on deeper distributed prey to "compensate longer transit times and optimize resource acquisition" (Mori,

1998; Doniol-Valcroze *et al.*, 2011). This is because deeper dives imply a higher oxygen consumption and a subsequent longer recuperation at the surface (Kramer, 1988). Thus, to make deeper foraging dives energetically efficient, prey density at depth must outweigh the costs of deep diving. For this reason, diving predators continuously adjust their foraging behaviour depending on prey distribution to maximize their energetic gain.

NSS herring has been observed to carry out diel vertical migrations in its previous overwintering grounds in Vestfjord, Norway (Røttingen *et al.*, 1994; Huse & Korneliussen, 2000). Therefore, it could be expected that humpback whales modify their diving behaviour and foraging activity according to the herring diel vertical movements. Studies on humpback whales feeding on other diel vertical migratory preys have shown extreme diel changes in feeding behaviour (Friedlaender *et al.*, 2009; Friedlaender *et al.*, 2013)

The main objective of this study was to provide the first description of the diving behaviour of North-East Atlantic humpback whales during the seasonal feeding aggregation in North-Norwegian fjords. The second aim was to assess whether the diving behaviour and presumed foraging activity of these humpback whales varied on a diel basis.

MATERIAL AND METHODS

Study area

The study was conducted in Kaldfjord (69° 45′ 14.4″ N, 18° 40′ 42.1″ E) and Vengsøyfjord (69° 48′ 56.5″ N, 18° 39′ 8.2″ E) in Troms County in Northern-Norway. These two fjords are connected and are characterized by a relative steep slope close to the shoreline with some shallow areas close to the openings of Vengsøyfjord and at the inner part of Kaldfjord. Main depths commonly range from about 50 to >200 m depths, with a maximum depth of 279 m in Vengsøyfjord. The length of Kaldfjord is about 16 km and Vengsøyfjord 13 km (Figure 1).

. This area was optimal to carry out the study because of the large aggregation of animals that otherwise spend most of their time spread in the open ocean.
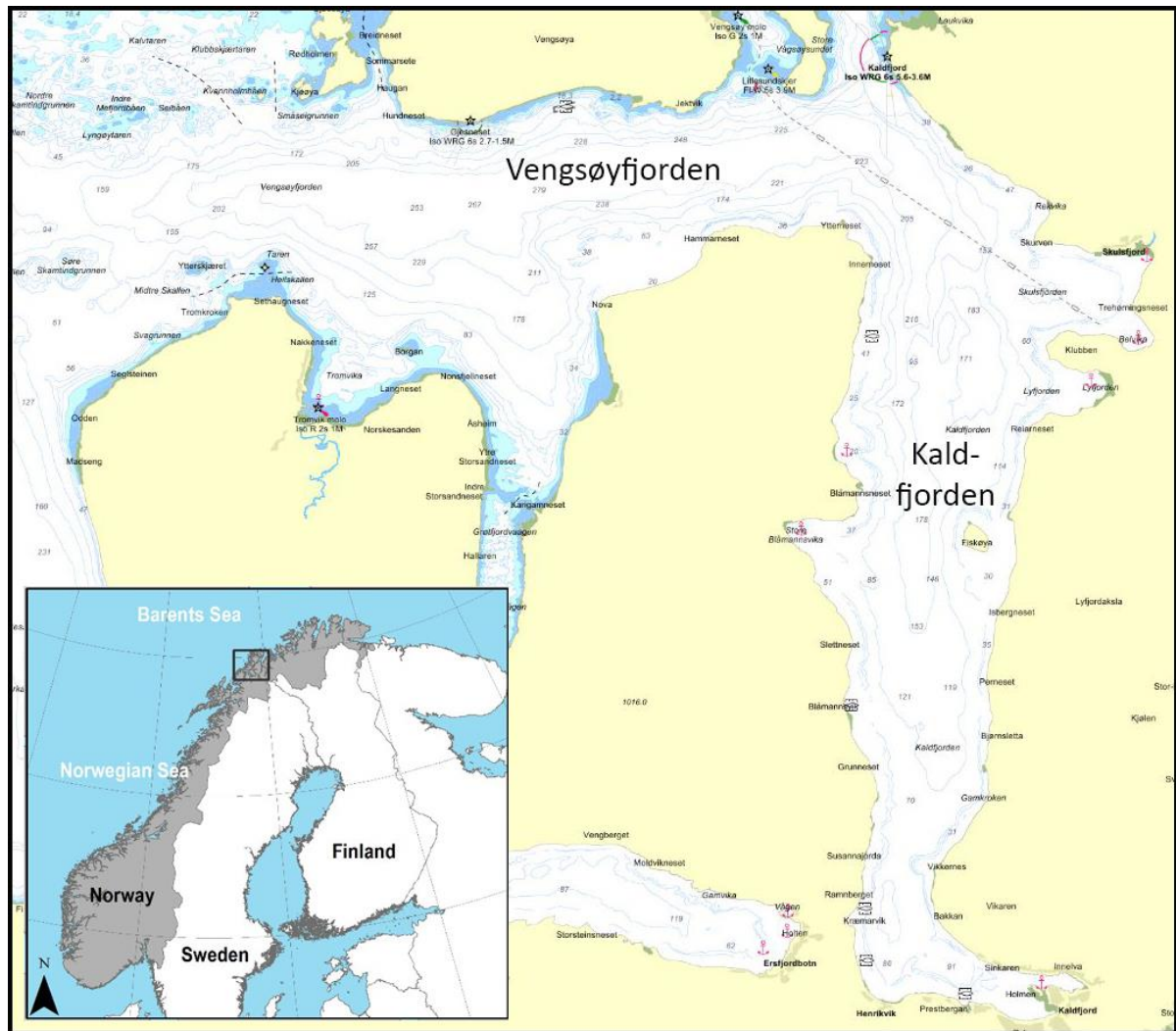
Figure 1. Map of the study area. The inset shows the study area at a larger scale. © Audun Rikardsen & Marie-Anne Blanchet. Bathymetric map retrieved from https://kart.gulesider.no/s%C3%B8k/sj%C3%B8kart

Tag description

Time-depth recorder archival tags (TDR10-F-297C, Wildlife Computers. Redmond, Washington, US) were deployed on humpback whales. The tags were attached to the whales with suction cups (Figure 2) and set to record and archive depth every second (±0.5 m resolution), temperature every 10 seconds and Fastloc® GPS position each time the whale surfaced. These tags did not have any data transmission system and had to be retrieved. Hence, each tag was equipped with a VHF transmitter (model MM110 or MM120, Advanced Telemetry Systems. Isanti, Minnesota, US) with an antenna that sent a constant signal on a specific frequency (148-149 Hz). The tag and the transmitter were placed inside a floating plastic case, which had four suction cups as non-invasive attachment mechanism. The entire package attached to the whales weighed less than 200g in air.
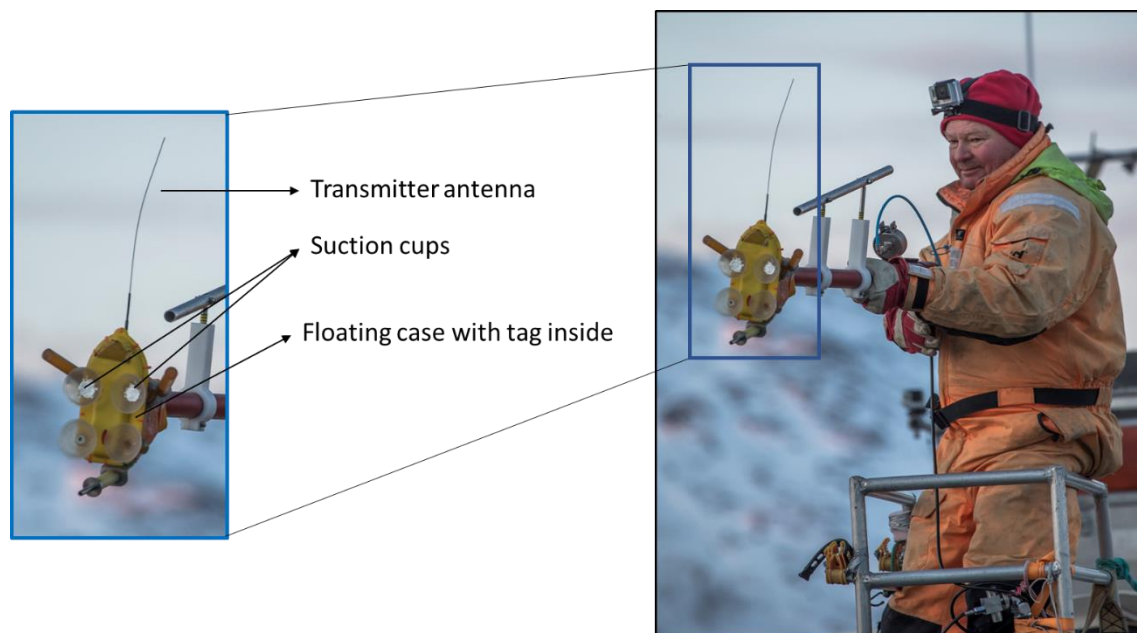
Figure 2. Photo showing the tag package used for this study and the tagger (Lars Kleivane) about to tag a humpback whale. © Audun Rikardsen.

Tagging procedure and tag retrieval

An 8 m steel cabin cruiser boat was used. Approaches to the whales were made from the side and behind the animal to minimize avoidance reaction. When closer than 20 m away from a whale, an airgun (ARTS Whale tagger. Restech-Norway AS, Bodø, Norway) loaded at 7-11

Bars of pressure adjusted for the distance to the whale was used to shoot the case containing the tag targeting the area under the dorsal fin (Figure 3).

Figure 3. Time-depth recorder attached to a humpback whale under the dorsal fin. ©Audun Rikardsen

After a variable attachment period, the suction cups on the tag-case lost the grip due to the whale's activity. They detached from the whale and the tag-case package floated at the surface with the antenna of the transmitter sticking out of the water. Keeping the antenna out of the water was essential because radio waves vanish in seawater, so this allowed us to track and retrieve the tags.

The boat was equipped with four 3-element Yagi antennas (148-151 MHz) (Figure 4), connected to a digital radio direction finder unit DDF2011 (ASJ Electronic Design, Norway) and to a VHF receiver R-1000 (Communications specialists, Inc., US & Canada). The fixed directional antennas received the VHF signal sent by the transmitter adhered to the tag. Then, the DDF2011 processed the intensity of the signal received by each antenna and indicated in which direction the tag was located.

Once found and retrieved, some tags were deployed again in another whale if the previous was a short attachment period.
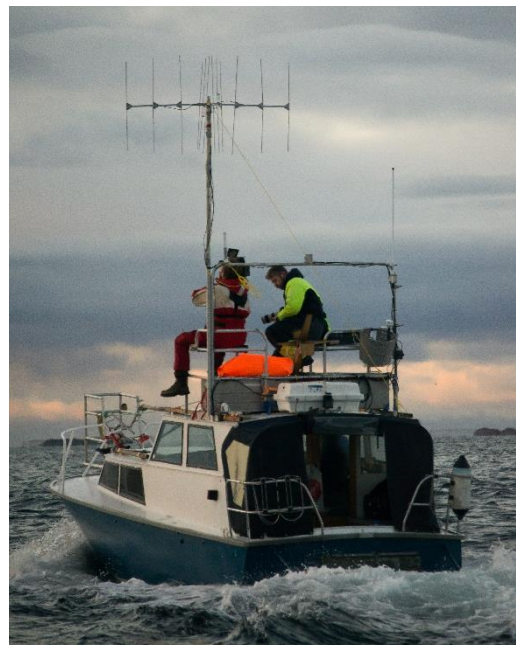

Figure 4. Boat used for tagging and tracking with the Yagi-antennas on the top. ©Kevin Ochoa

Project and procedures were accepted by the Norwegian Food and Safety Authority (permit FOTS 8165).

