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HABITAT USE AND FEEDING BEHAVIOUR OF HARBOUR SEALS (*PHOCA VITULINA*) IN VESTERÅLEN

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ABSTRACT: A pilot project was carried out by the Institute of Marine Research (IMR) to test the functionality of GPS phone tags (by SMRU) on harbour seals (*Phoca vitulina*) in the Vesterålen archipelago, Norway. Acoustic surveys were performed to investigate the abundance of fish in these waters and scat sampling was used to assess the diet composition of the seal population inhabiting the area. Five juvenile females were tracked between August 2007 and March 2008 and their diving behaviour and habitat use was studied. The dive profiles recorded from the tags were classified in the attempt to identify the dives connected with feeding behaviour. The tagged seals foraged close to the coast and at relatively shallow depths (50% of the dives between 12-32 m) showing marked individual differences in the choice of feeding grounds. Analysis of scat sampling suggested that gadoids dominated the diet (62%) followed by herring (*Clupea harengus*) (35%). Comparison between the abundance of fish species in the study area and in the diet composition indicated that harbour seals have no prey preference. Harbour seals appeared to prey on small size classes of gadoids. Therefore fish size, rather than species, could be a potential selection criterion in foraging. The local abundance of fish in the area is likely to allow harbour seals to feed on what is available close to the haul out sites. Targeting of small size classes might therefore be a consequence of habitat selection based on accessibility rather than size selection.

KEY WORDS: harbour seal, *Phoca vitulina*, habitat use, tracking, diving behaviour, feeding habit, prey preference.

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1. INTRODUCTION

The harbour seal (*Phoca vitulina*) is a common phocid species widespread all along the coasts of North Atlantic and North Pacific; this species lives in coastal environments and performs small migrations connected to feeding but is considered relatively stationary (Bigg 1981). It is typically colonial and large aggregations are to be found during the breeding and moulting seasons (June-July and August-September, respectively, for Norwegian populations) (Haug et al. 1998).

In Norway, the total number of harbour seals was estimated to be minimum 6700 individuals (Nilssen *et al.* 2006). The Gavlfjord area, in the Vesterålen archipelago situated at about 69°N, hosts one of the most abundant colonies in Norway.

The ecological role of the harbour seal in the coastal ecosystem is of particular interest. Due to their resident behaviour they are likely to interact with the local fisheries directly and/or indirectly by feeding on fish in fishing-gears and/or competing for the same resources. It is therefore important for management purposes to understand this species prey and habitat use in both time and space.

The feeding habits of harbour seals have been investigated by studies on diet composition based on scat sampling in many areas of the North Atlantic, such as: Svalbard (Andersen *et al.* 2004), the Vesterålen (Berg *et al.* 2002) and southern Norway (Olsen *et al.* 1995); the Skagerrak and Kattegat, Sweden (Härkönen 1987); the Shetland (Brown *et al.* 1998), the Moray Firth (Tollit *et al.* 1996) and western Scotland (Pierce *et al.* 2003); eastern England (Hall *et al.* 1998). Scat sampling can give an idea of the harbour seal diet at the population level and, if coupled with estimates of the available fish resources at sea, allows study of prey preference in these pinnipeds. Telemetric and 'mark-recapture' methods have been used to give insights on the animals' movement patterns and habitat preference in the some of the forenamed areas (Thompson *et al.* 1989, Thompson *et al.* 1990, Bjørge *et al.* 2002). Few studies, however, have combined the two approaches (diet and movement analysis) at the same time to investigate the

influences of both habitat preference and prey preference on the feeding behaviour of harbour seals (Thompson *et al.* 1991, Bjørge *et al.* 1995, Tollit *et al.* 1998).

This master thesis was based on the data collected during a pilot project carried out by the Institute of Marine Research, Tromsø. For this project, GPS phone tags (Sea Mammal Research Unit 2008) were deployed on harbour seals to gather information on diving behaviour and distribution of this species in the Vesterålen area.

The GPS phone tags were created by the instrumentation group of Sea Mammal Research Unit (SMRU) in University of St. Andrews, Scotland. They are equipped with a traditional 'animal data logger' (that records dive profiles and other environmental and behavioural data) and a new technology for position sampling (using Fastloc GPS receivers (Wildtrack Telemetry System Limited 2006)), all combined with a mobile phone network connection, on which data-download is based on. These tags relay in fact on GSM network rather than satellite connection to transmit the data ashore.

The prime objective of this pilot project was to test the functionality of these GPS phone tags at the Norwegian coast, since, until recently, the GSM network coverage along the coast has been restricted to only parts of it. The project had in addition some resources to carry out preliminary acoustic and scat samplings in the area of interest.

This master thesis study was aimed to construct an analytical approach to the telemetric data obtained from the tags and compare them to the resource and diet analysis in order to make inferences on the feeding behaviour and habitat use of harbour seals in the Vesterålen area.

Several aspects were investigated:

    i.   the habitat use of the seals tagged with GPS phone tags

    ii.   their diving behaviour (in relation to environmental factors like bathymetry and bottom topography)

    iii.   harbour seals diet composition

    iv.   prey preference.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The present study was carried out on a population of harbour seals resident in the area around the north western part of Langøya and the western part of Andøya (Gavlfjord), in Vesterålen, northern Norway (Fig. 1). The archipelago is located between 68.5°-69.5° N and 14.0°-16.0° E. It is exposed to the open Atlantic Ocean on the west and is characterized by the presence of many small islands and skerries (favourable haul out spots for the species) which partly become submerged during high tides. In the study area, the continental shelf break is situated 20 to 30 km from the coast. The shelf is relatively shallow and the most of it not deeper than 100 m.

2.2 DATA COLLECTION AND ANALYSIS

The data collected can be divided into three main categories: telemetry, diet and resource. Bathymetric data for the study area were provided by Statens Kartverk (25 m grid resolution).

2.2.1 Tag deployment

Data about position and diving behaviour of harbour seals were collected by means of GPS phone tags (provided by SMRU Instrumentation, University of St. Andrews, Scotland). The tags were deployed on five females, on the 30th-31st of August 2007. Four animals were assumed to be about one year of age, one probably two years (examining body mass). Two 15 ft Zodiacs fitted with outboard motors (Yamaha 30 hp) were used for catching operations. The seals were caught by using two bottom gillnets (mesh size ca. 20 cm and each about 25 m long and 9 m high) designed to catch Greenland halibut (*Reinhardtius hippoglossoides*). These were adapted to float and sewed together into one (approximately 50 m long). The net was then deployed in front of the haul out site; it was visually controlled from the inflatable boats in order to promptly pull the animal out of the water to avoid drowning. Each attempt lasted no longer than

five to ten minutes. By that time every seal had either been entangled in the net or avoided it, but in any case escaped from the haul out site. Seals that had been caught were taken onboard and brought to land at a temporary land station, where all veterinary and tagging material was hold.

The animals were weighted, standard length was measured and gender determined. They were then sedated with an intramuscular injection of 0.01 ml Zoletil® (Virbac) per kg body mass (Fig. 2a). To minimize stress the eyes were covered by means of a fabric bag applied on their head that allowed breathing. The tagging followed a standard procedure. An area on the neck, corresponding to the surface needed to apply the tag, was marked with a colour pen. In that area the fur was dried by help of highly absorbent paper and 70% ethanol, then with warm air by use of a hairdryer (Fig. 2b). Fat excretions were removed with acetone (this leads to longer lasting gluing). A two-component epoxy glue, Araldite® (Huntsman), was used to attach both the tag to a piece of synthetic net (of bigger diameter to increase the gluing area) and the forenamed net to the animal's fur (Fig. 2c). The net increments the surface in contact with the animal and allows the fur to anchor better by passing through the net holes. The whole package, glued to the fur, will be shed during moult in August-September 2008.

During all the procedure a sensor was kept in the gluing area to measure the temperature that was released in the chemical process of the two components coming together (maximum allowed 45° C) (Fig. 2d). It is important that no skin-burns arise, which would lead first to injury on the animal and possibly to the consequent loss of the tag together with the fur. The animal's eyes were also well protected against ethanol, acetone and glue by the use of the bag and additional paper.

The procedure lasted about 45 min per individual. The animals were then kept around 60 min in a large aluminium box before release (Fig. 2e). The condition of the seals was checked by releasing them on a sandy beach at around 20 m from the sea (Fig. 2f), allowing to control if muscular activity was completely restored and to check if the antenna was positioned correctly. The release location is marked on Fig. 1 and more details about the procedure and the individuals are

listed in Tab. 1. Several specifications about the functioning of the tag, such as protocols for data collection and methodology of connection and data transfer, are described in the following chapter.

2.2.2 Technical information about the tags

The GPS phone tags used were designed for being applied to seals which are mainly distributed within GSM range (McConnell *et al.* 2004). The innovative technique of data download using the GSM channel, provided by regular telephone companies, allows sending highly resoluted data at low battery costs, something that is not possible with satellite relayed loggers.

The tag is applied to the fur on the back of the seal right behind the head, so that the antenna can come in contact with Argos satellites for positioning and the network for sending as soon as the animal surfaces. The tag processor is housed in a solid epoxy body and is equipped with temperature, pressure and wet/dry sensors and a real time clock. The wet/dry switch registers the position of the tag above or below the water and detects surfacing and haul out events while the pressure sensor allows computing the depth during the dives. A very resoluted picture of the animal's behaviour is drawn by the sum of all these data, which are organized by type by the processor and stored into the temporal memory of the logger, waiting to be sent.

The use of traditional GPS tags in determining marine mammal positions at sea has been impractical due to the brief surfacing intervals in these animals' dives. To overcome this problem, SMRU integrated Fastlock GPS receivers into the tag. This system allows to take a snapshot (<0.2 sec) of the satellite data, while the calculation of position from this information, is done partly by the tag processor and partly after the data have been relayed ashore. This results in a higher probability of successful contacts with the satellite and more precise positioning of the seals.

The tag's software is highly configurable and sampling design can be decided and set before deployment. Depth and temperature are recorded every 4 sec. Depth is automatically reset to zero whenever the wet/dry sensor detects the

surface. Rapid sampling of the wet/dry sensor (every 0.5 sec) is initiated when approaching the surface, starting at 6 m depth. Profiles of dives shallower than 6 m were not logged due to the potential error in depth calculation close to surface. Behavioural categories (dive and haul out) were defined as following based on information on wet/dry, depth and time: dive started when wet and below 1.5 m for 8 sec and ended when above 1.5 m for 0 sec or dry at any time; haul out begun when dry for 10 min and ended when wet for 40 sec.

A summary record of behavioural state (relative frequency of time in each of three states: surfacing, diving, haul out) was logged every 2 hours. GPS-locations were set to be taken every 20 min. However, since positioning is dependent on satellite availability and the animal being at surface, the process can be delayed until favourable conditions arise. Water-column temperature profiles were reconstructed for each 2-hours period. Single dives were summarized in 9 points time/depth profiles, the points being selected by the processor prior to sending as the 9 most informative inflection points of a higher resoluted profile. This allows to data compaction, and thus energy saving in the transmission, by discarding redundant data.

A detailed description of the functioning of the GPS phone tags can be found online (see Sea Mammal Research Unit 2008).

2.2.3 Analysis of tag data

A complete database of all records sent from the five tags was continuously updated and was available for download at any time from a protected website provided by SMRU. The results presented in this study were last updated on the 24th of March 2008, when two out of five transmitters were still working (see Tab. 2 for telemetry data collection period).

Several analyses were performed on the different data types. In order to eliminate the GPS-locations that result from errors in position calculation (McConnell *et al.* 1992), the GPS data were filtered by a function that calculates maximum distances travelled at a plausible sustained horizontal speed of 2.0 m/sec.

Data on diving behaviour were classified into seven categories (called 'dive classes') based on the shape of the underwater profile (Tab. 3). When possible, a behavioural state was assigned to the different dive classes. The classification (i.e. the choice of the different categories and their possible behavioural interpretation) was based on references (Schreer *et al.* 1996, Lesage *et al.* 1999, Fedak *et al.* 2001), suggestions (Martin Biuw, Norwegian Polar Institute, Tromsø, Norway, pers. comm.) and trials.

Fig. 3 shows the generalized shape of a dive profile belonging to each class in a time-depth scale. In square dives (SQ), the animal swims down to a certain depth at high vertical speed (steep line in Fig. 3-SQ), it stays at a constant maximum depth for a period and surfaces with around the same vertical speed. SQ dives are assumed to be feeding dives at the sea-bottom (Le Boeuf *et al.* 1988, Hindell *et al.* 1991, Bengtson *et al.* 1992). Wiggled dives (W) have the same pattern but account for minor depth changes during the submerged deeper phase, something that was considered in some studies as indicating feeding in the water column (Le Boeuf *et al.* 1988, Bengtson *et al.* 1992). V-dives present the same proportion of time at all depths, which is interpreted as searching through the water column for prey without any successful finding (Fedak *et al.* 2001). U-dives are similar to SQ dives but smoothened out in their shape; those can also account for feeding or, as hypothesized in Schreer *et al.* (1996), travelling. Left root and right root classes (LR, RR) were skewed, mostly V-shaped profiles. LR and RR presented higher uncertainty in classification with respect to other classes (Fig. 4) and are of unknown behavioural interpretation. The previous classes' names were created to recall their shape and have no particular meaning; drift dives (DR) on the other hand were named after their assumed behaviour, where the animal sinks passively in the water due to the negative buoyancy. This particular diving pattern was discovered in a study on elephant seals (*Mirounga leonina*) by Le Boeuf *et al.* (1992). For DR only one shape (DR(a)) was originally created, but during classification a mirror shape (DR(b)) was found and both were assigned to the same bin (Fig. 3).

