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Spatial and temporal patterns of foraging of harbour seals (*Phoca vitulina*) in Porsangerfjord
from behavioural interpretation to resource selection

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Virginie Ramasco
A dissertation for the degree of Philosophiae Doctor – May 2015

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SPATIAL AND TEMPORAL PATTERNS OF FORAGING OF HARBOUR SEALS (*PHOCA VITULINA*) IN PORSANGERFJORD

FROM BEHAVIOURAL INTERPRETATION TO RESOURCE SELECTION

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This PhD thesis is dedicated to many, known and unknown:

to my family
who has been incessantly questioning when I would finally be finished with my
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the first person with whom I shared pure love for curiosity

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'If you want to be a dolphin- or a seal-hugger, do your maths'
– Dr. Sophie Bestley

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LIST OF PAPERS

PAPER I Ramasco V, Biuw M, & Nilssen KT. (2014). Improving time budget estimates through the behavioural interpretation of dive bouts in harbour seals. *Animal Behaviour*, *94*, 117–134.

PAPER II Ramasco V, Barraquand F, Biuw M, Mcconnell B, & Nilssen KT. (2015). The intensity of horizontal and vertical search in a diving forager: the harbour seal. *Movement Ecology* 3:15*.

PAPER III Ramasco V, Lindström U, & Nilssen KT. The dynamics of resource selection of harbour seals in a subarctic fjord ecosystem. *Manuscript intended for Marine Ecology Progress Series.*

GENERAL SUMMARY

The coastal cod stock of the Porsangerfjord has drastically declined in the 80's and never fully recovered since. A population of harbour seals, known to be resident in the fjord all year round, has been hypothesised to act as predator-pit for cod in the area, affecting its lack of recovery. In order to understand the role of these seals in this local marine ecosystem, their foraging behaviour was investigated by assessing the presence of preference for certain prey and the behavioural response to the seasonal dynamics of prey distribution in the fjord. The movement patterns of individual harbour seals (n = 15) were followed between 2009 and 2013. The data obtained (*i.e.* GPS location, time-depth dive profiles, etc.) were first thoroughly analysed to provide a robust interpretation of the behavioural patterns of activities of the single individuals and identify the methodological caveats in the detection of foraging behaviour. Among the major results, two types of resting behaviour at sea were described, in the form of prolonged periods at surface but also as resting dives, a behaviour never documented before for this species. The patterns of activity suggested that harbour seals mainly forage during daylight in autumn and spring in this area.

The foraging locations identified were then compared to the availability of potential prey in the fjord (*i.e.* herring, capelin, small and large codfish and sculpins). The availability of prey was assumed to be dependent on their biomass densities, their distance from the seals' haulout sites and the accessibility of the areas where prey was located. The latter could be restricted for example by the presence of sea ice in winter and spring. Results on the analyses of prey selection suggested that harbour seals in Porsangerfjord had a preference for small size fish (< 25cm). Small codfish was preferred during autumn, but a response to the presence of pelagic fish was seen when the latter aggregated to overwinter in cold deep waters in the inner parts of the fjord. The formation of ice in these areas during the winter season, however, provoked a shift in preference to small codfish, due to the sudden inaccessibility of the pelagic fish. A strong reversed trend was observed in late spring when the ice melted and pelagic fish was preferred again. The results suggest the preference for small aggregated fish close to the haulout areas. The impact of harbour seals on the cod population of Porsangerfjord can be therefore hypothesized to change across seasons and to be lowered by the availability of highly aggregated pelagic fish during winter and spring.

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1. Introduction

1.1.   The Porsangerfjord: a coastal ecosystem under change

The structure and productivity of the marine coastal ecosystems of the Finnmark county, northern Norway, have been affected by several environmental, biological and anthropogenic factors in the last decades. Global warming has contributed to a general northward movement of Atlantic species and affected abundances, distributions and community compositions in the Barents Sea, and consequently in the adjacent marine coastal systems (Drinkwater *et al.* 2011). The northern Norwegian fjords have additionally experienced in recent times a sequence of large scale invasions. These were the slow but constant westward movement of the invasive red king crab population from Russian waters (*Paralithodes camtschaticus,* Falk-Petersen *et al.* 2011), and the short term harp seal (*Pagophilus groenlandicus*) invasions in years of low capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) abundance in the Barents Sea (Haug & Nilssen 1995). These coastal ecosystems have been affected, not only by such large scale changes, but also by local factors, in particular fishing pressure, which in some cases has had a large impact on economically important fish stocks (ICES 2013).