Data collected

A total of 42 whales were tagged during three winter seasons (November-February from 2013 to 2016). Attachment duration ranged from four min to 62 h and 28 min averaging 10 h and 6 min (Table 1). Approximately 459 h of time-depth data were recorded. From the 42 whales tagged, the time-depth data from 38 whales were kept for further analyses (Table 2). Four records were removed because of their short attachment duration (<15 min). The remaining 38 dive records yielded 8497 dives which were further analysed. (

Table 2). The average number of dives recorded per individual was 224 ($\pm$ 272), but it ranged from 4 to 1106 dives (Appendix 4).

Table 1. Overview of the data collected split by winter season. Number of deployments (n), range of attachment duration (min – max) of the deployments and mean duration in hours ± standard deviation.

WINTER SEASON	ATTACHMENTS			
	n	Range duration min-max (h)	Mean duration (h)	±SD (h)
S1 (2013-2014)	9	0,07 – 12,45	3,97	4,62
S2 (2014-2015)	15	0,18 – 43,25	8,76	13,09
S3 (2015-2016)	18	0,42 – 62,8	16,23	16,74
TOTAL	42	0,07 – 62,8	10,10	13,35

Table 2. Number of dives recorded by month and by season for the 38 whales analysed. The number of individuals in brackets and same individuals providing data two months are marked with *. NAs indicate the months when data was not collected.

Winter Season	Nov.	Dec.	Jan.	Feb.	Total
S1 (2013-14)	210 *(2)*	338 *(5)*	*NA*	*NA*	**548**
S2 (2014-15)	168 *(5)*	196 *(3)*	520 *(1)*	2161 *(3)*	**3045**
S3 (2015-16)	1342 *(9)*	2591 *(8*)*	971 *(4*)*	*NA*	**4904**
Total	**1720**	**3125**	**1491**	**2161**	*8497*

Data analyses

Neither GPS positions nor temperature measurements recorded by the tags were used because they were not relevant for the objectives of this study. All numerical and statistical analysis were performed using R Software version 3.3.2 (R Core Team, 2016). Diving data visualization was done with the program Mk10 (Wildlife Computers Inc.) and in R.

Pre-processing of raw diving data

Raw data were downloaded from the tags using Mk 10 software (Wildlife Computers Inc.). The records were then truncated with a customized function to remove the parts of the dive records when the tag was not attached onto the whale. Finally, each dive record was individually calibrated to correct for drift in the pressure transducer using "diveMove" package (Luque, 2007). The calibration method applied was "Zero-offset correction = filter" following the recommendations of Luque and Fried (2011).

Dive detection and calculation of dive metrics

A dive was defined as every time the whale was submerged deeper than 5 meters. This depth threshold was considered the most appropriate due to variable tag position on the body, whale's size and tag resolution. Then, dive detection and calculation of dive metrics was performed using customized functions. The dive metrics described hereunder were calculated for all the dives and used to describe the whales' diving behaviour.

Median depth was defined as the median value of the depths traversed by the whale in a dive. Maximum depth, the deepest point the whale reached during the dive. Dive duration was the time spent by the whale from its departure from the surface to its return to the surface (Figure 5). Post-dive duration was the time spent within the 5 first meters of the water column after each dive. Percentage of surface time (PCST) (Dolphin, 1987) (Equation 1) was used as an indicative of how the whale allocated its time between the surface and diving.

Equation 1

$$PCST = \frac{Post\text{-}dive\ dur}{Dive\ dur\ +\ Post\text{-}dive\ dur} \cdot 100$$

The bottom phase of a dive was defined by using the broken stick method (Fedak *et al.*, 2002; Heerah *et al.*, 2014; Photopoulou *et al.*, 2015). The first inflection point where the whale showed a significant change in behaviour represented the end of the descent, whereas the last inflection point indicated the beginning of the ascent. The part of the dive between both

inflection points was considered the bottom phase. Bottom phase duration was calculated as time spent at the bottom phase of the dive (Figure 5). Then, that bottom phase duration was standardized by the total duration of a dive and this new variable was called standardized bottom phase duration (Equation 2). This last variable reflected the proportion of time allocated by the whale to the bottom phase of a dive.

Equation 2

$$Standardized\ bott.ph.duration = \frac{Bottom\ phase\ duration}{Dive\ duration}$$

The ascent and descent phases were defined as the periods between the surface and the inflection points calculated for the bottom phase (Figure 5).
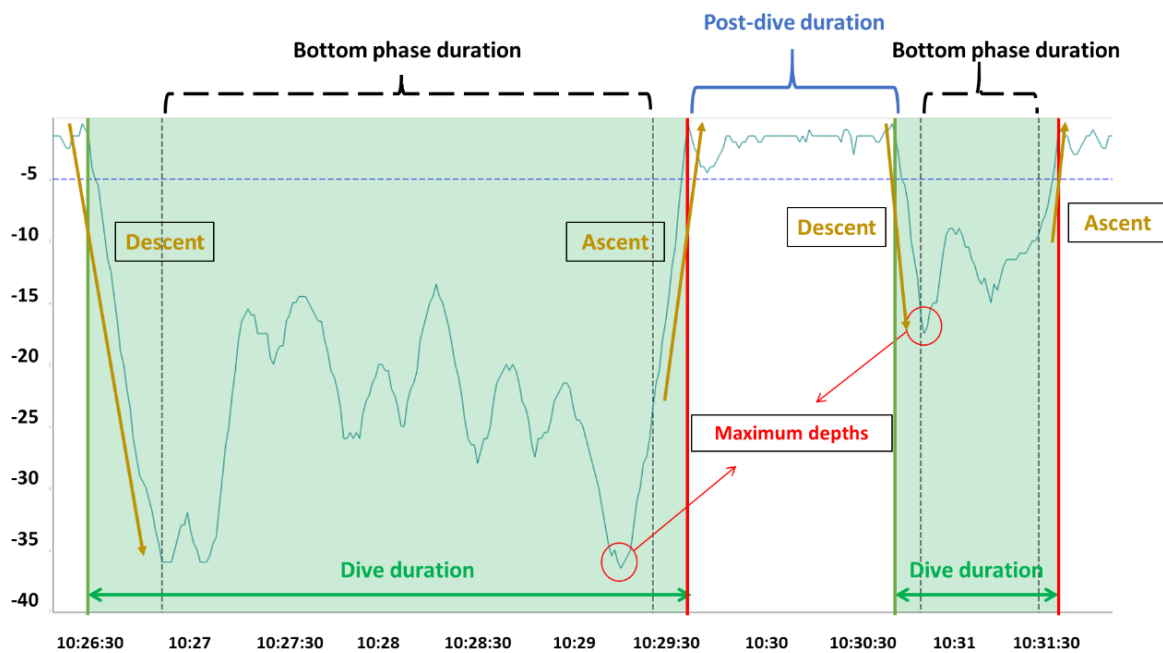
Figure 5. Example of two dives and graphic description of dive metrics from a TDR record of a humpback whale. Depth in meters (y axis) against time (x axis). Vertical lines: green solid indicates start of the dive, red solid indicates end of the dive, black dashed line indicates end of the descent and beginning of the ascent. Dashed blue horizontal line indicates the 5 meters depth threshold applied to dive detection.

Sun elevation was calculated at the beginning of each dive. The sun rose above the horizon during early November, late January and February at this latitude during the period of data collection. The rest of study period was polar night, so the sun remained below the horizon. Consequently, the average sun elevation during this study was –19 (±15°) ranging from -43° to + 10.8°.

Diel periods were defined according to the sun angle with respect to the horizon. Night was defined as a solar elevation below −12° (McCafferty et al. 1998; nautical twilight, US Naval Oceanography Portal 2011); twilight was the period with sun elevation between –12º and 0º; and day was defined as a solar elevation >0°. The value 0 of sun elevation corresponded to sunrise and sunset, indistinctively, and twilight comprised both dawn and dusk in the analyses of diel patterns.

Foraging Index

Three different methods to assess foraging activity were tested:

First, a wiggliness index was calculated as the vertical distance that the whale travelled within a dive standardized by the maximum depth of that dive (Equation 3). This represented the sinuosity of the whale in that dive and it was considered as a proxy for foraging activity in the water column.

Equation 3

$$Wiggliness\ index = \frac{\sum |\Delta Depths|}{maxDepth}$$

However, this index was eventually discarded from the analyses because it was found to be biased. Shallow dives got the highest values of this Wiggliness index (Appendix 1) due to tag resolution (±0.5m) (Appendix 2).

Two other foraging indexes were tested to estimate the foraging activity of each whale per dive:

    Foraging Index 1. The first axis of a Principal Component Analysis (PCA) that combined the "ascent rate" of a dive and the "descent rate" of the next dive and explained 76% of the variance (Vacquie-Garcia *et al.*, 2012).

    Foraging Index 2. The standardized residuals of a multiple regression of "bottom time" ~ "maximum depth" + "duration" for each dive. (Bailleul *et al.*, 2008; Dragon *et al.*, 2012; Blanchet *et al.*, 2015). Dives with positive values of this index were considered as "foraging" dives, whereas negative values indicated presumed "non-foraging" dives (Blanchet *et al.*, 2015).

Each foraging index provided a different result in the preliminary analyses (Appendix 3). Therefore, a selection of the foraging index which best represented the behaviour of the whales was done according to the optimal foraging theory. The trend that each index showed was visual compared with the time-depth data whale by whale and it was assumed that

increasingly deeper consecutive dives had foraging purposes. The presumed foraging behaviour of the whales was better reflected by *foraging index 2*. Thus, *foraging index 2* was chosen to analyse the diel patterns in the foraging behaviour of the whales.

Diel pattern analysis

From all tagged individuals, 19 had a sufficient spread in sun elevation data ($> 25°$) to be analysed for diel patterns. Four of those 19, provided data for sun elevation values higher than $0°$ from which two had data for sun elevation higher than $5°$. Furthermore, a total of 121 dives had to be removed from different whales because the calculated values of some dive metrics prevented the calculation of the foraging index.

A 95% quantile regression was computed for each of the remaining 19 individuals on each dive metric against sun elevation. Then, a smoothing B-spline line was plot over them for visual analyses of potential diel patterns in diving behaviour using the package "cobs" (Ng & Maechler, 2007). A special focus on the maximum depth and duration of the dives was taken to observe how the whales allocated their deepest and longest dives with respect to sun elevation (Bennett *et al.*, 2001).

To assess diel changes in the presumed foraging activity of the whales, *foraging index 2* was used as weighing factor in a similar 95th quantile regression". This quantile regression was computed again on each dive metric for each individual because the observed diel pattern in the deepest and longest dives was not necessarily an indicative of diel changes in foraging activity. Deep and long-lasting dives may also serve other purposes such as exploration.