To perform this classification, the dive data were first uploaded into the statistical computing program R 2.6.2 (Hornik 2008), where preliminary calculations were made to generate additional variables that were subsequently used for characterizing the generalized profiles (i.e. slopes of the segments and number of wiggles). The computer supported classification was performed in R 2.6.2 by means of a script created by Biuw (by use of 'randomForest' package in R 2.6.2) that calculates a generalized profile for each class defined by the user. This calculation is based on a preliminary visual classification, manually performed on a sub sample. The software then statistically assigns a class to each record in the database. It also calculates residuals and an error parameter, to check for quality (Fig. 4). The visual manual classification was performed on a sub sample of 1000 dives; an error value of 0.2 for a class, for example, would mean that 200 dives (20%) were statistically assigned by the program to a class different from the one chosen by the user in the manual classification.

For each dive, the start time was recorded but not the geographical position, since GPS-locations were taken at fixed time intervals. In order to determine the position of a dive happening between two consecutive GPS-locations, it was assumed that the seal had been swimming on a straight line and at constant speed between the two points. The position of the dive was then extracted from this line based on its timing in relation to the timing of the previous and subsequent GPS-locations. Moreover, in order to reduce errors on the position estimates, the dive records that were not close in time to a GPS-location (±1 min) were discarded (the process is referred to as 'filtration'). The dives were then plotted in gridded maps of 100x100 m roots (referred to as pixels). This resolution accounts for the potential errors introduced both by the positioning of the dives in relation to the GPS-locations and the inaccuracy of the GPS-locations themselves (median of residuals 10.3 m). The same procedure was used for haul out events.

R 2.6.2 was used for database management, data selection and all statistical computations. ArcGis 9.2 (Gorr *et al.* 2005) was used for all the mapping and for the spatial two-dimensional calculations. Among the analytical functions available in ArcGis 9.2, 'cost-distance' was used to generate a map, in which every point in

space (100x100 m pixel) had a value equal to its distance from the closest haul out site. This function does not calculate the Euclidean distance between the point and the closest haul out site, but, by considering land as a barrier, it computes the distance that a seal would have to swim to reach the point by going around land.

The seals' habitat use was estimated and plotted based on the density of dives per pixel. Consecutive returns to the same haul out site between feeding trips and diving associated with haul out activity usually increase the density of dives around the site and might overestimate the importance of the area when considering feeding behaviour (Thompson *et al.* 1994, Tollit *et al.* 1998). The 'cost-distance' map was used as a tool to correct for the concentrating effect of the haul out sites on dive density.

In habitat use maps, which are based on the density of dives in an area, the multiplication of the output values of the 'cost-distance' to the density of the dives for each pixel reduces the importance of the areas close to the haul out sites compared to farther areas.

2.2.4 Sampling of diet data

A total of 29 scat samples were collected on haul out sites around Stø during summer-autumn 2007 (30th June, 1st September, and 22nd October). No hard remains useful for prey identification were found in the samples from June (see Tab. 4). The material was sampled by visiting the haul out sites during low tide and the scats were collected from the substrate, conserved in plastic bags and frozen for later examination. The majority of the samples was collected above the intertidal zone.

Diet investigation by scats analysis is based on the recovery of the hard remains that overcome the digestive process. The samples were washed in warm water and then filtered through a system of three consecutive sieves of mesh width 2, 1 and 0.2 mm, respectively. The relevant remains, mainly fish otoliths, were conserved in alcohol and inspected under a lens (Wild Herrbrugg M3) for species identification to the lowest possible taxon with use of identification keys (Härkönen 1986, Breiby 1985) and reference material, conserved at the Institute

of Marine Research in Tromsø, Norway. The otoliths were measured and corrected both for erosion (digestion coefficient (dc)) and total loss (numerical correction factor (ncf)) during the digestive process. The correction factors used in the present study were taken from a study on grey seal (*Halichoerus grypus*) diet (Grellier *et al.* 2006). After correcting otolith length, known otolith length-fish length and otolith length-fish weight regressions were used to estimate the original length and weight of the fish species (Breiby 1985, Härkönen 1986). The harbour seal diet is presented as total (kg) and relative (%) biomass of the different prey species. For comparison, both uncorrected and corrected diet compositions are presented in the results.

2.2.5 Resource estimation

In June 2007 and January 2008, standard acoustic surveys were conducted using the research vessel 'Johan Ruud' in order to map the fish resources in the study area. Continuous acoustic recordings of fish and various planktonic organisms were made along a predetermined transect (Fig. 1) by a calibrated echo integration unit consisting of a 38kHz Simrad EK-500 splitbeam echosounding system (Bodholt *et al.* 1989) connected to a BEI post processing system (Foote *et al.* 1991). A minimum acoustic threshold of -88dB Sv was applied to detect smaller organisms (i.e. plankton, 0-group fish, etc.). The allocation of acoustic values (area backscattering coefficient (Sa)) was carried out on the basis of the acoustic character of species and the relative species size and composition in trawl samples (Simmonds *et al.* 2005). Both pelagic and demersal trawling was performed in response to potential changes in the echo sounder registrations. For pelagic trawling, a 10 fathom trawl fitted with a Scanmar depth recorder was used, while a Super Campelin 1400 mesh shrimp trawl was used for demersal trawling. Both trawls were fitted with an 8 mm net inside the codend thereby making it possible to sample fish juveniles. Pelagic and demersal trawling was standardized to 30 and 20 minutes duration, respectively. The trawling speed was approximately 3 knots.

Five and three trawl samplings were performed in 2007 and 2008 respectively (see Tab. 5 for details). No pelagic trawling was conducted in 2008 due to difficult weather conditions.

Individual weight (to the nearest g) and length (to the nearest cm) of the fish were recorded. The results from the trawling and the acoustic surveys were used to calculate the absolute biomass for the different fish species found on the survey transect. Since flatfish species lack swim bladder and hardly reflect echo, their abundance was estimated by a 'swept area' methodology (Jakobsen *et al.* 1997).

The 'swept area' estimate (A) of flatfish is simply the length of the trawl path (l) times the width (w) of the trawl times the catchability (c):

$$A = l \cdot w \cdot c$$

The catchability is defined as the proportion of fish captured within the 'swept area'. The catchability of flatfish in this study was assumed to be 0.5.

Sa-values were partitioned among the different fish species based on standard procedures (see Simmonds *et al.* 2005). They were converted to numbers (ρ) according to the relation:

$$\rho = \frac{Sa}{4\pi 10^{(0.1TS)}}$$

where TS is the mean target strength of scattering organisms, which varies between species and body length. The continuous recording of the values on the survey transect was averaged over one squared nautical mile (nm^2). Due to similarities in the acoustic signal of cod (*Gadus morhua*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*), these species were treated as a group (codfish). Identification of codfish at a lower taxon level is possible by use of species frequencies in the trawling results. The trawling samplings performed were not enough to provide a robust estimate of these proportions. The two-dimensional prey distribution was then modeled in ArcGis 9.2. A gridded map (1 nm^2 resolution) was created by interpolating the point values using Inverse Distance Weighting (Fisher *et al.* 1987).

2.2.6 Analysis of prey preference

Prior to statistical analysis of prey preference, the prey species were grouped into the following categories: codfish (cod, saithe and haddock), flatfish (plaice (*Pleuronectes platessa*), American plaice (*Hippoglossoides platessoides*), flounder (*Platichthys flesus*), witch (*Glyptocephalus cynoglossus*), lemon sole (*Microstomus kitt*)) and herring (*Clupea harengus*).

A combined index (C_i) was applied to estimate the diet composition (Nilssen *et al.* 2005):

$$C_i = \frac{B_i \cdot F_i}{\sum_{i=1}^{k} B_i \cdot F_i}$$

where B_i and F_i is percentage weight and occurrence of prey species *i*, respectively, and *k* is number of prey groups.

Harbour seals prey preferences were analysed by simply estimating the relative difference in prey composition between the diet and the resources

$$D_i = C_i\text{-}R_i$$

where C_i and R_i is the relative importance of prey *i* in the seal diet and in the resource estimates, respectively.

In order to test the null hypothesis (H_0), that harbour seals have no prey preference, the measure of difference (D_i), was tested for significant deviance from random feeding. This was accomplished by constructing approximate 95% confidence intervals (CI) for D_i for each prey species, by generating 5000 bootstrap replicates of the diet data. The CIs should be interpreted as follows: preference if the CI is above and does not overlap zero, random feeding if the CI overlaps zero, and avoidance if the CI is below and does not overlap zero.

The applied statistical methods were based on the following assumptions:

    i.   The examined scats were assumed to be the result of foraging in the study area, where the resource surveys were also conducted, and are a representative sample of the seals diet in the area.

    ii.   The composition and abundance of fish in the resources and in the seals diet are representative.

3. RESULTS

3.1 Telemetry

Five harbour seals were tagged with GPS phone tags for a total collection period of about 6 months. The life of the single transmitters varied; gp10-683-07 and gp10-684-07 sent the last data not long before the final update of the current database (24th March 2008), gp10-685-07 worked until the beginning of February 2008, while gp10-641-07 and gp10-655-07 stopped sending in December 2007. Four gave both GPS positions and dive/behavioural data, while gp10-683-07 provided only GPS positions. Details about the animals and their individual datasets are given in Tab. 6. A total dataset of 24246 GPS positions, 137019 dives, 794 haul outs and 8664 two-hour behavioural summaries was available for analysis.

A map of all GPS positions (Fig. 5) was generated to visualize the tagged seals' distribution (based on all the 5 tagged seals). There was a marked individual pattern in both direction and total length of the movement from the release location. Seal-684 (the individual marked with transmitter gp10-684-07) travelled north to Nordmela, Andøy, while seal-685 went south to the inner part of the western fiords of Langøy, travelling each a maximum of 30-35 km away from the release location. Seal-641 and seal-655 travelled mainly south-west during the tagged period but not further than 20 km from the release location, while seal-683 remained on site (less than 10 km from release location). The results of the last individual are surprising if considered that the recording time of this tag was the longest.

Results from the classification are listed in Tab. 3. The relative frequency of occurrence and the average maximum depth and duration of the dives are listed for each class.

The most frequent dives were SQ, W and U, which contributed for a total of 84.4%. The supposed feeding dives (SQ and W) make up more than 50 % alone.

LR and RR classes, which had unknown behavioural meaning, contributed only with 1.5 and 0.5% in frequency, respectively.

The maximal depth reached by any of the seals in this study was 177 m (seal-684) but 50% of the dives fell in the range of 12-32 m (average 24 m). The longest dive lasted 25 min (seal-684) but the majority of the dives performed were of 2-3 min. Differences in average dive duration and average maximum depth between individuals (Fig. 6) were tested and both found significant (ANOVA, P<0.001). The dataset used in this analysis was a randomly sampled subset of 100 dives per individual per dive class, with a total of 2800 records (7 classes x 4 individuals x 100). The subsample was used to reduce the number of outliers due to the size of the original dataset. From the same dataset, a pairwise comparison test (Tukey HSD) of the means of dive duration and maximum depth for all classes was run. The test allowed grouping the classes that had comparable means, but the results from the two response variables (dive duration and maximum depth) were not the same (Fig. 6). For maximum depth, SQ, W, U, LR, and RR were not significantly different, while DR dives were shallower and V dives deeper. On the other hand, SQ and DR were comparable in duration and the same was true for W and U, while all the others (V, LR, RR) differed (P<0.05).

Examining the distribution of maximum depths achieved in each dive class, however, showed that the values are not normally distributed around the means (Fig. 7). SQ, U and V dives had a bimodal distribution, peaking both at the minimum depths recorded (6 m) and at around 25-30 m, V and LR dives were most abundant at 25-30 m depths while RR and DR dives were most frequent at shallow depths.

Dive classes were also compared in spatial distribution. Before plotting, both dive data and haul out data were filtered to eliminate error in position calculation. The process reduced the dive records of 15% and the haul out events of as much as 87%. However, since the same haul out site was used several times, even such a large reduction in haul out events did not imply high loss of information on haul out locations. All the haul out events that were discarded were positioned at sea and not on land (due to error in position calculation), but all of them were close to

a point on land that had hosted several other haul out events and had been identified as a haul out site. Comparison of the plots of haul out events against filtered haul out events suggested that no haul out location was missed in the filtration process.

In Fig. 8 a selected area illustrates the different distributions of the dive types from one individual (seal-684) around the haul out sites (in orange). This particular individual and area were chosen because of illustrative purposes, but the same trend was observed also for the other tagged seals. In the figure, colours correspond to the density of the dives in roots of 100x100m. For each class the relative density was found to be particularly high around the haul out sites. The dive types differed from each other in concentration but not much in distribution, except for the DR, LR, and LR classes. These were not present in the areas north of the haul out site where, on the other hand, the other dives were very frequent. DR, LR and RR dives tended to happen only around haul out sites for all individuals and were then assumed not belonging to feeding or searching behaviour.

Average bottom depth for each dive class was extracted from the interpolation of the dive distributions and a bathymetry map (Statens Kartverk, see Tab. 7). No difference was found between average bottom depth and the diving maximum depth of each class, suggesting that on average harbour seals dive to the bottom. RR dives and DR dives were slightly shallower than average bottom depth. The same analysis was done on bottom slope. The tagged individuals seemed to prefer locations close to steep edges, but remaining on the shallower and less steep side of it (slope range: 0-50 deg, average: 5-7 deg, see Tab. 7).

From the comparison of the dive classes distribution, 4 classes (SQ, W, V, U) out of 7 were selected to best represent feeding behaviour (referred to as 'feeding dives'), and the sum of their distribution was used as a base for building a map of feeding grounds, which were well distributed accordingly to sea-bed topography (Fig. 9). The map of the 'feeding dives' was then processed to map habitat use. In order to correct for the concentrating effect of the haul out sites and reduce the importance of the areas around them, an analysis of 'cost-distance' from the

closest haul out site was performed and the output (Fig. 10) was multiplied with the density distribution of the 'feeding dives' for each individual. The generated habitat preference map is shown in Fig. 11. Several hotspots were found. It was interesting to notice that one of them is as the entrance of the harbour of Myre, a small village on Langøy Island.