The Porsangerfjord, which is located between 70° and 71°N, is one of the largest fjords in Norway (approximately 20 km wide and 100 km long) and opens to the north towards the Barents Sea. The Barents Sea is a productive ecosystem, which serves as feeding grounds for many boreal fish species (*e.g.* the three major codfish stocks, cod, *Gadus morhua*, haddock, *Melanogrammus aeglefinus,* and saithe, *Pollachius virens*), as an important nursery area for Norwegian spring-spawning herring (*Clupea harengus*) and as the main habitat for the Barents Sea capelin stock (Dragesund, Johannessen & Ulltang 1997; Gjøsæter *et al.* 1998). Many of those fish species range over large distances and move between oceanic and coastal waters at different seasons and life stages and therefore enter the coastal systems at certain times of the year. Juvenile herring moves towards the Finnmark coast to overwinter (Dragesund, Johannessen & Ulltang 1997) and capelin to spawn in spring (Jakobsen & Ozhigin 2011); codfish, which mostly spawns below 68-69°N, is rather abundant in the Barents Sea mainly during the feeding season (*i.e.* summer and autumn, Bergstad et al. 1987). In addition to long ranging species, these fjords also host several local fish stocks, such as coastal cod and local capelin stocks (Jakobsen 1987).

Porsangerfjord, in particular, has sustained a coastal cod fishery for decades. However in the 80's a large cod depletion was registered as a consequence of the combined effect of high fishing pressure and harp seal invasions (Nilssen, Grotnes

& Haug 1992; ICES 2013). These trends were registered in most of the fjords along the coast of northern Norway. In most of these areas the coastal cod populations recovered (Pedersen & Pope 2003), but this did not happen in Porsangerfjord. Different hypotheses for the lack of recovery have been put forward. The degradation of the kelp forest (*Laminaria hyperborea*), due to the grazing of an increasing sea urchin population (*Strongylocentrotus droebachiensis,* Norderhaug & Christie 2009), has been hypothesized to negatively affect cod recruitment, because the kelp forest serves as an important nursery habitat for cod. At the same time, the presence of a population of harbour seals (*Phoca vitulina*), resident in the fjord all year round, has been hypothesized to function as a predator-pit, preventing the cod population from recovering (Bakun 2006).

To understand the mechanisms that have affected the marine ecosystem of Porsangerfjord and that still are influencing its current and possibly its future states, an interdisciplinary research project was started (EPIGRAPH, www.imr.no/epigraph). Several components of the ecosystem were investigated simultaneously, such as macroalgal coverage, benthic fauna diversity and production, red king crab migration patterns, fish distribution, the physical oceanography and consequently the larval distribution of species spawning in the fjord, and the potential effect of top predators such as the harbour seal. The final aim of a multitude of synchronous studies on the different system components was to build an ecosystem biomass balance model, the Ecopath model (see www.ecopath.org, Christensen & Walters 2004). Such a model would allow assessing the major trophic relationships and identifying the mechanisms and perturbations that can alter the ecosystem's structure and impact the status of important resources, such as the coastal cod stock. Within this project, the present study was aimed at understanding the role of harbour seals as one of the major top predators in this ecosystem.

Understanding a system under change, however, implies investigating both the driving forces and the responses of the system to changes. Trophic relationships may vary with time, since animals may shift diet depending on the availability of food. Investigating ecosystems under change usually requires long term and large scale studies, but even these have limited predictive capabilities when the mechanisms at the basis of the system are complex and not fully understood (Schindler & Hilborn 2015). Dynamic systems however offer the possibility to assess responses also at small temporal scales, such as for example across seasons. In addition, animals live in a multidimensional space and the presence and strength of trophic links are affected by their distribution in space. Understanding the role of harbour seals in the ecosystem of Porsangerfjord is therefore a question with spatial and temporal perspectives.