RESULTS

Diving behaviour

The maximum and median depths of all dives showed bimodal distributions with two peaks at 5m and 30 m and at 3 and 20 m, respectively (Figure 6). Over 70% of the dives performed by the whales were shallower than 50 m, a median depth of less than 30 m, and lasted for less than 3 min. The average duration of the dives was 2.3 (±2.5) min. The longest dive lasted for 21.05 min and the deepest dive was recorded at 265.5 m. The bottom phases of the dives accounted for an average of 62% (±14%) of the total dive duration and the ascent and descent rates averaged approximately 1 ms^{-1} (Figure 6). In 5550 dives (65%) the bottom phases accounted for over half of the total dive duration and the descent and ascent rates were lower than 2 ms^{-1}. Most post-dive durations (73%) lasted for less than 1 min (Figure 6) and the median percentage of time spent at the surface by humpback whales in the study area was ~21%. This value varied among dives and among individuals (Figure 7). The other 73.5% of the time the whales remained deeper than 5 m. A summary table of the diving behaviour of each whale is presented in (Appendix 4).
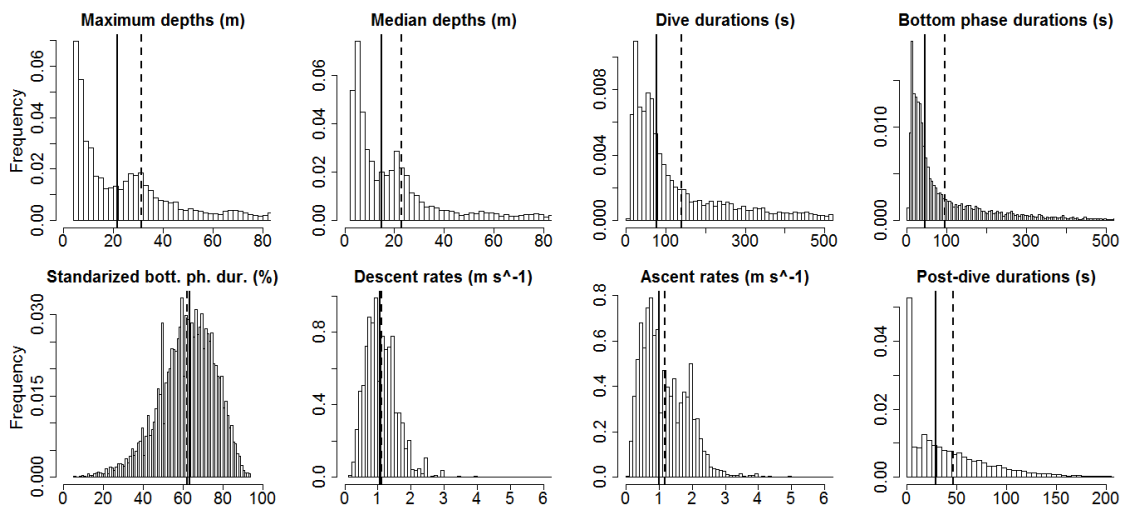

Figure 6. Histograms of frequencies from all dives and for each variable. Values on the x axis correspond to values for each dive metric and units are presented in the headings. Black solid line represents the median and black dashed line represents the mean.
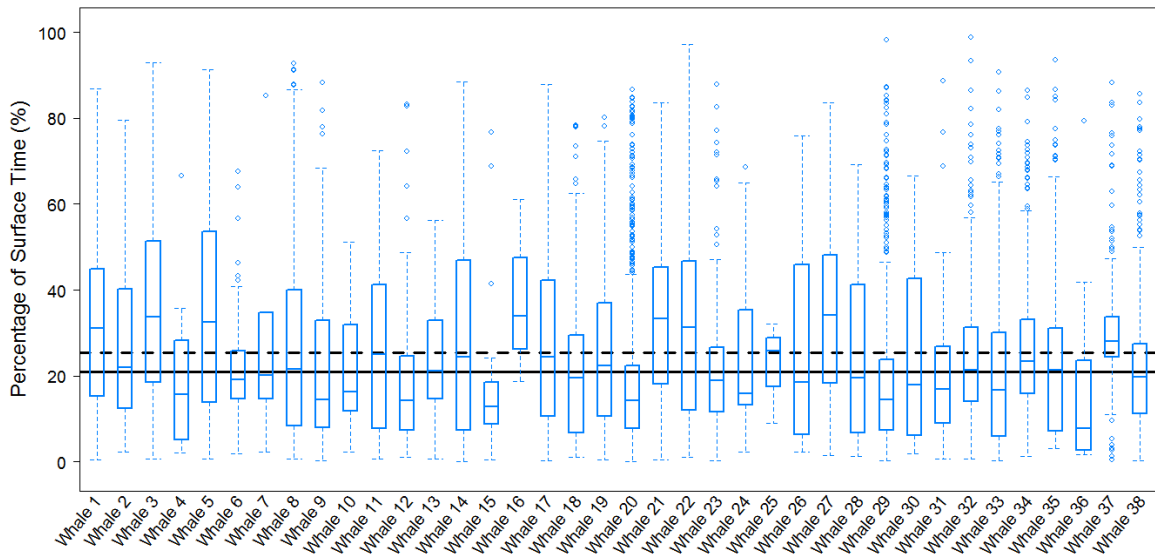
Figure 7. Median values (blue lines), 25 and 75% quantiles (box) and SE (whiskers) in percentage of surface time of all dives per whale. Black solid line represents the median and black dashed line represents the mean.

Influence of the month and the winter season was explored on the maximum depth, duration and percentage of surface time of the dives (Figure 8). No large changes were found between months or seasons in any of the dive metrics. However, the maximum depth and the duration of the dives was slightly shorter during season two (S2) than in the other two seasons. A subtle decrease could also be observed in the dive duration from November to February. The percentage of time at the surface showed a stable median value of ~20% (Figure 8).
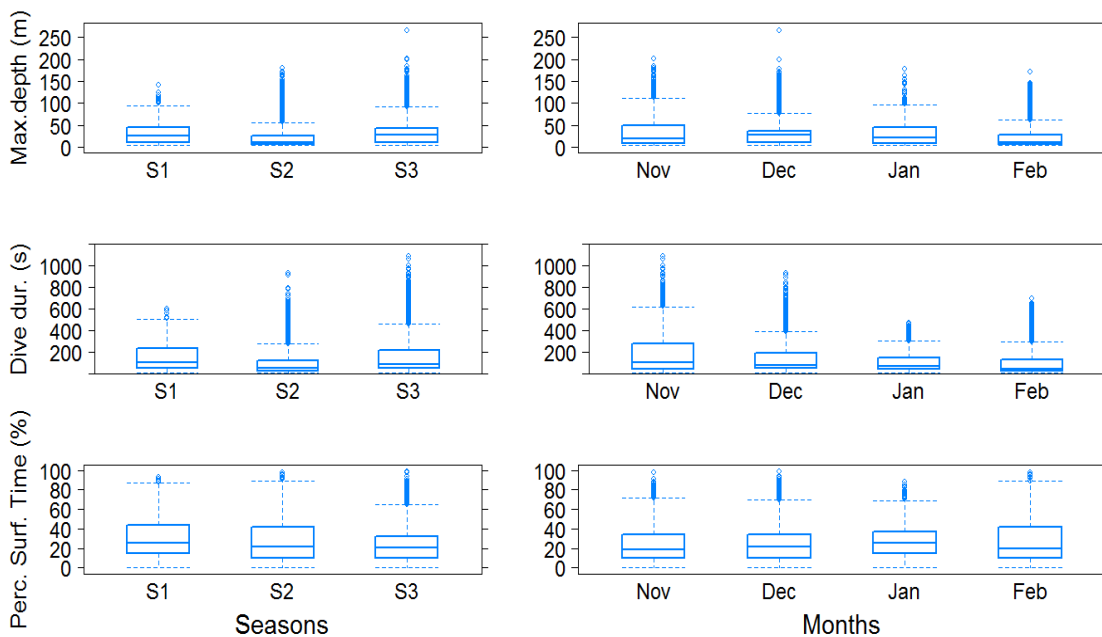

Figure 8. Median values (lines), 25 and 75% quantiles (box) and SE (whiskers). Maximum depths, dive durations and percentage of time at the surface of the dives performed by all humpback whales split by season (S1, S2, S3) and by month.

Diel patterns

Diel patterns in general diving behaviour

Visual inspection of the time-depth data of some individuals showed a clear distinct diving behaviour between day and night (Figure 9). Each whale was individually studied to assess how many whales performed a diel pattern in the maximum depth and duration of their dives.
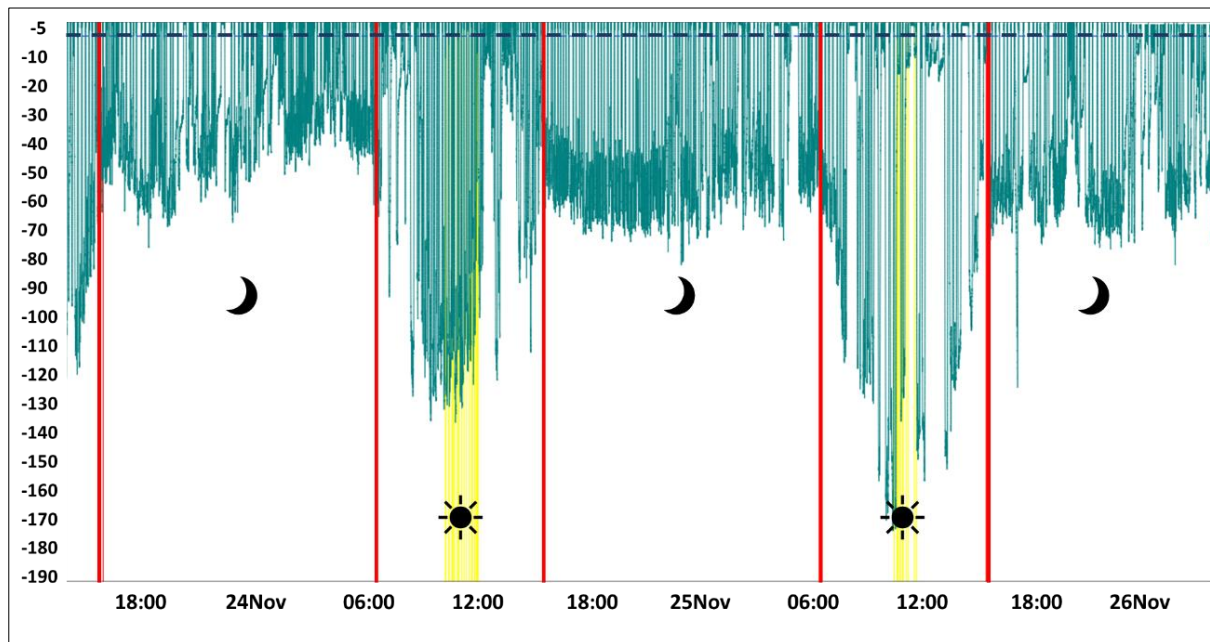
Figure 9.Dive profile of whale #29 as example of diel pattern observed in the diving behaviour of some humpback whales. Depth in the y axis and time in the x axis. Vertical red lines indicate the twilight limits (-12º) and yellow shaded area the day (>0º). Horizontal blue dashed line indicates the 5 m depth threshold used for dive detection.