3.2 Harbour seal diet

After discarding the scat samples without relevant hard remains, 26 samples were left for analysis (Tab. 4). Otolith analysis revealed the presence of a total of 5 fish families in the diet of a subsample of the harbour seal population of Vesterålen. Clupeidae, Gadidae, Pleuronectidae, Ammodytidae and Anarhichadidae were found. Among the gadoids three different species were recognized when possible: cod, saithe and haddock. Herring was also identified at the species level, while sand eel (*Ammodytes sp.*) and wolffish (*Anarhichas sp.*) at the genus level. Flatfish was considered as a group.

Codfish dominated the diet, followed by herring and flatfish. Tab. 8 shows the results of the back-calculated biomass (kg) of each prey taxon. The different gadoids are listed by species but their sum is also shown.

The corrections applied on the otolith length and number (Grellier *et al.* 2006), to account for erosion in the digestive process, had strong effects on the results. Fig. 12 compares the two datasets (uncorrected and corrected) both as relative values. In the figure only the most abundant groups are shown (codfish, herring, and flatfish). Wolffish is not included since the high biomass listed in Tab. 8 is due to a single prey item weighing 1.4 kg, which was assumed to be occasional. Moreover, specific correction factors were lacking for that taxon.

The correction affected the relative importance of the different groups in the diet. The proportion of herring increased from 18% to 35% while codfish and flatfish decreased from 73% to 62% and from 9% to 3%, respectively.

3.3 Resource abundance and distribution

Results from the acoustic surveys are presented in Tab. 9 as absolute biomass

(average and max. biomass given in tonnes per square nautical mile (t/nm^2)). The total average prey abundance varied much between summer (100 t/nm^2) and winter (17 t/nm^2). Codfish was the most abundant fish group in both surveys (summer 2007: 69 t/nm^2; winter 2008: 11 t/nm^2), followed by herring (summer 2007: 7.7 t/nm^2; winter 2008: 0.01 t/nm^2). Herring was by far the patchiest distributed prey in both surveys (low average, high max. in Tab. 9).

The distribution of the most important preys found in the harbour seals diet (codfish and herring) was plotted together with selected telemetric results (Fig. 13). Only the 'feeding dives' of two periods, September 2007 and January-February 2007, are shown. These periods were selected, when possible, to overlap the acoustic surveys in time. The spatial distributions of codfish and herring, obtained from the resource estimates, were found to be well correlated. The distribution of the tagged seals' dives on the other hand did not show an evident pattern in relation to their potential preys' distribution.

3.4 Prey preference

Results from prey preference analysis (Fig. 14) suggest that harbour seals have no strong preference for any of the prey groups analyzed. In fact, despite the CI of herring does not overlap zero, there was no significant difference in preference among the groups (the 95% CIs of the different groups overlap).

An evident discrepancy in fish length distribution was found between the diet and resources results (Fig. 15). Harbour seals appear to exploit smaller codfish more intensively than it would be expected by random feeding. Ninety % of the codfish in the seals' diet was smaller than 30 cm (median 14 cm), while the codfish sampled in the acoustic surveys fell in the range of 25-85 cm (2.5% and 97.5% quantiles, respectively), with a median value of 50 cm.

All herring in the scat samples was smaller than 35 cm (uncorrected values), with higher frequencies of individuals between 10 and 15 cm, but no length range estimates are available from the acoustical surveys due to the low frequencies of occurrence of this species in the trawl haul.

4. DISCUSSION

4.1 Telemetry

The choice of deploying GPS phone tags to monitor harbour seal behaviour and habitat use was based on the known resident and costal behaviour of this species (Bigg 1981, Würsig 2002).

This innovative combination of animal data loggers with mobile phone communication technology allows transmission of information at lower battery costs and higher rates with respect to Satellite Relayed Data Loggers (SRDL) (McConnell *et al.* 2004, Sea Mammal Research Unit 2008). The potential high resolution of some data, though, was lowered by the relatively low frequency of GPS positions, which sometimes brought to significant reductions in the original database. Both this reduction and individual differences in logging frequency and life-time of the tags caused different individual contributions to the dataset. This may have introduced biases in those results that are based on data pooled for all animals tagged.

The five seals used in the present study, moreover, were all juvenile females, a sample which is not likely to be representative for the population. However, this was not the main goal of the study, which was conducted to explore if GPS phone tags were appropriate data samplers for harbour seals. The GSM coverage has earlier been relatively low along parts of the Norwegian coast but is now improving. The results from the present study show that GPS phone tags can provide good quality data in the study area.

In the classification process, the general shape of the dive profiles was used to separate the dives into classes which, by means of further studies, could be explained in the behavioural perspective.

The different classes were defined based on the geometrical shape that the dive profiles recalled. Several other methods are available to group dives. Schreer *et al.* (1995) suggested multivariate analysis to select among several descriptive variables (dive depth, dive duration, number of wiggles, rate of descent and

ascent, time spent at the max. depth, etc.) the ones that explain most of the variability between dives. Lesage *et al.* (1999) as well supported geometrical classification with Principal Component Analysis for variable selection.

In the present analysis, dive maximum depth and duration were not used as discriminative variables, but some of the classes (the ones that have a bimodal distribution) could be split based on the frequencies of depths achieved (see Fig. 7). Future analysis should be done to check for possible differences in spatial distribution between the shallow and deeper dives belonging to the same dive class.

In the classification, several geometrical shapes were found, some previously described in literature (Bjørge *et al.* 1995, Schreer *et al.* 1996, Lesage *et al.* 1999) and some new (LR, RR). LR and RR categories were created during classification to help reducing the error of behaviourally meaningful classes (SQ, W, U, V in Fig. 4) by sequestering skewed dives from these classes. Dives that are skewed on the right side (like RR) were interpreted, by Schreer *et al.* (1996) in Weddell seal (*Leptonychotes weddellii*), as rapid changes or abrupt ending of dives. In that study, skewed dives were also thought to be due to the seal swimming slowly from shallow waters, near haul out sites, towards deeper waters, following the descending sea floor. The slope and shape of the skewed side of these dives, however, were highly variable and comparisons were difficult.

In order to give an insight on the possible behavioural meaning of unknown dive types, without direct observation, examination of time-series is suggested. The dives happening on the time scale before and after a dive which is difficult to interpret can give an indication of its behavioural interpretation.

DR dives were thought to be similar in behaviour to elephant seals drift dives as described in Le Boeuf *et al.* (1992). Elephant seals are thought to perform passive dives (by sinking), most probably, to save energy for metabolic purposes during digestion (Crocker *et al.* 1997). Harbour seals are usually slightly negative in buoyancy, depending on their body condition (based on observation, Kjell T. Nilssen, Institute of Marine Research, Tromsø, Norway, pers. comm.), and therefore tend to sink in the water if not moving. DR(a) dives were thus possibly

explained as energy saving dives. This is just a suggestion and more analyses should be done in future to check if these are connected with diel/tidal cycle or other environmental factors.

The presence of DR(b) dives in the same category as DR(a) did not generate problems in the accuracy of classification, since the error for DR is still low (Fig. 4), but this was probably due to the small number of DR(b) profiles in the dataset.

The grouping of SQ, W, U, and V dives under 'feeding dives' was made based on the behavioural interpretation (feeding or searching for food) of similar classes found in literature (Bjørge *et al.* 1995, Schreer *et al.* 1996, Lesage *et al.* 1999, Fedak *et al.* 2001). The average classification error for these dives was low compared to the other three classes (LR, RR, DR), meaning that these dive types were well defined. Moreover, LR, RR, and DR were absent in the areas assumed being feeding grounds. These reasons alone, however, do not imply that all the classes defined as 'feeding dives' were related to feeding events or feeding trips.

Identification of feeding events by classification is difficult, but the problem could be reduced by combining classification to other methods in order to identify feeding events. Such methods, like the deployment of stomach temperature loggers (Bjørge *et al.* 1995, Lesage *et al.* 1999), or underwater cameras (Bowen *et al.* 2002), have been previously used to identify feeding events, but little work has been done on combining such data with a computer supported classification (as in Lesage *et al.* 1999). A more clear interpretation of the different dive classes could also be achieved by deploying 3D-accelerometers in association with time-depth recorders. This would register not only movement related to depth, but also three-dimensional movement and acceleration bursts connected with feeding behaviour.

SMRU is now working on combining GPS phone tags with 3D-accelerometers (Bernie Mcconnell, SMRU, University of St. Andrews, Scotland, pers. comm.), which will possibly improve the understanding of feeding behaviour in pinnipeds by use of telemetric methods.

The spatial distribution differed among dive types. The dive density was found to be particularly high around the haul out sites and this was thought to be

due to the concentrating effect of the sites themselves, where the animals always return after foraging trips.

Due to this concentrating effect and thus the overestimation of diving density per 100x100 m root around the sites, the dives were weighted proportionally to the distance from the haul out locations (Fig. 10). That also accounted for a reduction in importance of the dives performed at very shallow depths close to the haul out sites. Other studies totally eliminated the dives performed closer than a certain distance from haul out sites, since these were assumed to be associated with haul out activity (Thompson *et al.* 1994, Tollit *et al.* 1998). At the same time, Lesage *et al.* (1999), who deployed stomach-temperature recorders in harbour seals in the St. Lawrence River estuary in Canada, found that about 40% of the feeding dives happened at depths shallower than 4 m. This may indicate that also the areas very close to haul out sites host a relevant part of the feeding events. These differences might be due to prey availability around the haul out sites, and further studies must be conducted locally to understand the importance of the areas around haul out sites in relation to feeding.

Another potential bias in using only classification for determining feeding events can arise as a result of the nature of the data analyzed. Dive data are in fact strongly temporally correlated and random sampling of dive data with a time lag will reduce this dependency.

The maximum distances travelled from the initial release location by the seals tagged in the present study were around 30-35 km. Being the results based on juveniles, biases in home range could have arisen. Lowry *et al.* (2001) found that sub adults travelled longer distances from initial location than adults (maximum distance travelled on average 96.6 km for juveniles, 61.3 km for adults, for a total tracking period of 100 to 140 days). This was explained by dispersion theories. Bjørge *et al.* (2002) recorded maximum distances between site of tagging and site of recovery of more than 200 km in juvenile harbour seals along the Norwegian coast. The peak of median distances travelled was found at 5 months of age, thereafter, median distances were less than 100 km for all ages.

The relatively limited sample size might have caused a bias in estimation of home range for the harbour seals in the present study. However, it is assumed that the estimated home ranges, based on movements of the tagged seals, represent the real home ranges for juvenile harbour seals in that particular year at the study area. According to the results of Bjørge *et al.* (2002) it is unlikely that the home range of adult seals will exceed the home ranges of juveniles.

The comparatively small distances travelled, observed in the present study, could be due to the local abundance of fish in the area. This abundance is likely to allow harbour seals to forage on what is available close to the haul out sites, and reduce the energetic costs of travelling. The waters around Lofoten Islands, south of Vesterålen, are in fact important spawning and overwintering grounds for Northeast Arctic gadoids (cod, saithe and haddock) and Norwegian spring spawning herring, respectively (Bergstad *et al.* 1987, Bogstad 2008, Holst 2008, Mehl 2008, Aanes 2008). The Vesterålen area, moreover, sustains one of the most abundant colonies of harbour seals in Norway. This strongly indicates that not only the availability of suitable haul out sites but also relatively high food abundance is to be found there.

Strong individual preferences in spatial usage were observed in the present study. This is even more interesting considering that the tagged seals are of similar age and sex. Stronger differences are to be expected between sexes and especially between age classes (Lowry *et al.* 2001). Individual preference and site fidelity for feeding areas were reported in several other studies on harbour seals (Thompson *et al.* 1990, Bjørge *et al.* 1995, Lowry *et al.* 2001).

The habitat preference of the seals is likely to be slightly positively biased in the area around Stø. The simultaneous presence of all five seals in the area can partly be explained by this being the release location (and possibly the moulting area). Habitat use plots, moreover, show pooled data for all seals and the pixel values in the maps are based on the number of dives performed by any of the seal in each 100x100 m root (Fig. 11). This method does not take into account the difference in amount of records per individual. Some seals had in facts comparable recording periods but relatively different amounts of data received.

During analysis and plotting this was not corrected for, leading to possible biases of the pooled habitat preference estimates.

Differences between individuals in average diving maximum depths and duration (Fig. 6) can be explained by individual differences in feeding grounds. Generally, such differences could also be due to age and sex. It has been found that diving capacity in air-breathing diving vertebrates (marine mammals, birds and turtles) is proportional to body mass (Schreer *et al.* 1997), making thus deeper areas available to older individuals. Such differences are not present between the individuals tagged in the present study, making the choice of feeding areas probably due only to individual preferences. Based on the previous considerations, the average dive duration and maximum depth found in the present study cannot be considered representative for the population, having been able to tag only juvenile females.

Differences in average maximum dive depth and duration have been tested with parametric tests. Due to the nature of the distribution of the data around the means, which was not normal, non parametric tests would have been more appropriate.

In the attempt to understand from the telemetric results the feeding behaviour of a seal, dive maximum depth did not prove to be the most descriptive variable. The majority of the dives performed by the tagged seals in this study reached the sea bottom (compare Tab.3 and Tab.7). This is understandable considering that average bottom depth while diving ranged between 20-30 m, which is relatively shallow compared to the potential diving depths of harbour seals (see Bjørge *et al.* 1995 for comparison). It was assumed however that some pelagic feeding might have occurred. Herring, a pelagic shoaling fish, was in fact present in the diet results.