The presence of a local population of harbour seals in Porsangerfjord has been known for decades. In the period post-war, seals were severely hunted and Øynes (1964) reported that no seals were resident in the fjord at that time. The population has then increased to ca 340 seals in 1998 (Bjørge & Øyen 1999), but later decreased again, due to high bounty hunt in the period 2004-2008, to respectively minimum counts of 150 seals in 2005 (Nilssen *et al.* 2010), 217 in 2008 and 196 in 2013 (KT Nilssen, Institute of Marine Research, IMR, unpublished results). At present the population is therefore assumed to be at a low level with respect to historical numbers. Harbour seals are usually considered generalist predators, foraging largely on codfish (*Gadidae*), sandeel (*Ammodytes sp*), herring and flatfishes (*Pleuronectidae*) depending on the type of habitat in the surroundings (Härkönen 1987a; Olsen & Bjørge 1995; Bowen & Harrison 1996; Tollit *et al.* 1998). Their diet, however, has been observed to change seasonally, depending on the availability of key prey species (Härkönen 1987a; Pierce *et al.* 1991; Brown & Pierce 1998; Hall, Watkins & Hammond 1998). Harbour seals have also been observed in certain areas to respond to different prey pulses, such as seasonal concentrations of herring or salmon (*Salmo salar*, Middlemas *et al.* 2006; Thomas *et al.* 2011).

This thesis investigated the spatial and temporal patterns of foraging of harbour seals in Porsangerfjord and assessed the response of this species to seasonal resource dynamics in this subarctic ecosystem. First, the movements of tagged individual harbour seals were investigated to ensure robust interpretation of their behavioural patterns from telemetry observations (papers I & II). Then, foraging behaviour was compared to the dynamic distribution of harbour seals potential prey to assess the presence of a behavioural response to resources (paper III).

1.2. The foraging and movement ecology of harbour seals

Harbour seals are widespread in the coastal areas of the North Atlantic (Bigg 1981). Their foraging behaviour and diet have been described extensively both through the analysis of scat contents and observations at haulout sites (*e.g.* (Härkönen 1987b; Olsen & Bjørge 1995; Bowen & Harrison 1996; Tollit, Greenstreet & Thompson 1997; Berg, Haug & Nilssen 2002). In the past four decades, with the development of telemetry devices (Rutz & Hays 2009), its habitat use and movements have also been followed underwater, providing insights in their behaviour while foraging (*e.g.* Bjørge et al. 1995; Suryan & Harvey 1998; Tollit *et al.* 1998). Despite the improvement in data resolution, battery life, memory and sending capacities of these devices, the data recorded still need some

degree of interpretation to identify different behaviours from movements in time and space (Cagnacci *et al.* 2010).

The identification of when and where an animal is feeding is at the basis of the study of foraging strategies with respect to the distribution of potential resources and the environment (Goldsworthy *et al.* 2010). In free ranging foragers, behaviours such as moving in search for prey or exploiting a prey patch can be identified by comparing animals' displacement in space to expectations based on ecological and foraging theory. In marine environments in particular, resources are patchily distributed in space. In these conditions it is expected that animals increase their search effort in response to prey encounter, because of the higher probability of encountering prey in the nearby area, a behaviour that has been named Area Restricted Search (ARS, Kareiva & Odell 1987).

It is also generally accepted that an animal will adapt its foraging time budget in order to maximise energy intake, thereby spending more time in areas which are more profitable than others (Stephen & Krebs 1986). The time spent in a given area (or foraging patch) can therefore be related to the quality of the resources. However, with increasing time spent foraging on resources in a certain location, these will deplete and the animal will need to search for a new patch. The Marginal Value Theorem predicts that a threshold of patch quality exists, below which it would be more profitable to look for another patch rather than continuing feeding in the same area (Charnov 1976). Moreover, when the average quality of resources in the environment is high, this threshold should be optimally lower and animals are expected to spend on average less time per patch (Charnov 1976). Following this logic animals are expected to shift between extensive and intensive search (*i.e.* spending more time per unit space) when the quality of the resources is profitable enough with respect to the general status of the resources available.