From the 19 whales analysed, 13 (68%) performed their deepest dives towards twilight and sunrise /sunset. Nine of those whales dove more than 50 m deeper during twilight than during night. The other four also dove deeper towards twilight than at night, but the difference was smaller than 50m (Figure 10). In contrast, five whales performed their deepest dives during the night and one individual performed its deepest dives during the day. However, only four of the 19 whales provided data for sun elevation values higher than 0º, which made impossible to know the general behaviour of the whales during the day.
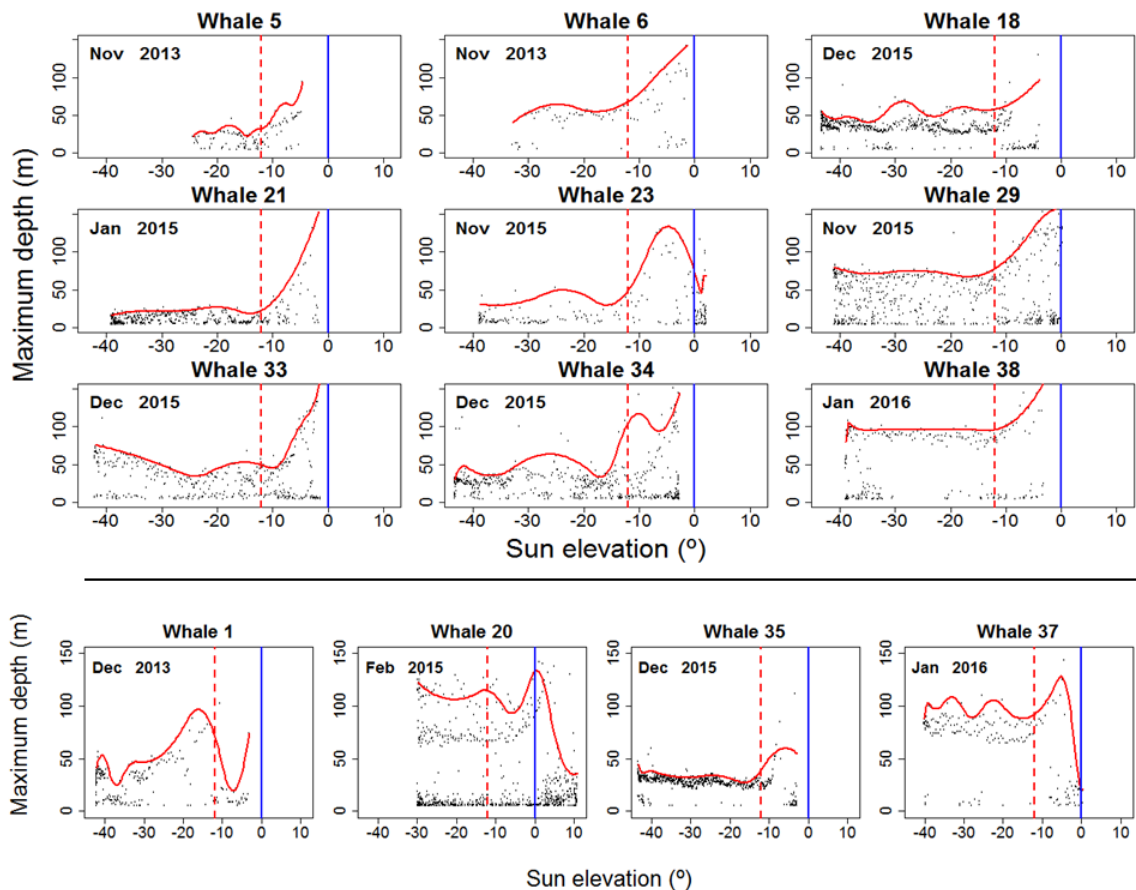
Figure 10. 95th quantile regression for 13 humpback whales on the maximum depth of their dives (y) against sun elevation (x). The top panel shows a diel increase in the maximum depth of their deepest dives of a difference greater than 50 meters and the bottom panel shows a similar increase but of less than 50 m difference. Vertical lines: Red dashed line indicates limit of twilight (-12º), blue solid line indicates sunrise / sunset (0º).

Most whales (79%) did not show a clear diel pattern in the performance of their longest dives. An increase in the dive duration with sun elevation was found in four individuals (21%) (Appendix 5). The other dive metrics were visually inspected but the no individual showed a clear diel pattern in all dive metrics. The median depths followed a similar pattern to the maximum depth of the dives. Post-dive durations seemed to increase during twilight.in 13 whales (68%). Eleven of those had shown the same pattern in the maximum depth of their dives. The bottom phase duration showed a similar pattern to the dive durations and the percentage of surface time followed the same pattern to dive duration in one individual. Descent rates and ascent rates did not show any consistent diel pattern. Examples of how the

95th quantile regression looked for each dive metric against sun elevation are presented in Figure 11 and they were calculated for the diving profile presented in Figure 9.
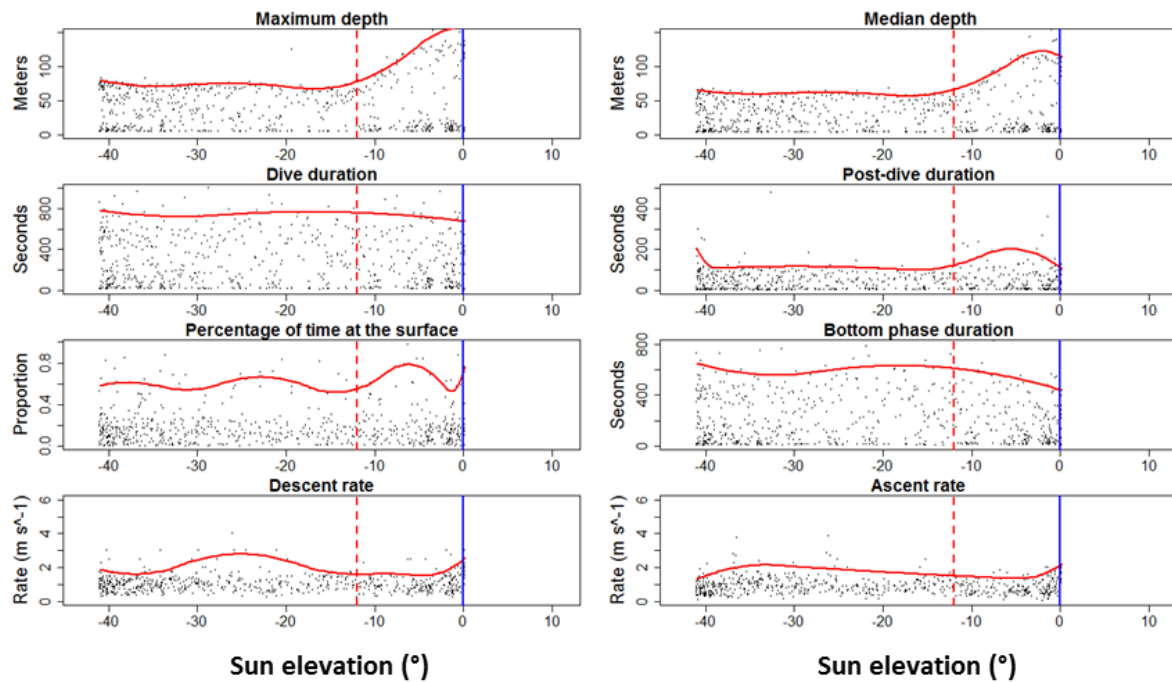
Figure 11. Example of 95th quantile regression for the different dive metrics against sun elevation calculated from humpback whale #29. Vertical lines: Red dashed line indicates limit of twilight (-12º), blue solid line indicates sunrise / sunset (0º).

Diel patterns in presumed foraging activity

From the 19 whales which contained enough data to be analysed for diel patterns, nine performed higher foraging activity at greater depths during the night, changing to surface foraging activity during twilight and day (Figure 12). Two of those individuals (Whales #17 and #29) seemed to forage at depth also right before sunrise or shortly after sunset. Five whales dove deeper as sun elevation increased (Appendix 6) and other five individuals did not show any diel pattern in their foraging behaviour. They seemed to forage constantly at depths shallower than 50 meters, regardless of the sun elevation, and two of those individuals performed a few foraging dives at depths slightly greater than 50 meters.
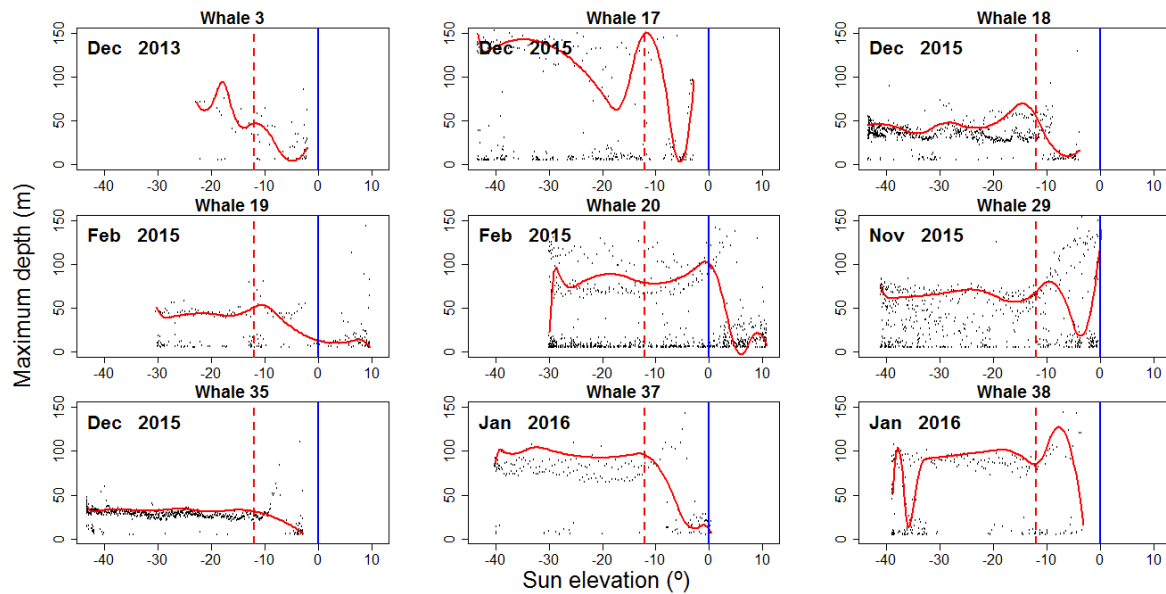
Figure 12. 95th quantile regression with foraging index 2 as weighing factor for 9 humpback whales on the maximum depth (y axis) of their dives against sun elevation (x axis). Vertical lines: Red dashed line indicates limit of twilight (-12º) and blue solid line indicates sunrise / sunset (0º).

Regarding the duration of foraging dives, nine of the 19 whales analysed (47%) did not show any diel pattern. Five whales (26%), performed their longest foraging dives during the night and shorter foraging dives towards sunrise or right after sunset. In contrast, four individuals (21%) performed the opposite pattern taking shorter dives during the night time and showing a slight increase in the duration of their foraging dives towards sunrise or right after sunset (Appendix 7).