The depth range at which a seal spends most of the time during dive (called focal depth) might be more informative in an analysis of feeding behaviour. Change in diving focal depth with time of the day was found in some phocid species, which are assumed to follow the diel vertical migration of some preys of interest (Hindell *et al.* 1991, Folkow *et al.* 1999). This has not been reported in

harbour seal (Frost *et al.* 2001). This species, on the contrary, adjusts feeding times (rather than depths) in relation to diel and tidal cycles (Thompson *et al.* 1989, Thompson *et al.* 1991, Frost *et al.* 2001).

To better understand the depth ranges, and thus the prey species, that harbour seals target, it is important to take into consideration both the focal depth and the temporal scale at which the dives are performed. The data obtained from the GPS phone tags give this possibility and that should be taken into account for future analyses on these data.

Another interesting result of the tags' deployment was the potential interaction of harbour seals with human activities. Seal-685 repeatedly visited the entrance of the harbour of Myre, a small fishing village on Langøy Island. The area probably hosts a local abundance of fish which could be feeding on the discards from small fishing vessels. It is possible that the seal was feeding on this fish or on the discards themselves (of which, although, no observation was reported).

4.2 Harbour seal diet

Studies of harbour seal diet in Northern Europe (Härkönen 1987, Tollit *et al.* 1996, Brown *et al.* 1998, Berg *et al.* 2002, Pierce *et al.* 2003, Andersen *et al.* 2004) indicate that this species is mainly piscivorous, even if crustaceans, cephalopods or molluscs have been reported in some areas (Tollit *et al.* 1996, Pierce *et al.* 2003).

In the present study only otoliths from scat samples were analyzed, while other hard remains were considered of little importance or possibly secondary prey remains from fish stomachs (Pierce *et al.* 1991). The pooling of some preys into higher taxons groups was due to the high degree of otolith erosion, resulting in uncertainty in the identification of a significant part of the samples. This pooling might have in some cases masked the seals preference for some species inside a group. Moreover, estimates of species that are represented by a low number of otoliths are likely to be less accurate than the ones that are represented by large numbers of otoliths (Pierce *et al.* 1991). Therefore, the importance of less

frequent and large species, such as the wolffish found in the diet, cannot be correctly estimated.

Results from the analysis of scats may refer to feeding events that occurred up to several days before collection. The scats themselves could be older than the sampling day, since the majority of them was collected above the intertidal zone, and each sample can potentially include the remains accumulated from several meals (Pierce *et al.* 1991).

The results suggested that gadoids dominated the diet composition. Results from Olsen *et al.* (1995) also suggested codfish to be dominant in the diet of harbour seals in southern (Oslo) and mid (Froan) Norway. Herring, a pelagic species, was also found in the diet, but its contribution is probably dependent on the time of the year.

The low number of samples collected and the restricted spatio-temporal span of the diet data analyzed in this study, however, can only provide an indication of this population's diet in a particular time of the year and restricted location. Seasonal differences in diet have been found in most of the studies on harbour seal diet (Härkönen 1987, Pierce *et al.* 1991, Tollit *et al.* 1996, Tollit *et al.* 1997a, Brown *et al.* 1998, Hall *et al.* 1998). Differences were also found by comparing two habitat types (rocky against sandy) in the Skagerrak-Kattegat area by Härkönen (1987). Seasonal variation on the importance of pelagic feeding was also observed and attributed both to prey availability and energetic content of the preys (Pierce *et al.* 1991, Tollit *et al.* 1996, Tollit *et al.* 1997a). All these studies indicate strong dependency of diet composition on the area and the time of the year, making generalizations and comparisons difficult.

Berg *et al.* (2002) studied the feeding ecology of harbour seal by analyzing stomach contents and scats in the same area as the present study. These authors concluded that gadoids, and particularly saithe, were by far the most important prey group. In the present study, a proportion of saithe higher than other gadoid species was found (Fig.12). There was, however, considerable uncertainty in the partitioning of gadoids between the different species, due to the high degree of digestion of the otoliths.

The diet results obtained in the present study were corrected with digestion coefficients and numerical correction factors in order to account for otolith erosion and re-estimate the prey species' relative proportions in diet. The factors used were developed for grey seals (Grellier *et al.* 2006). Tollit (1997b) made a similar experiment on harbour seals, but did not provide coefficients for several of the species found in the scat samples from the present study. In addition, Tollit (1997b) used a carrier species (herring) to present different otoliths to the captive seals. This was proved to be a large source of bias in the coefficient calculation, since erosion by gastric acids is much stronger when the otolith is put in the flesh and not protected by the head skull of the fish (Grellier *et al.* 2005). Berg *et al.* (2002) fed whole fish to harbour seals to avoid this source of error, but calculated numerical correction factors only for cod, haddock, and herring. We therefore decided to use Grellier *et al.* (2006) in order to be able to correct our values and maintain, at the same time, the most of the prey groups found in the analysis.

In a study on hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*), Christiansen *et al.* (2004) found that the digestive process was strongly influenced by the stomach's temperature and acidity ranges; the authors also suggested that temperature and acidity in phocids probably depend on diet composition. The diet of harbour seal is similar to the one of the grey seal both in species composition and size range of prey in northern Norway (Tuominen 2005), which may indicate that digestion rates of grey seals are comparable to the ones of harbour seals.

However, a comparison among the correction factors available for harbour and grey seals from different sources (Tollit *et al.* 1997b, Berg *et al.* 2002, Grellier *et al.* 2006) is strongly suggested for future work, in order to minimize biases in diet composition estimates due to methodological errors.

4.3 Resource abundance and distribution

In this study, the resource maps shown are a time point estimate of the real biomass and spatial distribution of fish at sea. This has to be taken in consideration when examining the resource distribution in space and comparing it,

for example, with the telemetric data (Fig. 13). Distances between the extremities of the study area could be swum in a day by fish schools (Erik Berg, Institute of Marine Research, Tromsø, Norway, pers. comm.), which means that their position at the time of sampling is not necessarily representative for the period.

The distribution of codfish in the area was found to overlap consistently with the one of herring, suggesting that codfish species prey on herring (as observed in Michalsen *et al.* 2008).

The resource surveys revealed considerable seasonal differences in prey biomass estimates (Fig. 13). This was unexpected, considering that the waters around Lofoten and Vesterålen are a important spawning and wintering grounds for Northeast Arctic gadoids and Norwegian spring spawning herring, respectively (Bogstad 2008, Holst 2008, Mehl 2008, Aanes 2008). Spawning starts at the end of the winter and a relative increase in biomass would be expected, due to the southward massive migration of fish from the Barents Sea to the spawning grounds along the Norwegian coast. However, the study area has a limited extension and lays slightly north of the hotspot area for spawning. It is therefore possible that the concentrating effect of spawning, which probably happens slightly outside the study area, leaded to a strong decrease in biomass inside the study area.

4.4 Prey preference

Due to difficult weather conditions during acoustic and scat sampling, the diet and resource samples were not temporally synoptic. As a result, the mean of the biomass estimates of the two acoustic surveys was used when calculating prey preference.

For this calculation, it was assumed that the scats used in estimating diet composition were the results of foraging in the area covered by acoustic sampling. This assumption was not robust and could have introduced some error. The telemetry results show in fact that the areas used by the tagged harbour seals are all shallower and closer to the coast than the resource sampling cruises (Fig. 13).

Making inferences on fish species composition in these areas, based on samplings in deeper waters, could have introduced bias.

The results indicate no strong preference for any of the prey groups analyzed (Fig. 14). Even if the CI for herring did not overlap zero, this result does not indicate a clear preference in comparison to the other species. It should be noticed, moreover, that the uncertainty in the resource abundance was not included in the CIs' estimates. Only the variability in diet was considered, resulting in potential underestimation of the CIs.

On the contrary, since the survey was not designed for 'swept area' assessment, the relatively few trawling performed in areas of denser echo registrations are likely to have overestimated the abundance of flatfish.

Results from the comparison of the length distributions of codfish, sampled in acoustic surveys and in scats, suggested that harbour seals might be size selective (Fig. 15). Similarly to previous years (Berg *et al.* 2002), harbour seals in the study area apparently exploited more intensively small preys. In the diet results in fact all herring was smaller than 35 cm and 90% of the gadoids were smaller than 30 cm (median 14 cm, see Fig. 15). Uncorrected otolith lengths were used to estimate fish lengths for herring, since the corrected values were leading to improbable high size ranges for this small species. Such bias might have been caused by the use of correction coefficients that do not take into account the degree of otolith digestion (Grellier *et al.* 2006).

Preference results are dependent on the relative frequencies of the fish species at sea; therefore, if the biomass of young age classes of codfish is proportional to the one of mature individuals, than results indicate no preference in the species groups analyzed. Data on resource distribution and availability, however, are still not accurate enough to make such an assumption. Although harbour seals are generally regarded as opportunistic feeders, taking prey according to local abundance (Olsen *et al.* 1995, Tollit *et al.* 1997a), this still remains to be tested for the study area. Use of additional resource sampling techniques, which allow sampling of smaller individuals at shallow depths (i.e. gillnets, beach seine), should be considered for future investigation on the subject.

The size range found for codfish species in the present study corresponds to juvenile age classes (age groups 0-2 in Bergstad *et al.* 1987). Generally, codfish species in the younger life stages are found in shallow waters (Godø *et al.* 1989). Norwegian costal cod, for example, is known to settle in waters shallower than 20 m and remain there during the first two years of life (Berg 2008). Following these considerations, the high abundance of small size classes of codfish in the diet, accordingly to the relatively small range travelled by the tagged seals, suggest that the harbour seal population of the Vesterålen area might rely on food sources that are abundant in the vicinity of haul out sites.

5. CONCLUSIONS

The deployment of GPS phone tags was a successful method to gather information on distribution and feeding behaviour of harbour seals in the study area.

The results of this study tend to indicate that diet composition in harbour seals is influenced by the relative abundance of prey species at sea, i.e. harbour seals have no prey preference at the species level. Age/size class of the prey appeared to be a criterion in prey selection rather than prey species.

The tagged seals foraged close to the coast and at relatively shallow depths. The local abundance of fish in the area is likely to allow harbour seals to forage on what is available close to the haul out sites. Targeting of small size classes might therefore be a consequence of habitat selection based on accessibility rather than prey selection.

Habitat use differed between individuals in the present study. This implies that potential individual differences in diet composition could arise, due to different choices of feeding grounds combined with site fidelity.

Analysis of diet composition at the population level indicated that gadoids dominated the diet. Herring, a pelagic species, was also found in the diet, but its contribution is probably dependent on the time of the year.

6. POSSIBLE FUTURE WORK

The analysis of diet composition by scat sampling coupled to resource abundance surveys is a powerful method to investigate feeding ecology in pinnipeds. However, the telemetric results of the present study, combined with observations on size composition in harbour seal diet, strongly indicated that resource sampling, for preference estimation, had to target different areas and size ranges of prey. Different methodologies are available to concentrate the sampling effort on fish species of smaller size in shallow waters. The use of gillnets or beach seine is therefore suggested to estimate the species composition and relative abundance of potential harbour seals preys in shallow waters.

Moreover, the combination of detailed resource samplings with the deployment of a new model of GPS phone tags, which allow measurements of acceleration bursts, will give the possibility to study in more detail the feeding behaviour of costal pinnipeds.

The integration of different sources of information, like GPS-positioning, feeding dive classification, determination of diving focal depth, and resource estimation for the different depth strata, could allow inferences on diet composition.

Such estimation, by use of telemetric methods, could give a spatial perspective to studies of seals diet and allow testing the relative importance of habitat and prey selection on food consumption.

7. AKNOWLEDGEMENTS

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TABLES

Table 1 Details on the individuals and on the tagging procedure for the five tagged seals (F=females).

Indiv. nr	Catch date	Catch time	Sex	Body mass (kg)	Length (cm)	Zoletil dose (ml)	Release time
gp10-641-07	30.08.2007	09:35	F	23	86	0.18	11:30
gp10-655-07	30.08.2007	11:40	F	22	92	0.22	13:30
gp10-683-07	30.08.2007	11:40	F	22	90	0.22	13:50
gp10-684-07	30.08.2007	20:20	F	32	108	0.32	22:00
gp10-685-07	31.08.2007	19:45	F	20	90	0.21	21:37

Table 2 Telemetry data collection period and lifetime of the tags.

Indiv. nr	Collection period		Lifetime
	from	to	(days)
gp10-641-07	30.08.07	16.12.07	108
gp10-655-07	30.08.07	07.12.07	99
gp10-683-07	30.08.07	14.03.08	197
gp10-684-07	30.08.07	04.03.08	187
gp10-685-07	31.08.07	10.02.08	163

Table 3 The dive classes and their assumed behavioural interpretation with the relative frequency of occurrence, average maximum depth (m) and average duration (sec) for each class.

Class name	Class code	Behavioural interpretation	Class freq. %	Average max depth	Average duration
drift dives	DR	drifting	4.02	11	132
left root dives	LR	unknown	1.49	25	87
right root dives	RR	unknown	0.50	20	67
square dives	SQ	feeding at bottom	31.10	24	136
u dives	U	searching or travelling	25.69	25	109
v dives	V	searching	9.64	31	92
wiggled dives	W	feeding in the water column	27.57	23	107

Table 4 Scat sampling dates and number of samples collected; the samples were discarded when no hard remain useful for identification was found.

Collection date	Nr. available samples	Nr. discarded samples
30.06.07	11	11
01.09.07	28	6
22.10.07	5	1

Table 5 Acoustic surveys and trawling stations details. The station numbers are plotted in figure 1.

	Survey period		Effort	Trawling stations		
	from	to	(nm)	nr	type	depth (m)
summer 2007	25.06.07	27.06.07	99	1	pelagic	30
				2	demersal	125
				3	demersal	112
				4	demersal	135
				5	pelagic	30
winter 2007/2008	29.01.08	31.01.08	119	6	demersal	132
				7	demersal	108
				8	demersal	201

Table 6 Number of telemetry records per individual in the dataset downloaded on the 24th March 2008; the filtered datasets were the output of a filtering procedure to eliminate the records with uncertain GPS positioning.