The intensification of search can be obtained by slowing the displacement speed, increasing the tortuosity of the movement path or a combination of both (Benhamou & Bovet 1989). The observation of changes between extensive movements and ARS has therefore been used to identify the response of animals to resources and their characteristics, but has been rarely tested in marine systems (*e.g.* Mori & Boyd 2004). Moreover, the activity of foraging may include searching for food, and, after prey encounter, following, catching and handling prey. The analysis of movement will only distinguish between extensive and intensive search in response to resources, but not between intensive search and the actual foraging success (*i.e.* prey consumption).

Animals are affected by several constraints in their time and energy budgets. This implies that they cannot allocate their time entirely to foraging related activities, but need to meet other requirements, such as seasonal processes (*e.g.*

reproduction and, in the case of seals, moulting), and daily needs (*e.g.* resting, digesting, socializing, avoiding predators, etc). The presence of a multitude of behaviours complexifies the constraints that affect animal movement in space and therefore the identification of foraging behaviour from those. Harbour seals are central place foragers, performing regular movements between foraging areas at sea and resting areas on land (*i.e.* haulout sites). These trips are regulated by the balance between the need to rest and to feed. The time and energy budgets of such trips are therefore highly affected by the distance between the haulout sites and foraging areas.

Moreover, harbour seals move not only on the horizontal plane but also in the vertical dimension, by diving. Dives, being excursions between the water surface for breathing and the foraging patch depth for feeding, can also be seen as a form of central place foraging behaviour (Thompson & Fedak 2001; Elliott, Davoren & Gaston 2008). Differently from the horizontal space, the time budgets of these vertical trips to the underwater foraging patches are affected by constraints of very different nature. The allocation of time in different parts of a dive is assumed to be related to the hunting strategies adopted (Bowen *et al.* 2002), as well as the quality of the patch exploited (Thompson & Fedak 2001), but are ultimately limited by physiological capabilities such as oxygen storage capacities and their speed of recovery (Carbone & Houston 1996).

Based on the theoretical expectations of movement in response to the profitability of the resources encountered, a multitude of indices have been created to identify the onset of ARS from either horizontal or vertical movements. Due to the different constraints that act on these two spaces, analyses comparing movement signals in the two dimensions have not shown consistent results among species (Austin *et al.* 2006; Robinson *et al.* 2007; Kuhn *et al.* 2009; Dragon *et al.* 2012; Bestley *et al.* 2015), or within the same species (*e.g.* Bailleul *et al.* 2008; Thums *et al.* 2011). To fully understand the strategies of allocation of time in space with respect to the profitability and distribution of resources, it is not only critical to identify where and when animals forage, but also how long these remain in foraging patches. In diving animals, in particular seabirds and otariids, it has been proved that a bout of successive dives can be considered as a unit of foraging behaviour, therefore bout duration and location should be related to patch size, quality and distribution (Mori & Boyd 2004). When resources are on average of lower quality (*e.g.* higher distances between patches), the Marginal Value Theorem predicts that animals should spend on average more time per patch (Stephen & Krebs 1986).

Many of the aforementioned concepts have been widely used in studies of marine mammals' behaviour at sea, but few have been tested and, if so, on species

with clear large range patterns or feeding on one prey only (Mori & Boyd 2004; Doniol-Valcroze *et al.* 2011). Harbour seals on the other hand are short ranged and relatively shallow divers and studying their behaviour requires high resolution data both in time and space. Their movements in the horizontal and vertical dimensions lack large variation, and therefore show a less clear behavioural separation than long ranging or deep diving species. In order to better understand how the theoretical frameworks of movement apply to this species, and how generally used foraging indices can be interpreted, the movements of tagged harbour seals were compared to two theoretical predictions:

a) that dives bouts correspond to units of foraging behaviour (as in Mori & Boyd 2004, paper I);
b) that changes in search intensity occur simultaneously in the horizontal and vertical spaces as the assumed response to resource profitability (paper II).