The proportion of presumed foraging *vs* non-foraging dives was higher at night (63%) than during twilight (53%) and day (51%). No large differences were found between the maximum depth and duration of dives performed at night, twilight and day, regardless of the presumed foraging activity. Slightly deeper presumed foraging dives were found during the night (33 ± 27 m) and twilight (35 ± 40 m) than during day (22 ± 30 m). Non-foraging dives were slightly deeper during twilight (36 ± 38 m) than during night (28 ± 27 m) and day (20 ± 27 m). However, most dives (>75%) remained in the 50 first meters of the water column and were shorter than 3 min, regardless of the diel period or the presumed foraging activity (Figure 13).
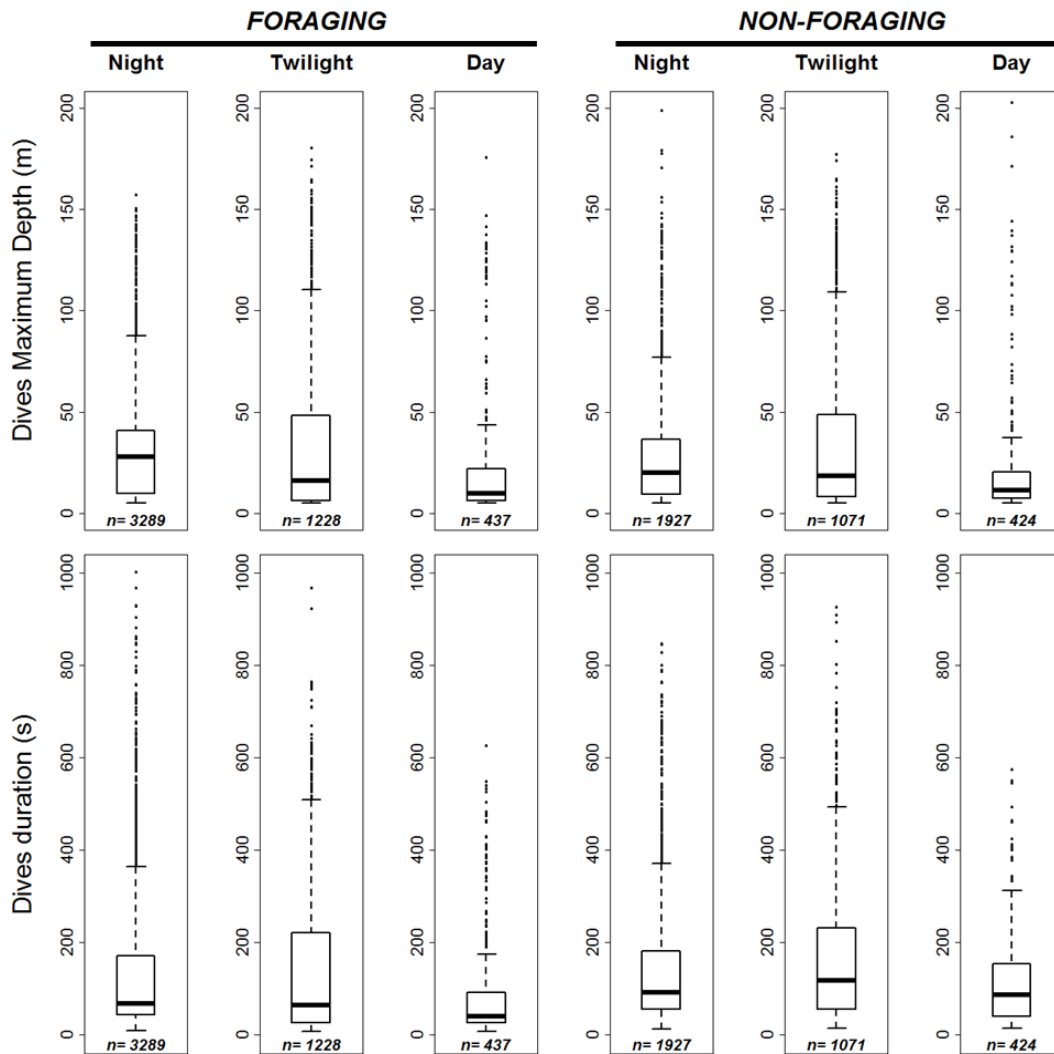
Figure 13. Maximum depth and duration of presumed foraging and non-foraging dives (based on foraging index 2) and split by night, twilight and day. Median values (black lines), 25 and 75% quantiles (box) and SE (whiskers). n=number of dives.

No differences were found in the percentage of surface time of the dives regardless of the presumed foraging activity or day / night period. The whales allocated a median of ~20% of their time at the surface than remained stable between the dive groups (Appendix 8).

DISCUSSION

The diving behaviour of these whales has been found to be dominated by short and shallow dives. More than 70% of the dives were concentrated within the first 50 meters of the water column with higher occurrence at 3 and 20 meters of depth. The dives with a median depth of 3 meters included shallow dives performed during respiration bouts between longer deeper dives. The other bulk of dives to a median depth of 20 meters probably indicated the most frequented foraging depth used by the whales throughout the winter feeding aggregation. The bathymetry of the fjords probably partly determined the diving behaviour of the whales. Several shallow areas are found at the inner part of Kaldfjord, close to the openings of Vengsøyfjord and around Vengsøya. The whales were often observed in those shallow areas displaying surface lunge feeding, which was probably more energetically efficient than deeper diving. The short duration of their dives is a typical characteristic of rorquals and it is thought to be caused by the high energetic costs of lunge feeding (Croll *et al.*, 2001; Acevedo-Gutierrez *et al.*, 2002). This particular feeding strategy has been found to limit foraging time and dive duration in other rorquals, leading to shorter dives than were expected from their large sizes (Acevedo-Gutierrez *et al.*, 2002).

The whales' diving behaviour was also characterised by high percentage of time at the bottom phase of their dives. This might be an indication of intense foraging activity. Diving predators are assumed to concentrate their foraging activity at the bottom phase of their dives and previous studies have associated similarly high proportion of time spent at the bottom with feeding activity in other marine mammals (Lesage *et al.*, 1999; Guinet *et al.*, 2014). The ascent and descent rates found in this study were similar to the values described for foraging dives of humpback whales in other feeding grounds (Goldbogen *et al.*, 2008), and the median percentage of surface time (~21%) was in accordance with other studies on other species of whales and on humpback whales in other foraging and breeding areas (Dolphin, 1987; Baird *et al.,* 2000; Baumgartner & Mate, 2003).

A high resemblance was found between diving behaviour displayed by the whales in this area (Appendix 9) and the whales in Frederick Sound, Alaska (Dolphin, 1987). This resemblance seemed to be independent of the prey targeted and of the season, since humpback whales in Frederick Sound feed heavily on euphausiids during July through September and humpback whales in the present study feed on herring from November to February. The only apparent similarity between both feeding grounds was the bathymetry of the area, characterized by

shallow areas in the inner part and on the sides of the sound. The shallows areas probably represent a dead end for the prey, keeping them concealed and more accessible for the whales. No large difference was found in the maximum depth, duration and percentage of surface time between months and winter seasons. However, maximum depth and dive duration were slightly lower in the second winter season (2014-2015) compared to the other two winter seasons, and a slight decrease in the duration of the dives was found from November to February. The lower values in season 2 were influenced by the high proportion of dives recorded that season during February (71%), when the maximum depth and duration of the dives were the lowest of all months. The subtle decrease in dive duration observed from November to February could be caused by changes in the environment between across months. The natural spatio-temporal fluctuation of the NSS herring biomass within the fjords might influence the behaviour of the whales (Appendix 10). However, the potential effect of sampling bias on these results cannot be discarded, since there was an unbalanced amount of data collected in different months and winter seasons.

Even though no common diel pattern was found among the whales, over 60% of the individuals performed their deepest dives towards twilight and sunrise /sunset. Nevertheless, half of the whales seemed to perform deeper foraging dives at night than during twilight and day and a higher proportion of foraging vs non-foraging dives was also found at night than at twilight and day. These results suggested that the whales foraged more intensely during the night, when the herring was likely to distribute closer to the surface. The whales which dove deeper during twilight probably attempted to continue feeding until the herring was too deep to be energetically profitable. During the day, when most of the herring was assumed to aggregate deeper in the fjords, the whales seemed to remain closer to the surface. This would be in accordance with the diel variation in feeding behaviour performed by humpback whales feeding on krill in Antarctica, where they seem to feed exclusively at night (Friedlaender *et al.*, 2013). A potential change of foraging strategy between night and day is also suggested. These whales may carry out underwater lunge feeding on dense herring shoals close to the surface during the night and change to opportunistic surface lunge feeding in shallower areas during the day. Similar bimodal feeding activity has been previously reported in other rorquals (Doniol-Valcroze *et al.*, 2011; Friedlaender *et al.*, 2013). However, the proportionally low amount of data collected during daylight compared with night and twilight periods could be biasing the results.

There was a high inter-individual variation in the diel diving patterns which was not influenced neither by the month nor by the winter season when the whales were tagged. Several factors may explain why some individuals performed diel changes in their diving behaviour whereas others did not. Inter-individual differences in body condition probably influenced the activity of the whales. Being herring their last abundant food source before they started long distance migrations, these whales probably tried to fill up their fat reserves during the winter seasons in Tromsø. Thus, whales with lower fat reserves may have needed to increase their foraging activity and had to dive deeper while the herring was in the fjords. On the other hand, whales which had been more successful foragers during the previous months, would have had better body condition and might not have needed to forage so actively. Another factor which probably determined the behavior of the whales was their sex and pregnancy status. These factors have been shown to affect the diving behaviour of other whales (Baumgartner & Mate, 2003). Pregnant female humpback whales probably had higher energetic requirements than males due to the costs of reproduction (Braithwaite *et al.*, 2015). Therefore, they might have dived deeper and more often to forage more frequently than the others.

However, the variable prey density and distribution was probably the most influencing factor which determined the diel patterns of the whales. A loosely spread herring shoal or the fish migrating too deep for the hunt to be energetically profitable could be reasons why some whales did not dive deeper during twilight. Furthermore, the presence of killer whales in the area where the humpback whales were feeding could have also influenced the diving behaviour of the latter. Regardless of the natural vertical migration of herring, the killer whales in the area tend to form small tight balls of herring that they push to the surface and display their typical carousel feeding (Similä, 1997). Several humpback whales were reported to often follow the killer whales and steal the herring that they had herded in Andsfjord, a fjord south from Tromsø (Jourdain & Vongraven, 2017). If killer whales did so in the area, there was no need for the humpbacks to involve in deep diving during the day.

Short tag attachments were another potential source of inter-individual variation in the observed diel diving patterns. Most individuals were tagged for less than 24 h, only 5 individuals were tagged longer than 24 h and only 1 was tagged for more than 48 h. With these short tag attachments, it is possible that individuals which might have performed diel behavioural patterns other days were tagged when they did not display them.

Despite all these potential explanations of the inter-individual variation in diving behaviour among the whales, it is likely that the performance of certain diel patterns varied both between and within individuals over time.

The presumed foraging activity of the whales, assessed by the bottom time residuals, could not be directly validated since there were no accelerometers in the tags data or cameras attached to the whales. The choice of using *foraging index 2* over the other indexes tested to estimate foraging activity was made by a visual comparison of the trend that each index showed with the time-depth data, whale by whale. Then, based on the optimal foraging theory, deeper and longer-lasting dives were considered to have foraging purposes. The presumed foraging behaviour of most whales was better reflected by *foraging index 2* than by the other foraging indexes, so that is why it was chosen. Previous studies have highlighted the limitations of inferring foraging activity from dive metrics (Viviant *et al.*, 2014; Carter *et al.*, 2016) and some have even pointed at the specific limitations of using the "bottom time" as a proxy of foraging activity (Viviant *et al.*, 2016). In view of these limitations I acknowledge the potential inaccuracy of estimating foraging activity solely from dive data.