Indiv. nr	Dive data	GPS data	Haul out data	Summary data	Dive data filtered	Haul out data filtered
gp10-641-07	17344	1870	110	1212	681	13
gp10-655-07	30838	3605	107	876	29841	17
gp10-683-07	0	5548	138	2352	0	11
gp10-684-07	48350	5933	220	2340	46975	30
gp10-685-07	40487	7290	219	1884	39654	29
SUM	137019	24246	794	8664	117151	100

Table 7 Statistics of sea-bottom depth (m) and slope (degrees). The depth and slope of the sea-bottom were calculated at the position of each dive record and the statistic of these values is presented for each dive class.

Class name	Max depth	Mean depth	Max slope	Mean slope
drift dives	158	14	43	5
left square root dives	165	24	48	8
right square root dives	102	24	45	8
square dives	167	23	52	6
u dives	184	25	52	6
v dives	168	28	52	7
w dives	184	23	52	6

Table 8 Diet composition calculated from scats sampled in autumn 2007. The biomass (kg) is presented both as values uncorrected and corrected for otolith erosion following Grellier et al. (2006), codfish is presented both at the species level and as a group.

Fish species	Latin name	Uncorrected biomass	Corrected biomass
TOT. CODFISH	(gadidae)	5.06	37.12
saithe	*Pollachius virens*	2.28	18.91
haddock	*Melanogrammus aeglefinus*	1.54	8.00
wolffish	*Anarhichas sp.*	1.40	NA
herring	*Clupea harengus*	1.25	20.58
unid. codfish	(gadidae)	1.03	8.47
flatfish	(pleuronectidae)	0.65	1.99
cod	*Gadus morhua*	0.22	1.75
sandeel	*Ammodytes sp.*	0.01	0.09

Table 9 Absolute fish abundance estimates (t/nm2) presented as average and maximum values. The values are the results of from the two acoustical surveys (June 2007 and January 2008). Flatfish and wolffish were estimated with a 'swept area' methodology. The biomass of these two groups is probably an overestimate due to sampling methods.

Fish species	Latin name	June 2007		January 2008	
		average	max	average	max
herring	*Clupea harengus*	7.66	246.80	0.01	0.47
sandeel	*Ammodytes sp.*	0.00	0.00	0.00	0.00
codfish	(gadidae)	68.82	326.91	11.07	113.83
redfish	*Sebastes marinus*	0.00	0.00	2.11	30.41
Norway pout	*Trisopterus esmarkii*	4.40	32.68	0.71	4.77
whiting	*Merlangius merlangus*	16.79	64.41	1.55	10.00
flatfish	(pleuronectidae)	1.94	NA	1.60	NA
wolffish	*Anarhichas sp.*	0.00	NA	0.03	NA
SUM		99.61		17.08	

FIGURES
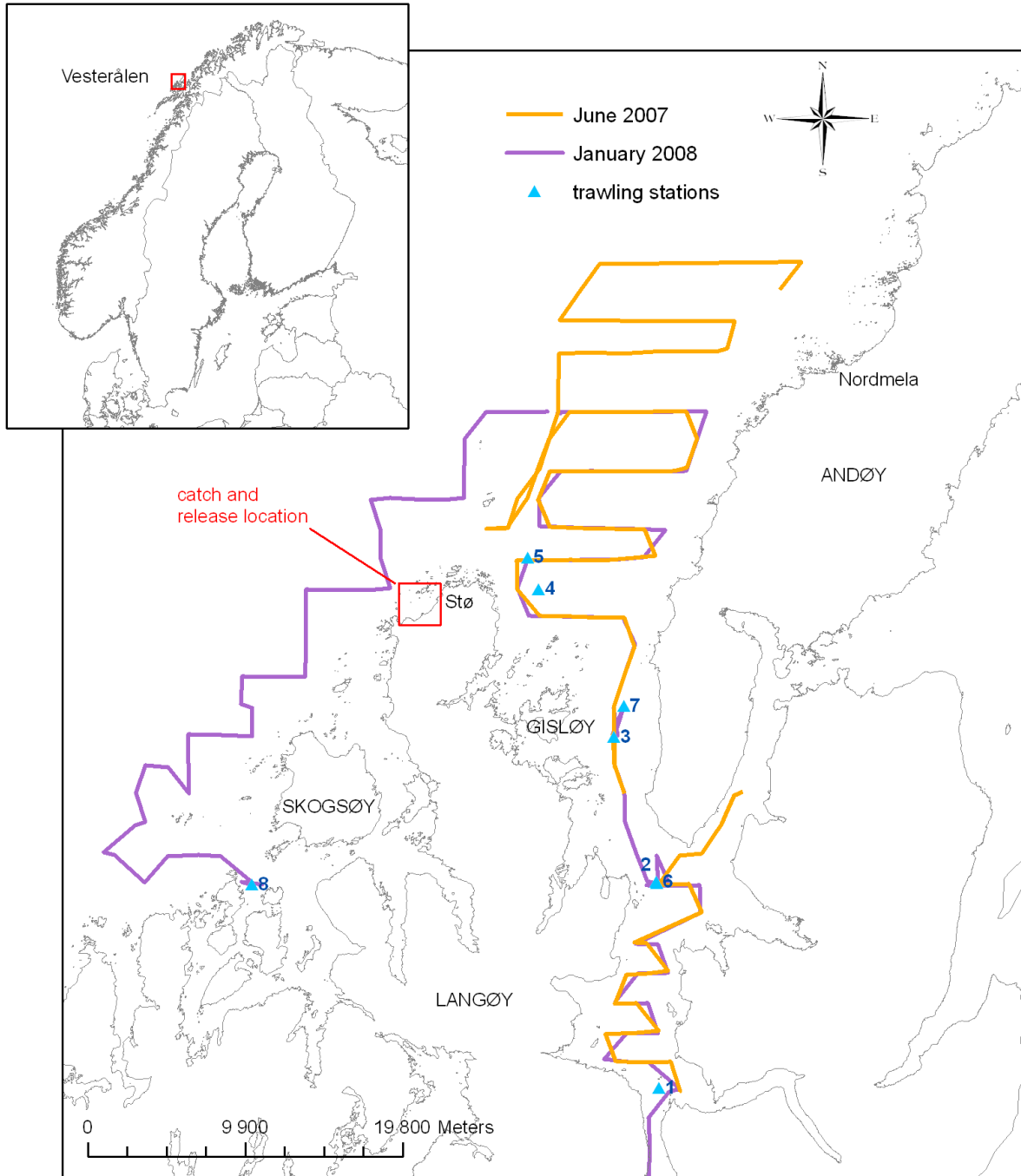
Figure 1 Study area; the lines show the acoustic transects, the triangles the trawling stations (stations 1 and 5 are pelagic trawl). The area in the red square is where both catches and releases of the tagged seals took place.