The first analyses contributed to a better understanding of activity time budgets in harbour seals, extending the commonly accepted dichotomous characterization of time at sea, as either travelling or foraging, by two types of resting behaviours at sea. The second analysis allowed identifying the principal factors affecting the allocation of time in horizontal and vertical dimensions, contributing to a better interpretation of the commonly used indices for the detection of foraging. These results were used to characterize the behaviour of harbour seals at sea and to make inference on the dynamics of resource selection.

1.3.   The dynamics of resource selection of harbour seals in Porsangerfjord

Resource selection is defined as a disproportional use of resources with respect to their availability and is related to the choice of a forager to use certain resources selectively more than others, depending on their characteristics (Manly *et al.* 2002). Understanding the mechanisms at the basis of resource selection gives insight on the foraging strategies of the animals and therefore allows better understanding, and therefore predicting their responses to change.

However, while the usage of resources is a commonly undisputed concept, the notion of availability is highly subjective and context dependent. The perception of resource availability for a forager can be conditional to its quantity (*e.g.* total biomass), as well as its quality (*e.g.* energy content, prey species, size), or distributional characteristics (*e.g.* density, patchiness, Figure 1). At the same time, animals forage in a multidimensional space and need to move in order to exploit their resources, therefore the spatial location of resources with respect to the

animals can affect their perception of how easily accessible the resources are (Figure 1). The main factor affecting resource accessibility in harbour seals, which are central place foragers, is the placement of resources conditional to the haulout sites, since foraging locations have a decreasing accessibility with distance from the sites (Matthiopoulos 2003). Other factors limiting the spatial accessibility of locations in space can affect resource availability. In the Porsangerfjord sea ice forms in winter and usually covers the inner parts of the fjord up to spring. Since harbour seals are breathing mammals, ice cover prevents these animals to access resources located far under the ice.

The response of harbour seals to changes in the availability of resources was expected to occur either at the level of the single foraging trips, with the selection of areas richer in a certain prey, or at the level of the placement of haulout sites, which in turn increases the availability of certain resources to the animals (Figure 1). Harbour seals are often described as opportunistic foragers, but several studies have demonstrated patterns of selection in this species, as for example the preference for energy rich, pelagic schooling fish, when occurring close to haulout areas, and the preference for small size fish.
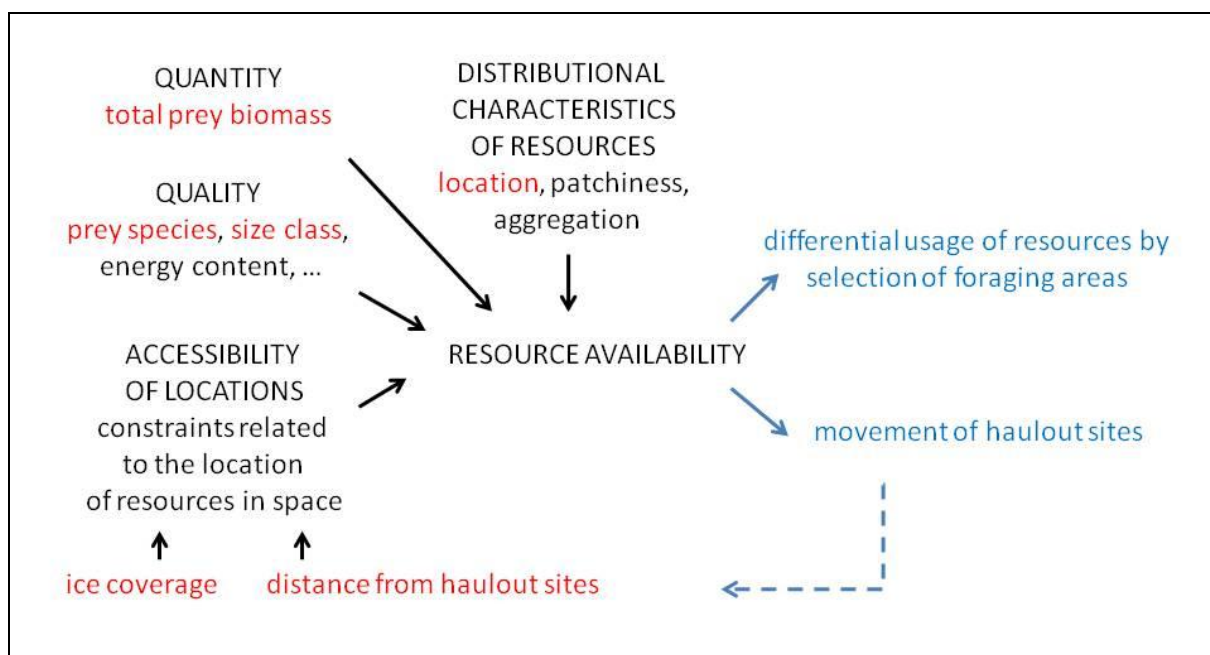
Figure 1 A conceptual scheme of the factors affecting the availability of prey resources for free ranging foragers (capital) and specifically for harbour seals in Porsangerfjord (low case). The figure shows the factors accounted for in this study (red) and the possible responses of the seals (blue) to alter these factors (dashed arrows).