Applicability and recommendations for future research

One of the findings of this study was that the whales spent a median of ~21% of the time at the surface. Although some inter-individual differences were found, this value seemed to remain stable between seasons or across months and it seemed to be independent of the day / night cycle and presumed foraging activity of the whales. Therefore, this value has a potential application as correction factor for abundance estimates of humpback whales in this and similar feeding aggregations by aerial surveys, either by airplane (Barlow *et al.*, 1988; Andriolo *et al.*, 2006) or with drones (Fiori *et al.*, 2017; Hodgson *et al.*, 2017). Once estimated the number of humpback whales that aggregate in the fjords and their consumption rate, it would be possible to calculate their herring biomass removal and assess their impact on the NSS herring stock. Adding accelerometers to the tags would improve the accuracy of the estimation of the whales' foraging activity and may allow to carry out bioenergetic studies. Concurrent spatial and temporal measurements of prey distribution and abundance in the area where the tagging is performed could be done using scientific echo-sounders (Witteveen *et al.*, 2008; Friedlaender *et al.*, 2009). Finally, the fluctuation of the whales' body condition throughout the feeding season could be assessed combining photogrammetry and

drones. This fluctuation may serve as indicator of foraging success of the whales within the fjords and throughout the months.

Since this is the first study carried out about this feeding aggregation of humpback whales, the results presented may serve as baseline for the assessment of potential anthropogenic impacts on the marine ecosystem in North-Norwegian fjords. In a context of constant anthropogenic disturbance (whale-watching industry, oil drilling, seismic blasting, shipping, etc.) and other interactions with humans (i.e. competition with fisheries, entanglement in fishing gear), future changes in the whales' diving behaviour may be used as indicators of anthropogenic impacts and lead to improved management. Moreover, since the NSS herring regularly change the location of their overwintering grounds, these results may also serve as a baseline for future comparative studies between the diving behaviour displayed by the same whales feeding offshore or in other fjords.

CONCLUSIONS

This study has shown that the humpback whales which feed on overwintering NSS herring during the polar night have large inter-individual variation in diving behaviour and diel patterns. Notwithstanding, there seemed to be a tendency amongst the whales to perform their deepest dives during twilight but to intensify their foraging activity at night. These results were in accordance with the herring diel vertical migration described in previous overwintering grounds. The bathymetry and the high density of herring (Gjelland, pers.comm) that aggregated within the fjords these last winter seasons, probably contributed to make Kaldfjord and Vengsøyfjord the perfect location for these humpback whales to top-up of their fat reserves prior to long distance migrations. The fisheries industry has also been intensively exploiting the NSS herring stock, which has made the pressure on this fish species twofold. There is a large paucity of knowledge regarding how many whales aggregate to feed within these fjords and how much herring they consume. Thus, there is a need for abundance and consumption estimates of these humpback whales to assess their potential impact on the NSS herring stock. That way, a better ecosystem based management of the NSS herring could be implemented in Northern-Norway and the quota for the fisheries industry could be adjusted in accordance to the whales' impact.

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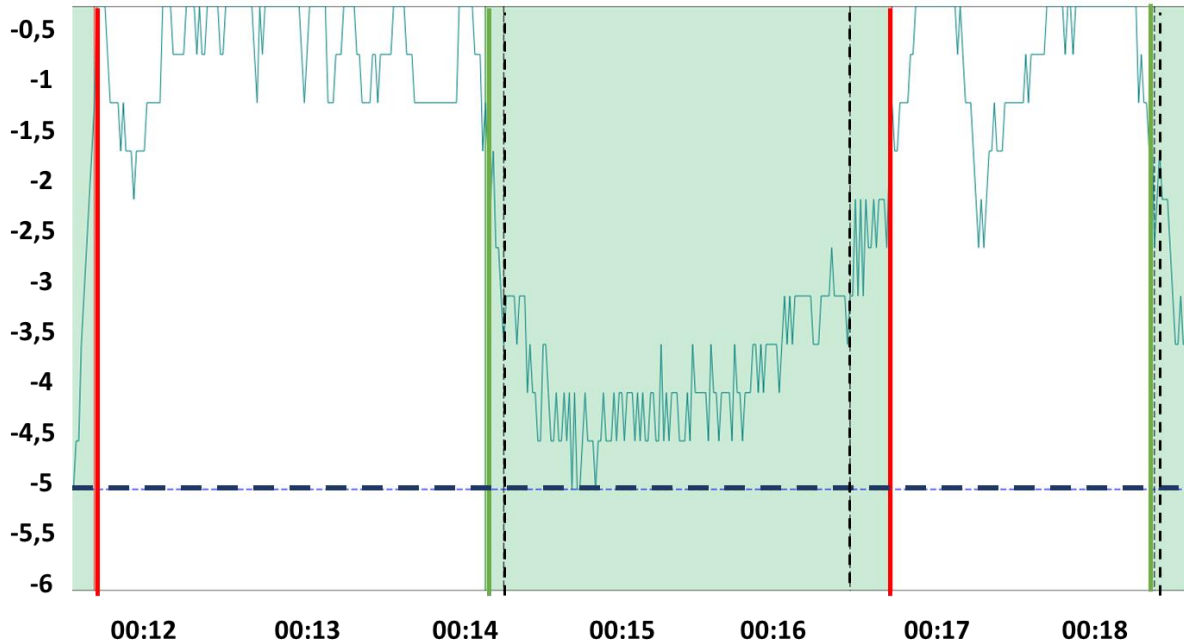
acoustic tags and concurrent fish surveys. *Marine Mammal Science, 24*(3), 516-534. doi:10.1111/j.1748-7692.2008.00193.x

APPENDIX

Material and Methods
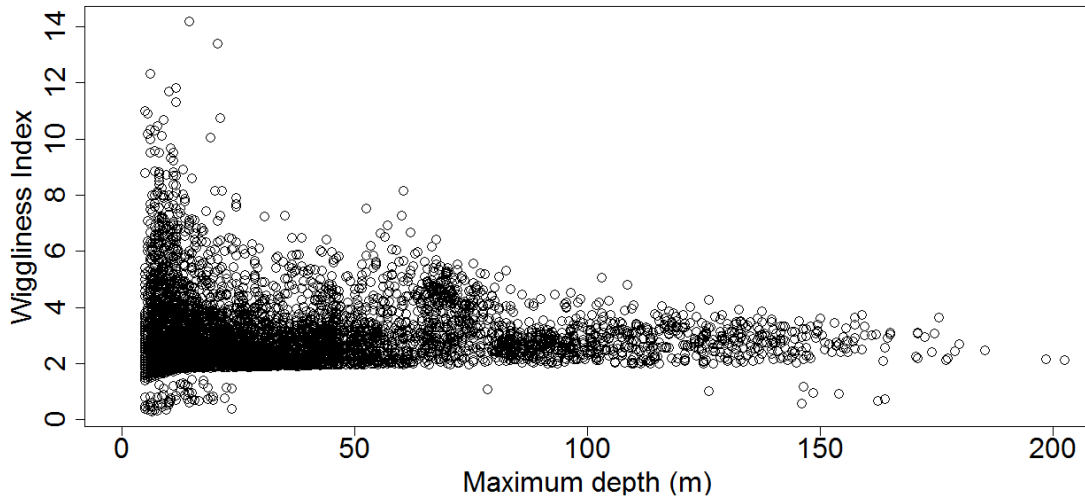
Appendix 1. Wiggliness index values (y) against maximum depth (x) of the dives showing (biased) higher values of wiggliness index for shallow dives.

Appendix 2. Example of a shallow dive performed by a humpback whale with high noise produced by the TDR tag resolution. Depth in the y axis in meters and time in the x axis. Blue dashed line indicates the 5 m depth threshold used for dive detection. Vertical lines: green indicate the beginning of a dive; red indicate the end of a dive and black indicate the end of the descent and beginning of ascent.
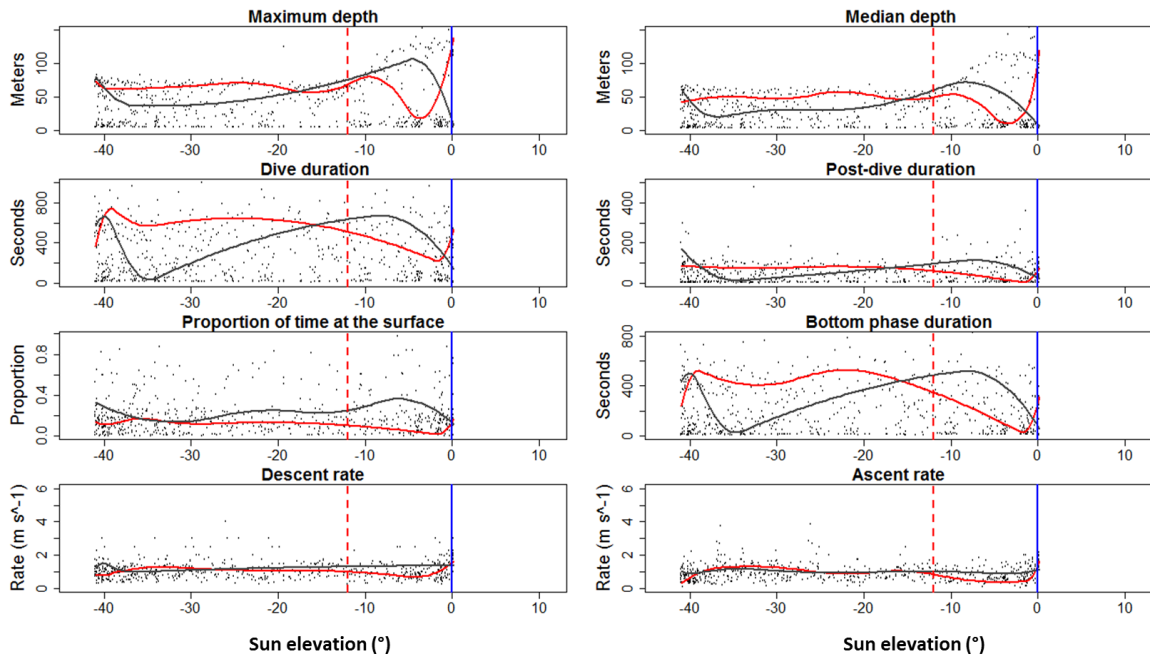
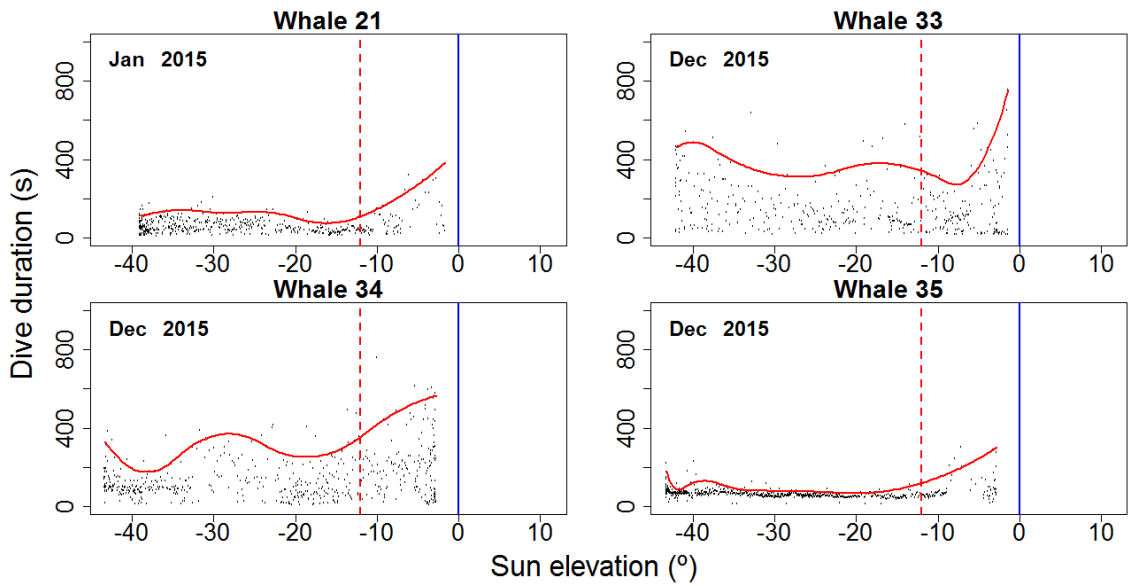*Appendix 3. Example of 95ᵗʰ quantile regressions with foraging indexe 1 (grey) and foraging index 2 (red) as weighing factor for the different dive metrics against sun elevation calculated from humpback whale #29. Vertical lines: Red dashed line indicates limit of twilight (-12°), blue solid line indicates sunrise / sunset (0°).*