Figure 2 Tagging procedure: a. Sedating the seal with an intramuscular injection of Zoletil[®] (Virbac), b. Drying the fur in a selected area behind the head, c. Applying the transmitter previously glued to a synthetic net, d. Measuring temperature during gluing, e. Waiting for the animal to restore muscular activity, f. Releasing the tagged seal.
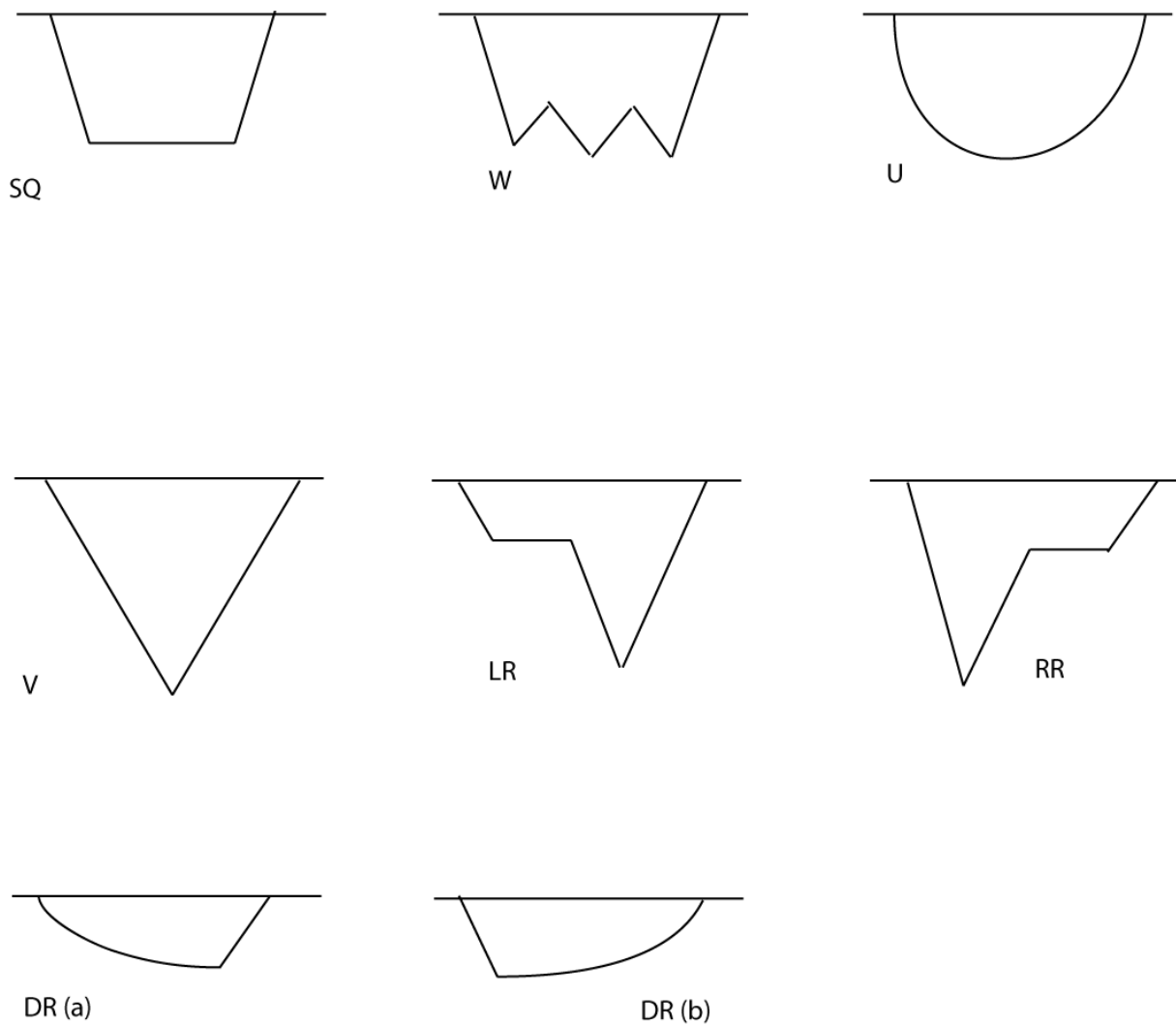
Figure 3 The generalized dive profiles used to visually classify the dives shown on the time (x-axis) vs. depth (y-axis) scale. SQ=square dives, W=wiggled dives, U=u-dives, V=v-dives, LR=left root dive, RR=right root dive, DR=drift dives. Drift dives were originally thought as (a) but a mirror shape (b) was found during classification and assigned to the same bin.
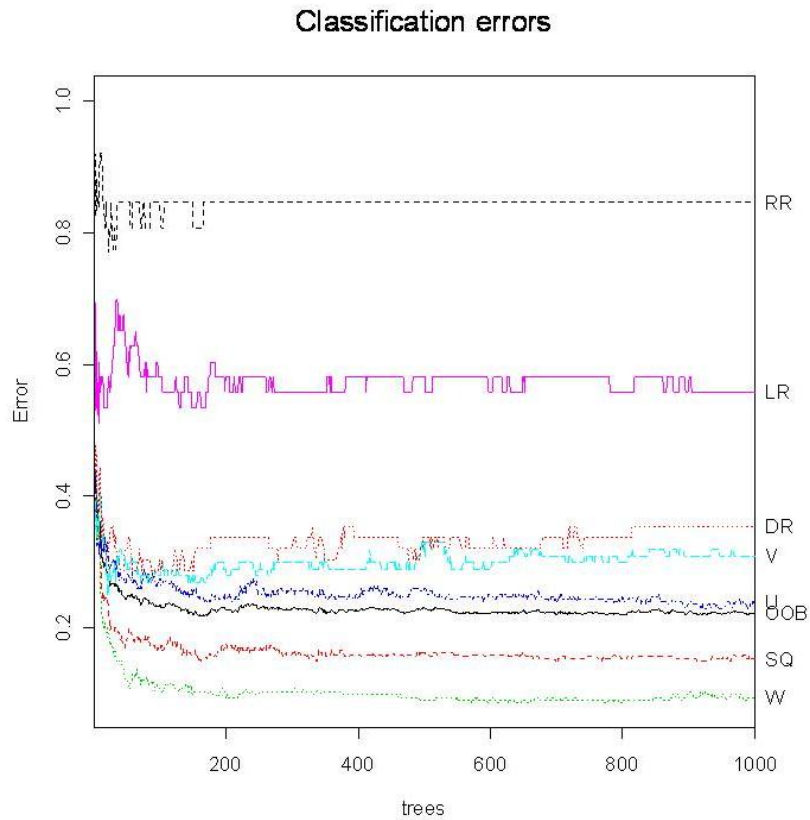
Figure 4 Output error parameter of the classification (y-axis) produces by 'random forest' in R 2.6.2. The value of the error corresponds to the proportion of the 1000 manually classified profiles (on the x-axis, named trees) that were statistically assigned by the program to a class different from the one chosen by the user in the manual classification. The letter codes on the right of each line define the class for which the error (corresponding coloured line) is calculated, OOB is the overall error.
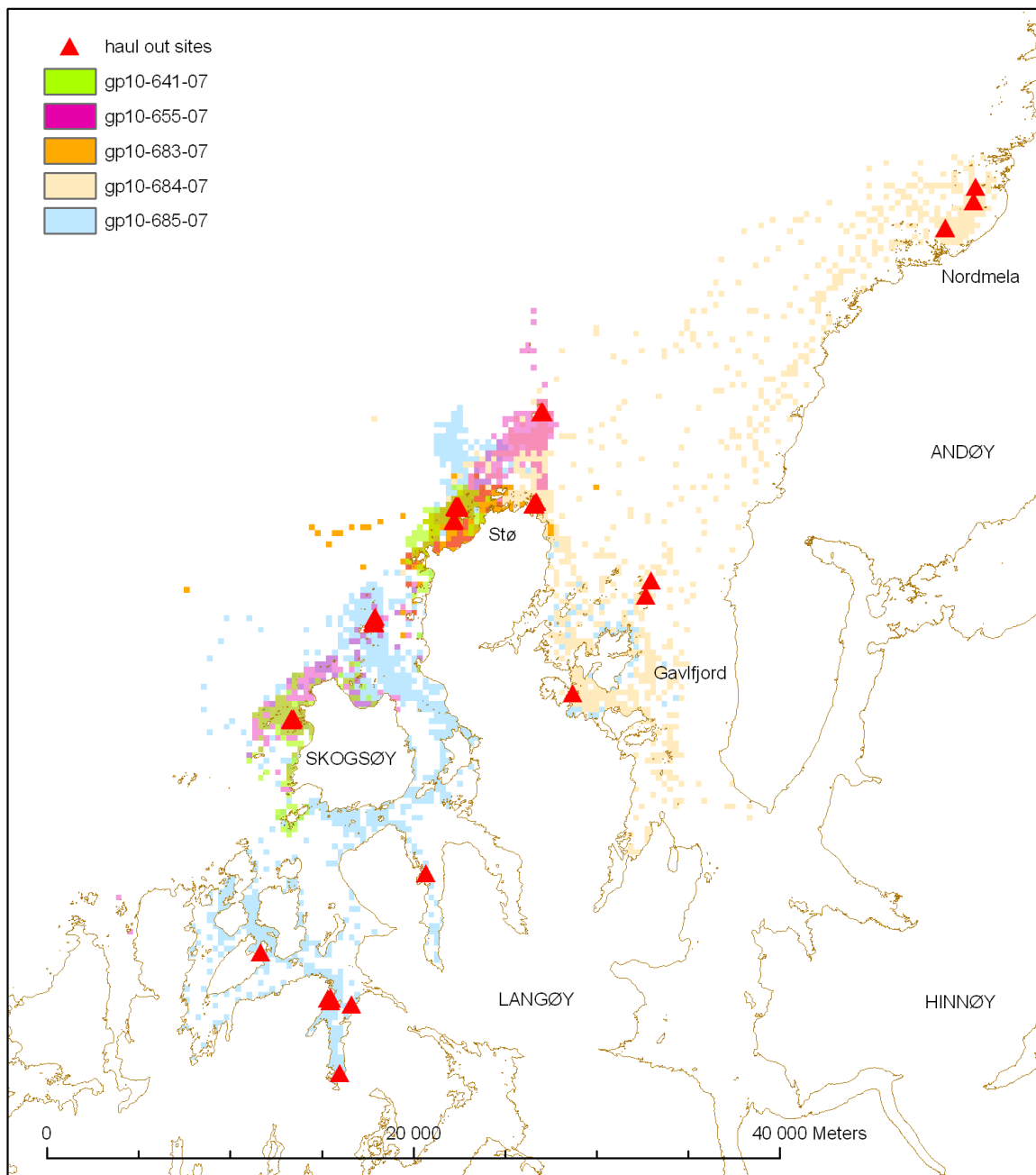
Figure 5 Distribution of the GPS positions received from the 5 tagged animals. The colours identify each individual, the red triangles the haul out sites.
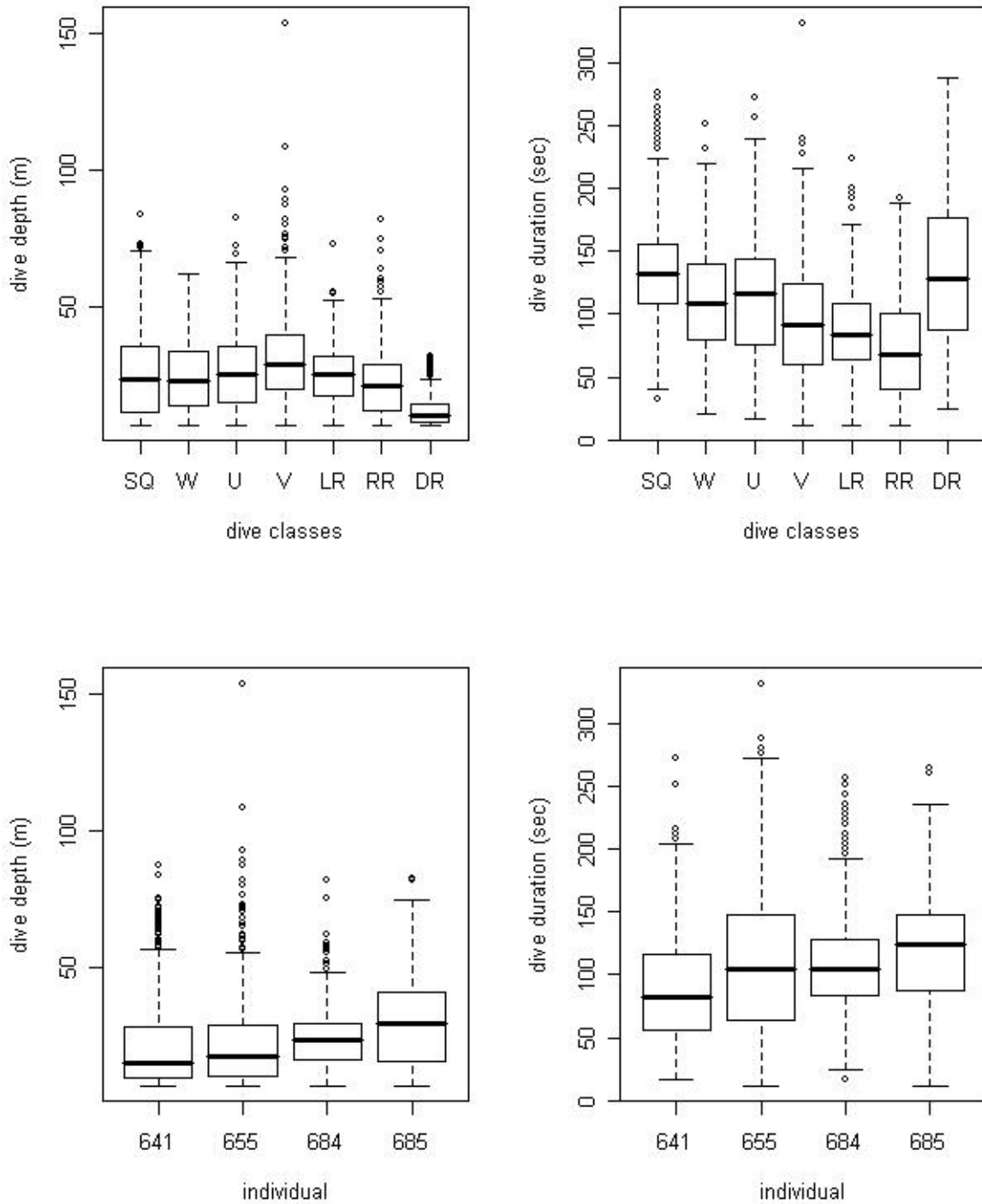
Figure 6 Plot of the mean of maximum depth and duration for each diving category (upper line) and for each individual (lower line) calculated from a random subsample of 100 dives per class per individual (total 2800 records). The box and the line contain 50% and 95% of the observations, respectively.
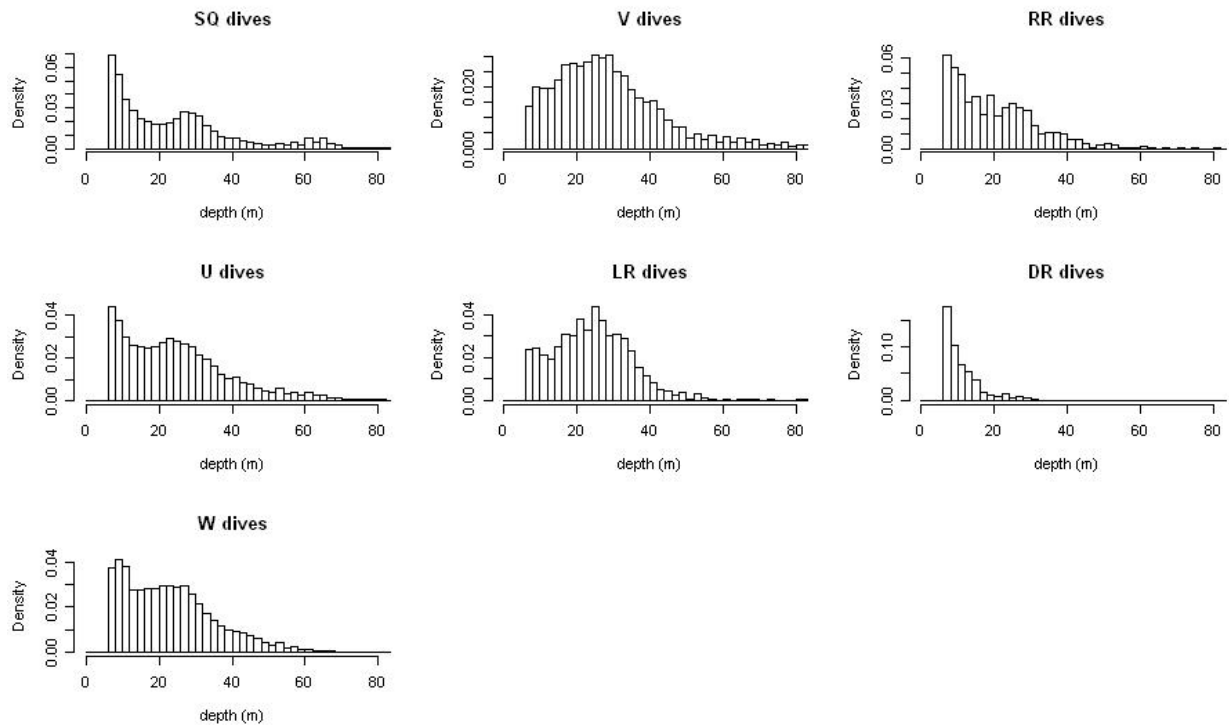
Figure 7 Distribution of diving maximum depths presented for each dive class; the data are pooled for all individuals. Dive classes on the left column have a bimodal distribution peaking both at minimum depths (6 m) and around 25-30 m. The classes in the central column peak at around 25-30 m and the ones on the right at minimum depths (6 m).
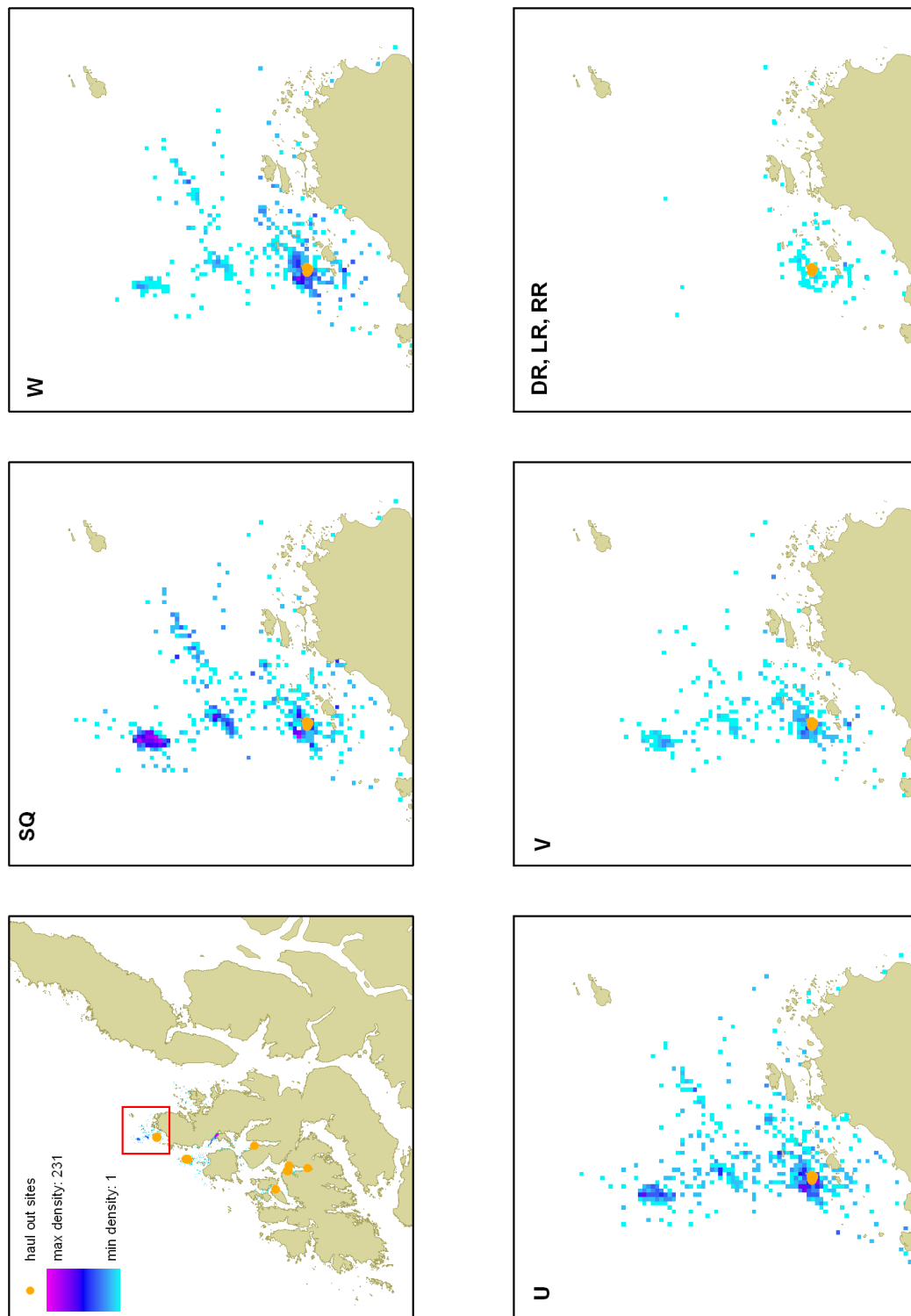
Figure 8 Comparison of the spatial distribution of all dive classes from seal-684 in a selected area north of Stø. The first map shows the area zoomed inside the study area (red square), the other maps show the distribution of the dive classes specified in the higher left corner of each map. DR, LR, RR are found only close to the haul out site.