Resource selection in this study was investigated along time in order to examine the seals' response:

  a) to the seasonal variation in resource distribution, and
  b) to the changes in the accessibility of the areas due to sea ice cover in winter and spring;

Selection was also examined at two different spatial scales to assess if harbour seals showed preference

  c) at the level of the single foraging trips or at the level of the home range by shifting haulout areas to increase the accessibility of certain resources.

Preference was moreover assessed for

  d) different potential prey species and
  e) size groups.

1.4. *Objectives*

The aim of this thesis was to understand the foraging ecology of harbour seals in a dynamic subarctic ecosystem, the Porsangerfjord. This was done by:

1) providing a robust interpretation of the behavioural patterns of harbour seals through the analysis of movement and diving data from telemetry observations (papers I & II);
2) through these findings, inferring on harbour seals spatial and temporal patterns of foraging with respect to the dynamics in the distribution of fish resources in Porsangerfjord (paper III).

Specific aims were:
  I.   To investigate the organization of dives and movements in time, and test the theoretical prediction of dive bouts being units of foraging behaviour (a). The results were aimed at providing a better estimation of activity budgets at sea in harbour seals (paper I);

  II.   To test the theoretical prediction that changes in search intensity occur simultaneously in the horizontal and vertical spaces (b) by comparing the indices of searching intensity derived respectively from horizontal and vertical movements. The results were aimed at providing a more robust behavioural interpretation of such indices when applied to this species (paper II);

  III.   To infer on the dynamics of resource selection for harbour seals in Porsangerfjord focusing on the spatial scales of selection and on the harbour seals responses to seasonal resource changes (paper III).

Glossary

ARS: Area Restricted Search, the tendency of a predator to restrict foraging in the vicinity of a capture (Kareiva & Odell 1987). This results in the sudden increase of searching intensity in space.

BT: Bottom Time, the time spent in the lower 15% of each dive.

Dive bout: group of dives occurring in a series with relatively short interdive periods at surface. Longer interdive periods divide a dive bout from the next. The threshold interdive periods duration determining a bout's end and start of the next is assessed statistically (Luque & Guinet 2007).

FI: foraging index (hFI = horizontal FI, vFI = vertical FI), a measure used for identifying foraging behaviour from

HS: horizontal speed (m/s).

Interbout period: time lag at surface between two successive dive bouts.

LMM: linear mixed models.

MT: movement types, output of the switching state-space models, classified as either resident (*i.e.* slow speed and high turning angles) or transient (*i.e.* fast directional movement).

Profitability: in this work is intended as the characteristics of a resource affecting the balance between the energy gained and consumed by the animal, therefore ultimately determining the animal's decision to forage on it. Profitability is therefore influenced by the quality of the resource, its location with respect to the animal and the quality and location of other resources.

Resource: what is needed by an animal to meet their requirements. In this work, focusing mainly on foraging behaviour, resources are considered what can be eaten by the animals (*i.e.* potential prey).