Results

Appendix 4. Summary table of each whale tagged and dive metrics analysed. The headings of the table correspond to Whale number (Nr.), Tagging date, start and end times of the diving record, attachment duration and number of dives detected. For the following dive metrics, the mean values are presented with the standard deviations in brackets: maximum depth of the dives, median depth, duration, bottom phase duration, standardized bottom phase duration, descent rate, ascent rate, post-dive duration and percentage of surface time.

| Nr.	Tag.date	Start rec. (UTC +1)	End rec. (UTC +1)	Att. dur (h)	Dives	Max. Depth (m)	Median depth (m)	Duration (s)	Bott.ph.dur (s)	Stdz.bott. ph.dur. (%)	Desc.rate (m·s⁻¹)	Asc.rate (m·s-1)	Post-dive dur. (s)	PCST (%)
1	01/12/2013	12:12	0:34	12,4	222	28 (±18)	20 (±14)	135 (±105)	91 (±86)	62 (±16)	1 (±0,4)	1,2 (±0,7)	66 (±112)	31 (±20)
2	03/12/2013	11:38	12:45	1,1	27	11 (±7)	8 (±5)	104 (±67)	74 (±57)	66 (±14)	0,7 (±0,3)	0,5 (±0,4)	48 (±70)	26 (±19)
3	05/12/2013	9:33	17:08	7,6	69	35 (±24)	27 (±18)	220 (±131)	156 (±103)	67 (±13)	0,9 (±0,4)	0,9 (±0,6)	179 (±339)	38 (±25)
4	06/12/2013	11:09	11:42	0,6	13	34 (±35)	21 (±19)	129 (±109)	78 (±77)	60 (±15)	1,1 (±0,5)	0,9 (±0,3)	29 (±29)	20 (±18)
5	28/11/2013	12:56	17:28	4,5	120	23 (±15)	14 (±10)	82 (±57)	53 (±43)	62 (±17)	0,9 (±0,3)	2 (±1,4)	54 (±55)	35 (±24)
6	30/11/2013	10:36	19:12	8,6	90	52 (±31)	37 (±22)	276 (±141)	187 (±110)	66 (±13)	1,1 (±0,4)	0,8 (±0,4)	69 (±40)	22 (±12)
7	01/12/2013	11:07	11:23	0,3	7	26 (±30)	19 (±22)	98 (±101)	59 (±59)	61 (±8)	1 (±0,3)	0,9 (±0,1)	43 (±57)	30 (±29)
8	02/12/2014	9:13	11:47	2,6	87	30 (±28)	20 (±20)	81 (±78)	53 (±54)	61 (±14)	1,7 (±0,5)	1,7 (±0,6)	26 (±31)	28 (±25)
9	06/12/2014	9:44	15:02	5,3	80	65 (±56)	46 (±42)	191 (±171)	119 (±125)	58 (±15)	1,4 (±0,6)	1,3 (±0,6)	48 (±50)	22 (±21)
10	24/11/2014	8:22	9:22	1,0	16	58 (±67)	46 (±58)	202 (±251)	126 (±165)	58 (±12)	1,4 (±0,3)	1 (±0,4)	22 (±18)	22 (±16)
11	27/11/2014	12:27	14:51	2,4	64	23 (±25)	16 (±19)	97 (±109)	62 (±76)	62 (±11)	1,1 (±0,4)	0,9 (±0,3)	38 (±47)	26 (±21)
12	28/11/2014	10:23	14:20	4,0	56	56 (±51)	40 (±38)	214 (±213)	143 (±154)	63 (±15)	1,5 (±0,6)	1,3 (±0,6)	41 (±46)	20 (±20)
13	29/11/2014	11:49	13:36	1,8	24	53 (±41)	41 (±35)	214 (±182)	137 (±135)	60 (±13)	1,2 (±0,5)	1,3 (±0,6)	54 (±40)	24 (±14)
14	30/11/2014	9:05	9:55	0,8	8	82 (±77)	70 (±68)	286 (±273)	200 (±196)	65 (±9)	1,3 (±0,4)	1,4 (±0,5)	95 (±80)	32 (±33)
15	01/12/2014	12:14	16:37	4,4	29	65 (±58)	51 (±50)	474 (±281)	317 (±208)	66 (±15)	0,9 (±0,5)	0,6 (±0,4)	71 (±49)	18 (±18)
16	30/12/2015	10:04	10:25	0,4	4	56 (±58)	49 (±51)	233 (±215)	160 (±150)	67 (±2)	1 (±0,5)	1 (±0,6)	126 (±70)	38 (±21)
17	30/12/2015	10:48	7:09	20,3	314	46 (±56)	35 (±45)	163 (±167)	104 (±118)	61 (±14)	1,1 (±0,5)	1 (±0,7)	71 (±86)	29 (±22)
18	31/12/2015	12:08	7:50	19,7	646	35 (±15)	24 (±10)	85 (±55)	49 (±39)	56 (±11)	1,4 (±0,3)	1,6 (±0,6)	25 (±28)	21 (±15)
19	21/02/2015	10:27	22:24	12,0	240	25 (±23)	17 (±16)	132 (±104)	85 (±76)	61 (±14)	1 (±0,4)	0,8 (±0,5)	47 (±49)	26 (±18)
20	23/02/2015	13:23	8:36	43,2	815	30 (±36)	23 (±28)	161 (±180)	113 (±137)	62 (±13)	1 (±0,3)	0,9 (±0,5)	30 (±38)	20 (±19)
21	25/01/2015	13:11	3:56	14,7	520	14 (±11)	10 (±8)	65 (±43)	43 (±31)	65 (±13)	1 (±0,4)	1,2 (±0,6)	37 (±37)	33 (±19)
22	01/02/2015	10:21	19:37	33,4	1106	19 (±16)	14 (±12)	68 (±59)	43 (±41)	61 (±13)	1,3 (±0,5)	1,3 (±0,8)	40 (±48)	32 (±21)
23	15/11/2015	9:55	0:52	15,0	233	23 (±25)	17 (±18)	184 (±129)	132 (±104)	68 (±13)	0,8 (±0,4)	0,6 (±0,4)	47 (±34)	21 (±15)
24	17/11/2015	10:47	11:57	1,2	18	60 (±70)	42 (±52)	187 (±159)	99 (±84)	56 (±18)	1,2 (±0,5)	0,9 (±0,5)	49 (±54)	24 (±19)
25	18/11/2015	11:04	11:23	0,3	4	102 (±55)	79 (±51)	220 (±133)	124 (±106)	49 (±21)	2 (±0,8)	1,7 (±0,4)	89 (±79)	22 (±12)
26	20/11/2015	12:47	13:19	0,5	15	14 (±11)	10 (±6)	96 (±61)	67 (±50)	66 (±10)	0,9 (±0,4)	0,9 (±1)	36 (±34)	26 (±23)
27	20/11/2015	14:32	23:47	9,2	288	17 (±11)	11 (±7)	75 (±61)	46 (±48)	58 (±16)	1 (±0,6)	1 (±0,7)	40 (±36)	34 (±19)
28	22/11/2015	11:51	14:22	2,5	79	21 (±17)	13 (±12)	89 (±98)	57 (±77)	59 (±19)	1,2 (±0,4)	1 (±0,4)	27 (±31)	24 (±19)
29	23/11/2015	13:05	3:05	61,9	656	42 (±37)	32 (±29)	284 (±254)	209 (±204)	68 (±14)	1,1 (±0,5)	0,9 (±0,5)	56 (±116)	19 (±18)
30	23/11/2015	9:59	11:04	1,2	32	31 (±34)	20 (±24)	96 (±89)	55 (±53)	60 (±16)	1,2 (±0,6)	1,5 (±0,9)	27 (±27)	24 (±20)
31	01/12/2015	10:02	12:06	2,1	20	75 (±72)	66 (±65)	302 (±268)	210 (±198)	64 (±12)	1,1 (±0,4)	1,1 (±0,6)	73 (±69)	26 (±26)
32	01/12/2015	12:40	23:50	11,2	390	36 (±37)	23 (±25)	236 (±185)	161 (±139)	66 (±17)	0,8 (±0,4)	0,8 (±0,5)	89 (±267)	25 (±16)
33	01/12/2015	10:17	9:39	23,4	411	35 (±31)	23 (±23)	160 (±137)	107 (±108)	62 (±15)	1,1 (±0,5)	0,9 (±0,6)	45 (±104)	21 (±19)
34	30/12/2015	9:44	16:46	31,0	560	28 (±25)	20 (±18)	151 (±117)	102 (±89)	65 (±14)	0,9 (±0,5)	1,1 (±0,6)	48 (±44)	26 (±15)
35	31/12/2015	10:43	4:45	18,0	649	28 (±9)	20 (±6)	70 (±30)	41 (±21)	58 (±8)	1,2 (±0,3)	1,8 (±0,5)	30 (±73)	23 (±15)
36	18/11/2015	10:04	10:34	0,5	17	30 (±39)	20 (±31)	92 (±75)	63 (±53)	69 (±17)	1,7 (±0,8)	1,4 (±0,7)	18 (±24)	17 (±21)
37	21/01/2016	11:41	6:21	18,7	212	61 (±34)	52 (±29)	225 (±116)	156 (±90)	66 (±10)	1,3 (±0,4)	1,6 (±0,7)	92 (±47)	31 (±14)
38	26/01/2016	13:43	10:04	21	356	46 (±43)	38 (±37)	160 (±131)	119 (±99)	64 (±13)	1,4 (±0,5)	1,5 (±0,8)	46 (±43)	23 (±17)