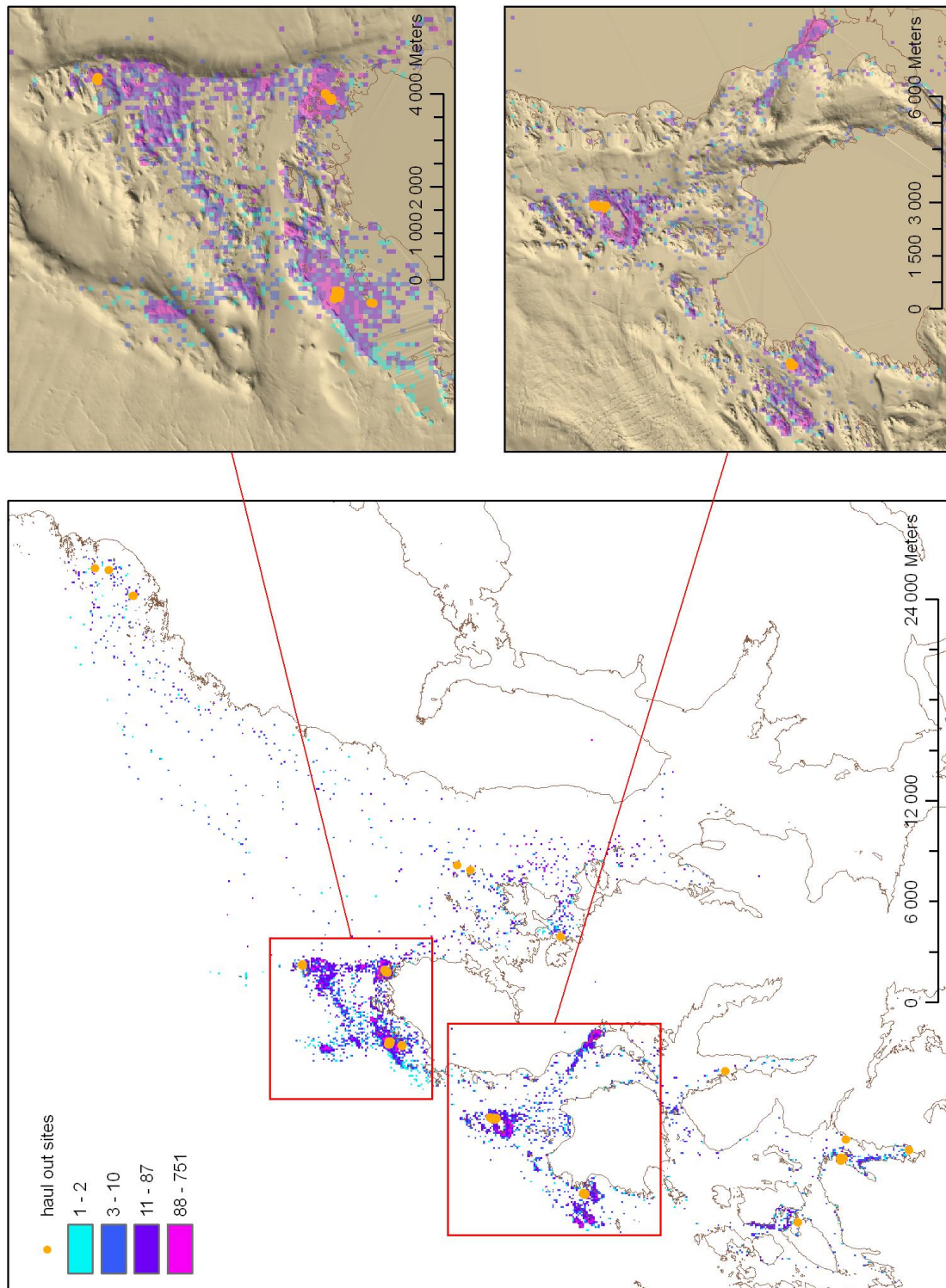
Figure 9 Distribution of the "feeding and searching dives". Two areas are zoomed and presented with bottom topography in order to show the relationship between dive distribution and bathymetry. The data were pooled for all individuals (seal-641, seal-655, seal-684, and seal-685). The values correspond to the number of dives per 100x100 m root.
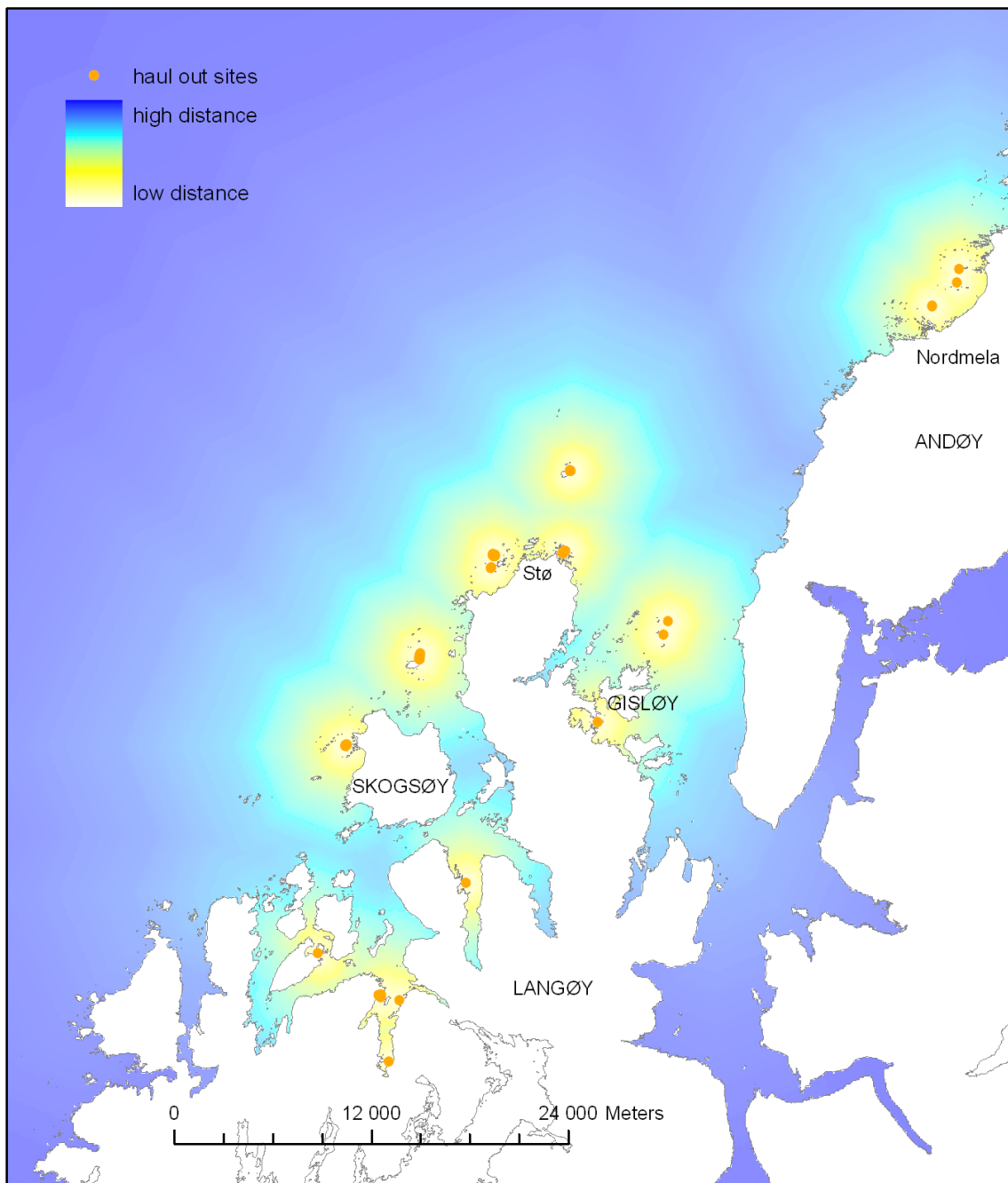
Figure 10 Plot of "cost-distance from the closest haul out site". In this figure, every pixel has a value proportional to the cost of swimming from the closest haul out site to that point going around land. The further the point is positioned the higher its value.
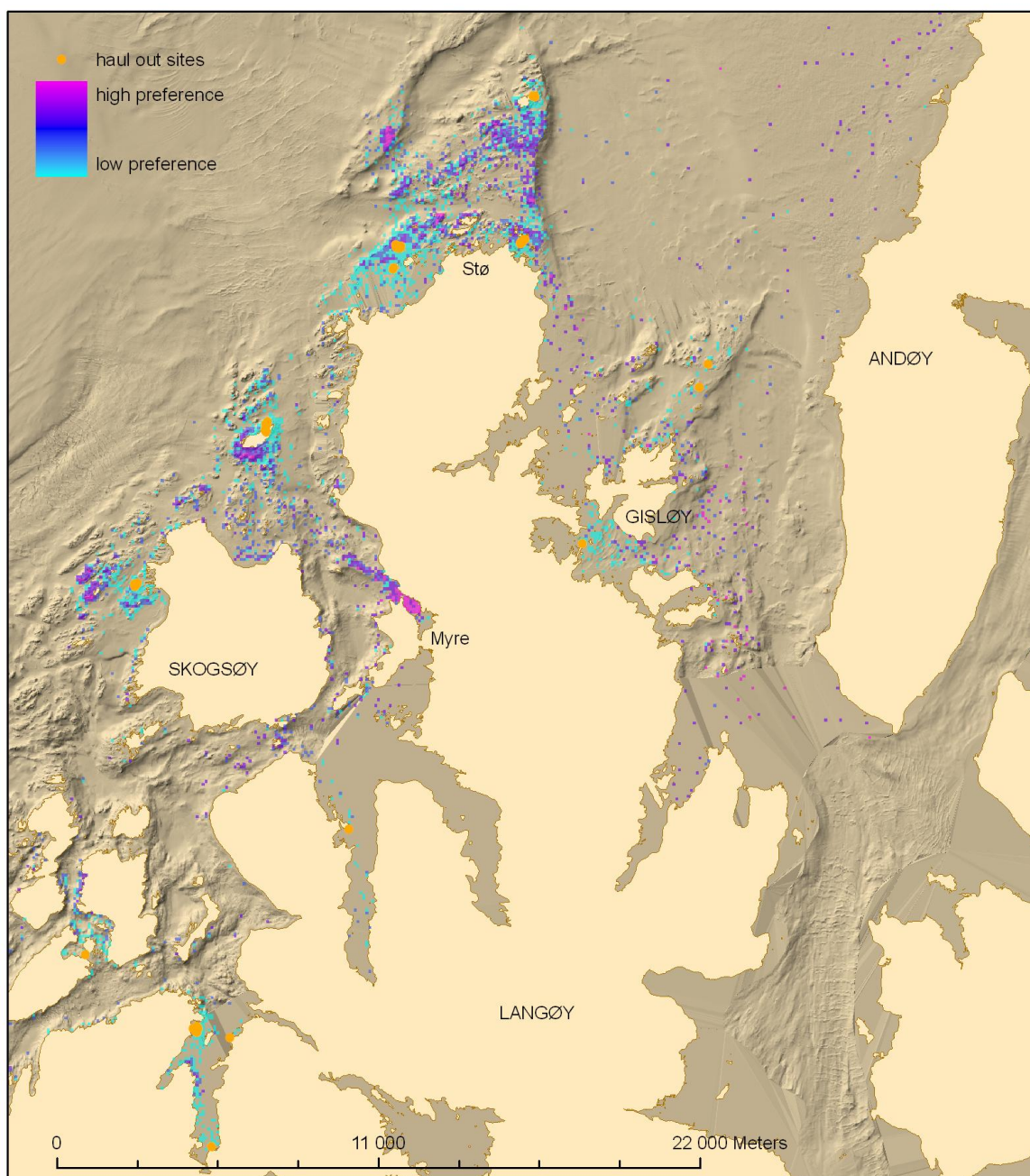
Figure 11 Habitat preference map calculated on the 'feeding dives' distribution times 'cost-distance' from the closest haul out site. The data were pooled for all individuals (seal-641, seal-655, seal-684, and seal-685). Absolute values of preference are not shown in the legend since they have no particular meaning; they are the result of the multiplication of number of dives (per 100x100 m root) times distance (m) from the closest haul out site.
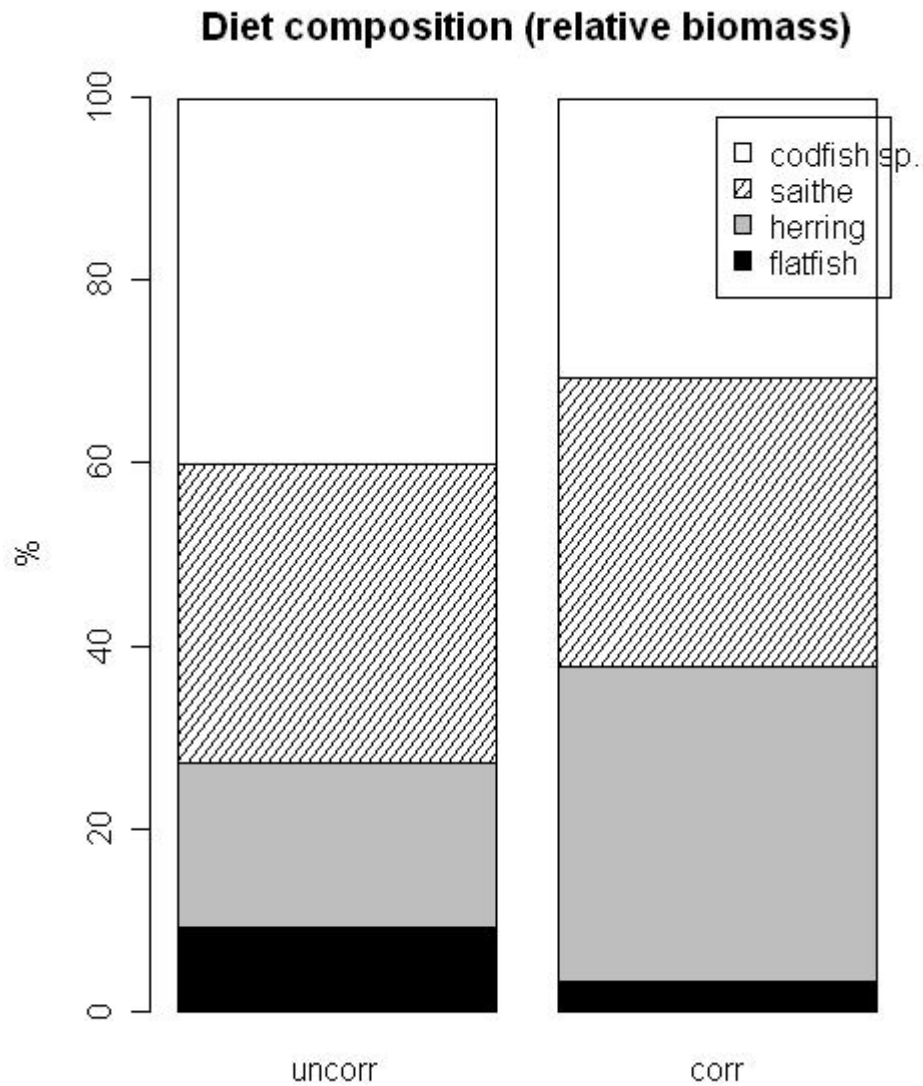
Figure 12 Relative frequencies of selected prey species groups found in harbour seal diet. The codfish sp. group includes identified cod and haddock, and unidentified codfish species. The unidentified codfish group was probably dominated by small eroded saithe otoliths that could not be identified with accuracy. The contribution of saithe in diet composition could therefore be higher than shown. Flatfish was not identified at the species level. Wolffish and sand eel were also found in the diet but not included in the plot, the first was assumed to be an occasional prey and the second contributed with very little biomass.
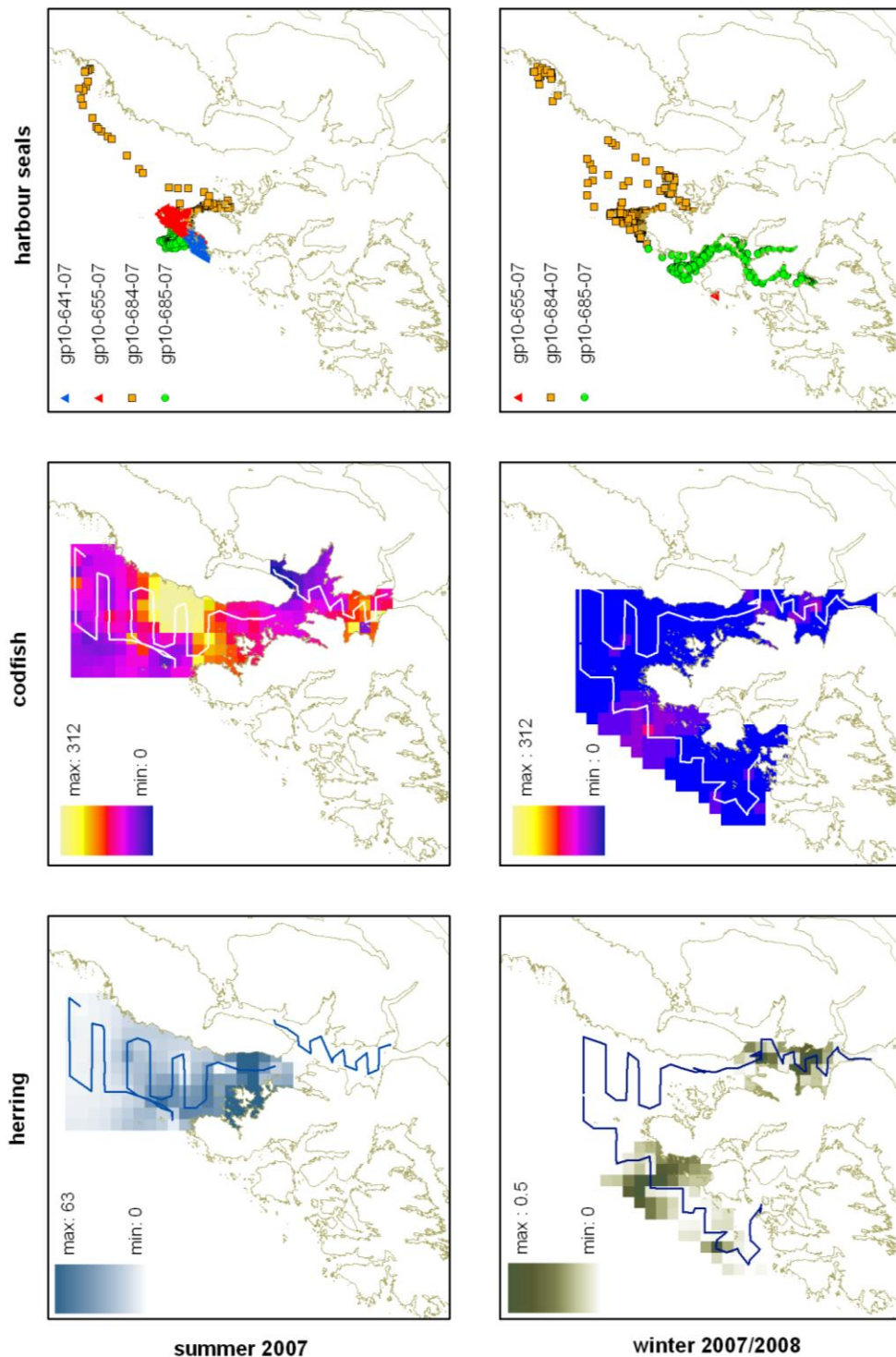
Figure 13 Comparative distributions of herring, codfish and tagged harbour seals in two periods. The resource data are point estimates in time (taken on the 26-27th June 2007 and 29-31st January 2008), while the telemetric data were extracted for a time period (September 2007 and January-February 2008). The colour-range (and this the scale) for the codfish abundance in the two seasons is the same. For herring, two different scales were used due to large differences in abundance between seasons.
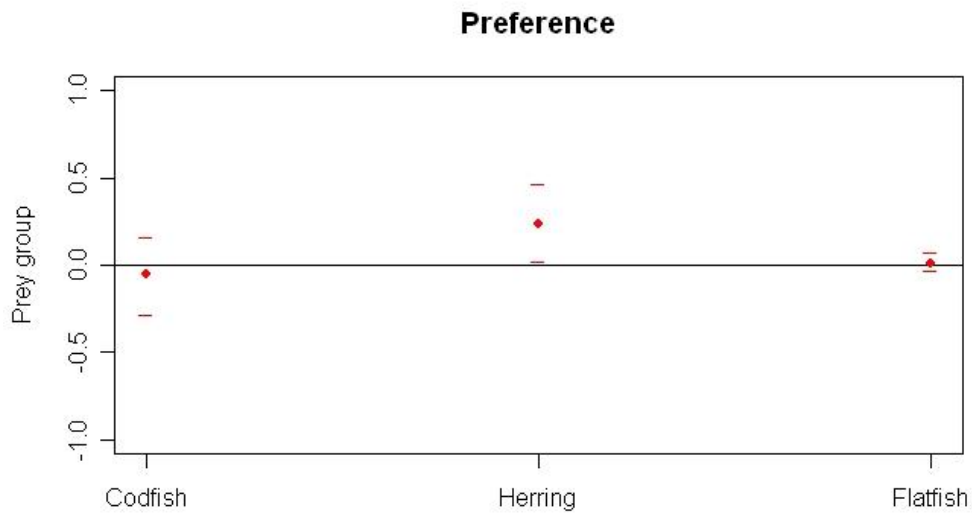
Preference