Resource accessibility: the ease at which an animal can reach a point in space, where a resource is located.

Resource availability: the amount of resources that can be encountered by the animal. Since the main currency of foraging decisions is ultimately the net energy gained by the animal, this quantity could be represented by prey biomass, but also by other characteristics of the prey (see Figure 1).

Resource selection: the disproportional use of resources with respect to their availability (Manly *et al.* 2002).

Resource use: in this work, the act of foraging in a specific location in space, that hosts a set of resources.

RT: Residence Time, the time elapsed from the moment the animal enters a circle of a given radius (r) to the moment it leaves it for longer than a given time threshold (t).

Searching intensity (in space): the time spent searching per unit space.

SK: dive skewness, the proportion between the ascending and descending speeds in a dive.

stBT: standardised Bottom Time, BT standardized across dive depths and durations (*i.e.* % of maximum potential BT for a given dive depth and duration).

2. Methods

2.1. Data sampling and preparation

2.1.1. Sampling of animal movement, diving and behaviour

Data on harbour seals movements and behaviour in the Porsangerfjord were collected by deploying GPS phone tags (SMRU Instrumentation, University of St Andrews, U.K.) on 15 individuals during the falls of 2009, 2010, 2011, and 2012 (paper I, table 1). The animals were captured in the water in the vicinity of haulout sites by means of specially designed nets, sedated and equipped with a tag, which was glued on the animals' fur below the neck. The tagging procedure (~ 2 hours) is described in paper I. The animals were then released from the shore at a location nearest to the catch site (Figure 2).

The tags were attached to the seals' fur right after moulting (September) and were expected to fall off at the next moult (July-August), giving a maximum sampling duration of 10-11 months. The tags recorded GPS positions, dive depth, and the time spent at surface or hauled out (see Table 1 for tag settings). GPS data were filtered to retain only good quality positions (maximum error of 50 m, Russell et al. 2011). Errors in the registration of the seals' vertical movements could arise due to temporary failures of the tags' pressure or conductivity sensors and implausibly long dives were excluded from further analysis (see Methods in paper II).

Figure 2 Releasing a harbour seal individual equipped with a GSM phone tag.

2.1.2. Horizontal movement models

Different movement models were fit to the location data depending on the purpose of the analysis. A switching state-space model was fit to the GPS positions, with the purpose of estimating behavioural states (paper II and III, Jonsen *et al.* 2005). Two states (or movement types, MT) were allowed, assumed to correspond to fast directional movements (extensive or transient movements, MT = 0) or slow

and tortuous movements (intensive or resident movements, MT = 1), indicative of ARS behaviour. From the models, HS was predicted at regular 20 min intervals (*i.e.* the maximum temporal resolution of the tags, see Table 1). The same data were also fitted with a correlated random walk model (*i.e.* non-switching state-space model) to predict horizontal speed (HS) at a higher resolution (5 min intervals, package `crawl`, R Development Core Team 2010; Johnson *et al.* 2008). The predicted HS were then classified, for each individual separately, into a fast and a slow group through a k means clustering procedure (k = 2, see paper I), to distinguish between transiting and resident movement phases. The latter procedure is computationally simpler than the first and was used to be able to estimate HS at such high resolution in manageable time.

Table 1 The type of information and data sampled by the GPS phone tags, their frequency and the required onboard technology used for measuring each data type. The tags were equipped with a GPS receiver for positioning; a pressure sensor estimating water depth; a wet/dry sensor, detecting at any time whether the animal was submerged or not; an inner clock, registering the time at which any event occurred; and a GSM transmitter, allowing the data to be transferred via the GSM network.

Sampled behaviour	Sampled data	Sampling design	Set sampling frequency (actual mean freq.)	Onboard technology used
Horizontal movements	GPS position and timing	Regular when tag not submerged and satellites available	20 min (53 min)	GPS receiver, clock
Vertical movements (diving)	Time-depth registrations	Regular when submerged	4 sec	Pressure sensor (depth), clock (time)
Surfacings	Start and end times	Start: any time dry, end: when below 6 m for more than 10 s (*i.e.* diving).	anytime	wet/dry sensor, clock
Haulout events	Start and end times	Start: any time dry for more than 10 min, end: wet for more than 40 s after start.	anytime	wet/dry sensor, clock

2.1.3. *Foraging indices derived from horizontal or vertical movements*

Several variables were computed and used as foraging indices. These were either measures of residence in the horizontal plane or at the assumed patch depth, usually the maximum depth of a dive.