Appendix 5. 95th quantile regression for 4 individuals on the duration of their dives against sun elevation. Vertical lines: Red dashed line indicates limit of twilight (-12º); blue solid line indicates sunrise / sunset (0º).
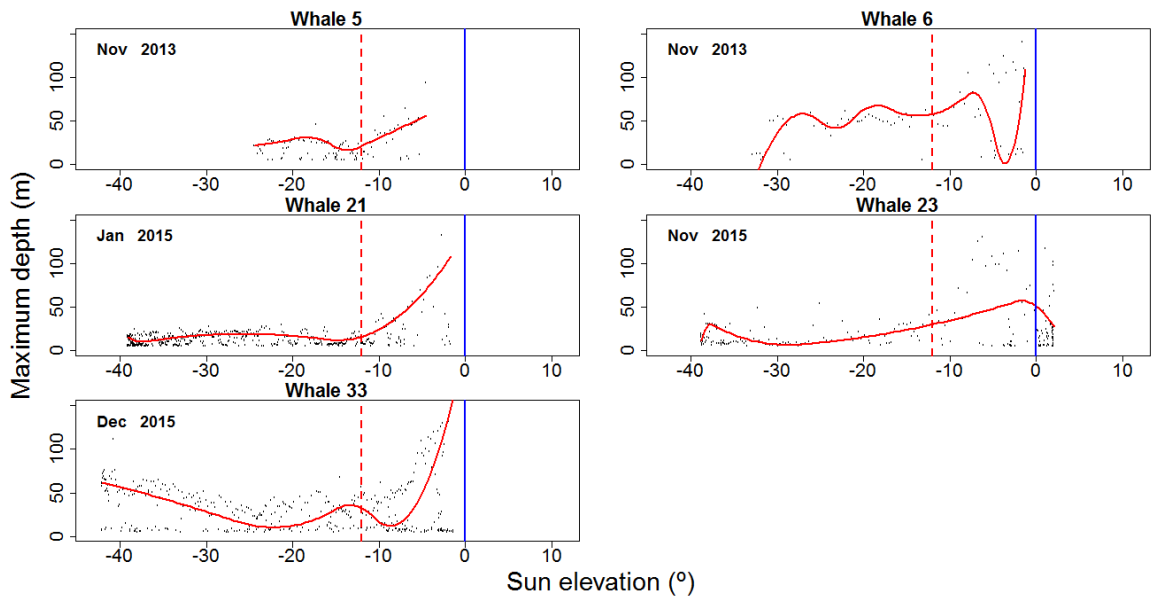
Appendix 6. 95th quantile regression with foraging index 2 as weighing factor for 5 individuals on the maximum depth (y axis) of their dives against sun elevation (x axis). Vertical lines: Red dashed line indicates limit of twilight (-12º) and blue solid line indicates sunrise / sunset (0º).
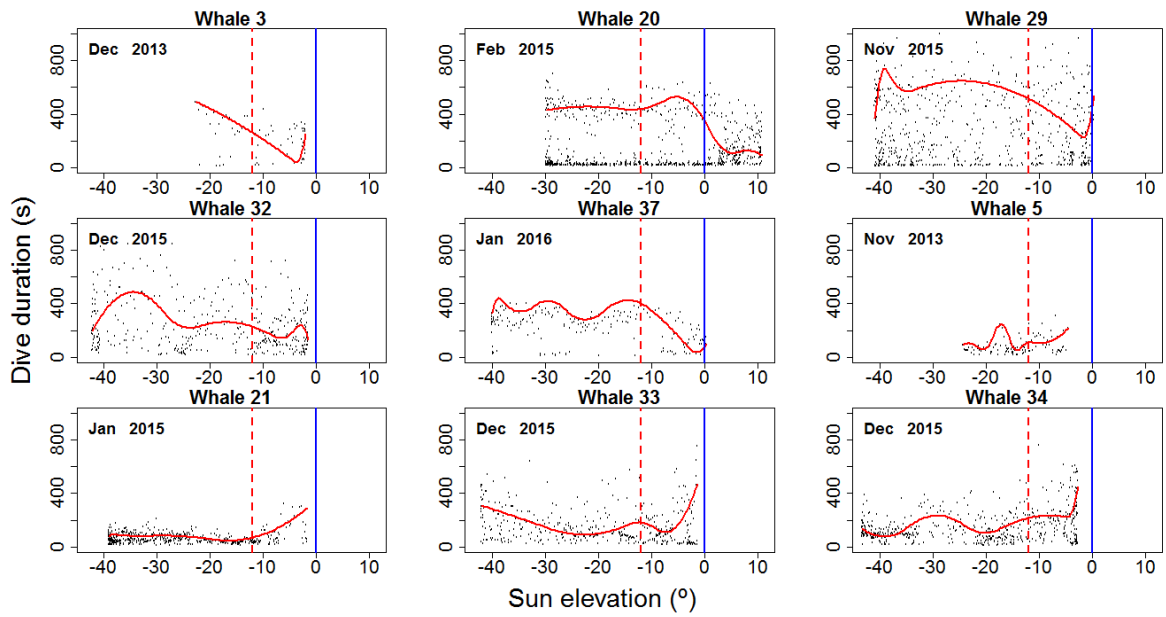
Appendix 7. 95ᵗʰ quantile regression with foraging index 2 as weighing factor for 5 individuals on the dive duration (y axis) of their dives against sun elevation (x axis). Vertical lines: Red dashed line indicates limit of twilight (-12º) and blue solid line indicates sunrise / sunset (0º
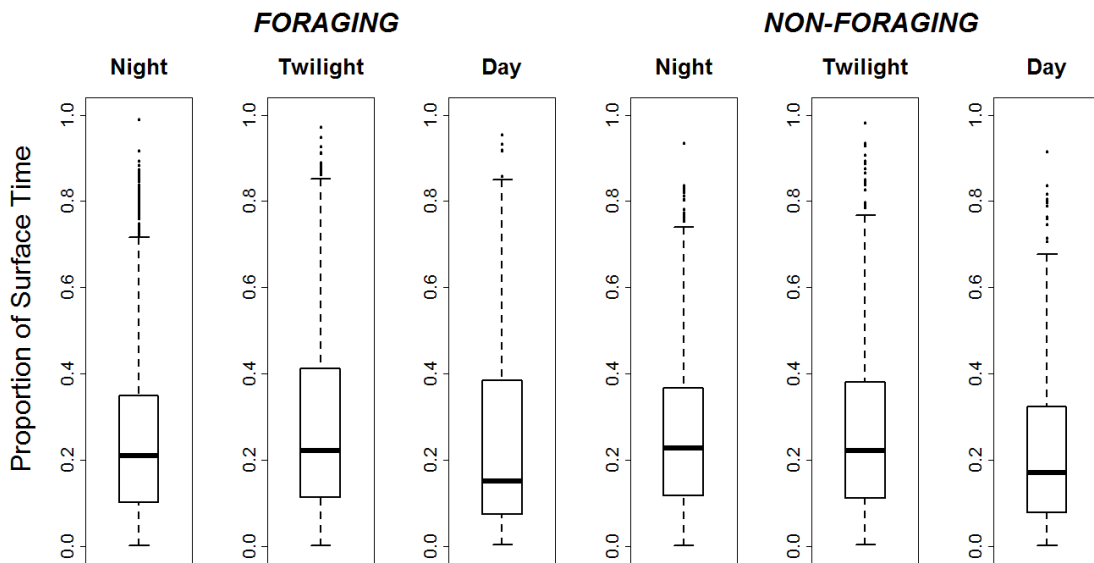

Appendix 8. Proportion of Surface Time of presumed foraging and non-foraging dives organized by night, twilight and day. Median values (black lines), 25 and 75% quantiles (box) and SE (whiskers. Proportions relative to 1.

Discussion
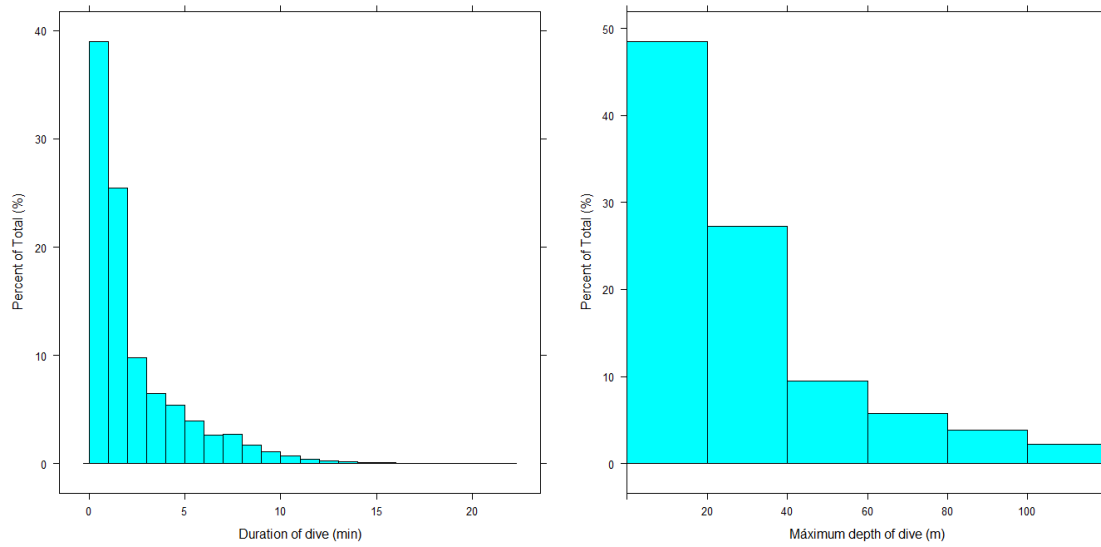
Appendix 9. Histograms of relative frequencies of dive duration (left) and maximum depth (right) from all dives recorded in our study area in Troms, Norway.
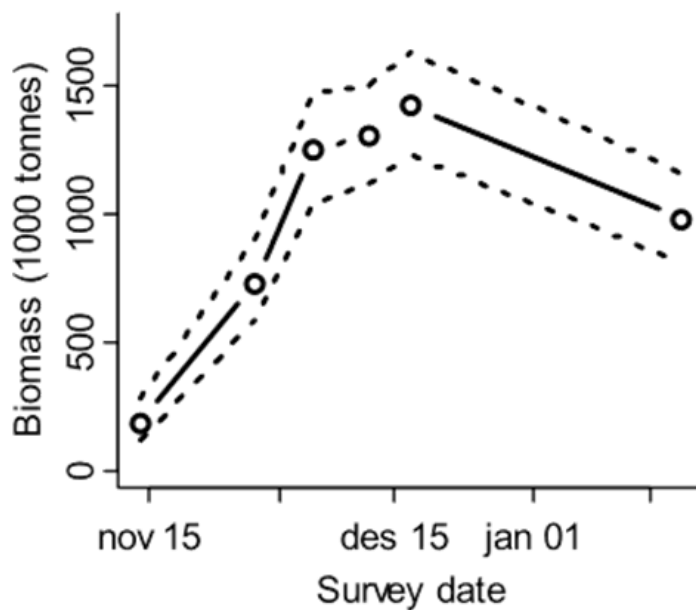
Appendix 10. Herring biomass in Kaldfjord and Vengsfjord, 2014-2015. Unpublished data from Karl Øystein Gjelland (NINA).