Figure 14 Plot of prey preference in harbour seals, calculated as the difference (D_i) between the relative importance of prey groups in the diet and in the resources (averaged between June 2007 and January 2008). The dashes represent the 95% CI; if the CI interval overlaps zero (line), no preference is observed. The position of the value and its CI above the line indicates preference, below the line, avoidance. Here a slight preference for herring was observed.
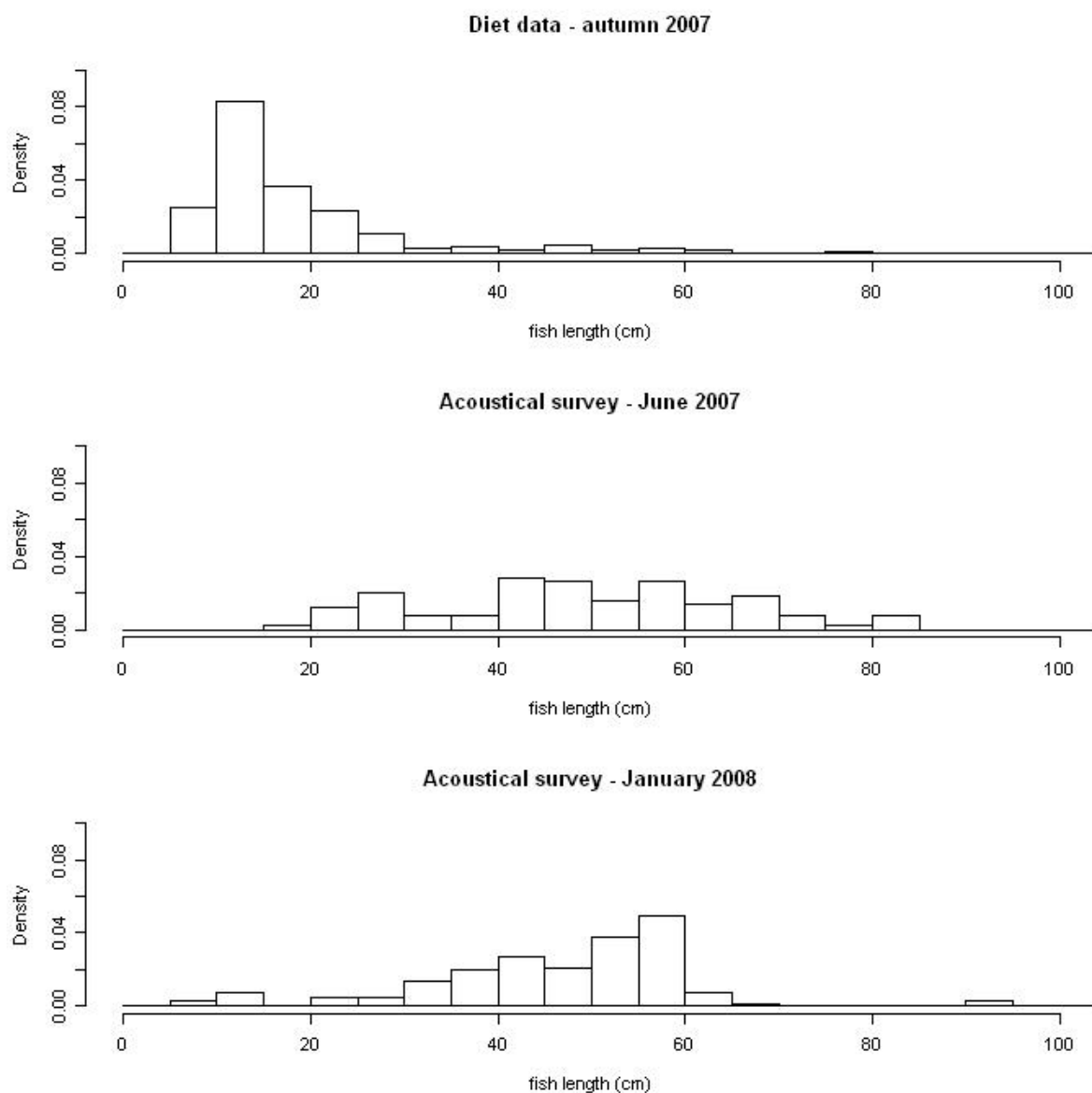
Figure 15 Distributions of fish length (cm) for codfish sp. in diet data and resource samplings. The fish length values in the diet data are estimated from corrected otolith lengths (from Grellier *et al.* 2006).