As an indication of residence in the horizontal plane, HS (continuous) and MT (categorical) were used. In addition, Residence Time (RT, Barraquand & Benhamou 2008) was computed. RT is a measure corresponding to the time an animal spends within a circle of a given radius (r) centred on each point along the

movement trajectory. The relationship between the different indices (high correlation after non-linear transformations) is presented in Additional file 3, paper II.

In the vertical dimension, the time spent at the bottom of a dive (Bottom Time, BT) has been associated to foraging behaviour (Austin *et al.* 2006), since an animal is assumed to spend more time at depth when in a foraging patch. BT was then standardized across dive depths (stBT) by transforming it into a % of maximum potential BT for a given dive depth and duration (paper II).

2.1.4. *Additional behavioural characterization*

The behaviour of harbour seals at sea was investigated further to extend the simple dichotomous classification of time at sea into foraging or travelling. The characteristics of time-depth dive profiles were analyzed to assess the potential presence of resting behaviour while diving, which has been previously documented in many phocid species but never in harbour seals (Crocker, LeBoeuf & Costa 1997; Page *et al.* 2005). Two independent analyses were performed, both based on the assumption that potential resting dives would be characterized by one of the two vertical displacements being constant and slow, indicative of potential prolonged gliding driven by buoyancy (Watanabe *et al.* 2006).

First, the joint distribution of the mean and variance of multiple vertical speed measurement during each dive was examined (independently for the descending and ascending phases of the dives) to assessed the presence of dives with slow and constant speed (*i.e.* respectively low mean and variance, see Figure A2, paper I). Then, the proportion between mean vertical ascent and descent speeds, further called dive skewness (SK), was inspected. Dives with pronounced skewness in either direction were considered resting dives, with the direction of the skewness reflecting the positive or negative buoyancy of the animal. Series of consecutive skewed dives were identified through a multiple changepoint method (Killick, Fearnhead & Eckley 2012) as periods of resting while diving. The results of the two analyses were compared to strengthen the inference on the potential presence of resting dives and to test the robustness of the independent detection methods (see Appendix 3, paper I).

The underwater foraging behaviour of the seals was characterized relatively to the depth of the sea bottom and periods of benthic and pelagic diving behaviour were identified. For each dive the distance between its maximum depth and the depth of the sea bottom (expressed as the depth of the water column at mid tide) was computed. A mixture of *n* normal distribution functions ($1 <= n <= 5$) was fitted to the frequency distribution of bottom distances and the probability of each dive to belong to any of these distributions was modelled. The distribution having its mean closest to zero was then assumed to be the distribution of bottom distances for benthic dives (see Figure 6, paperII).

As a proxy for the satiation state of the animals, a categorical variable was computed, based on the major movement direction with respect to haulout sites. The major trip directions were identified (*e.g.* outward, inward, transiting between haulout sites, etc.). Satiation was assumed to be higher when the animals were

returning to haulout sites rather than on their way to the foraging areas (see Methods and Figure 7, paper II).

2.1.5. *Sampling and modelling of potential prey distribution*

Several types of sampling campaigns were performed during the EPIGRAPH project to map the distribution of various ecosystem components in the fjord (see Table 2 for a list of all additional data sources, sampling designs and data ownership). The biomass distribution of pelagic and semipelagic fish species was sampled during February, April/May and August of both 2009 and 2010 by continuous boat-based acoustic measurements along the entire fjord, when possible (*e.g.* the inner part of the fjord was not sampled in February and April 2010 due to the presence of ice). Acoustic measurements were integrated at each 1 nm of transect and scaled by the catches at pelagic and benthic trawl stations (see Figure 1, paper III, for the sampling design, and Appendix 1, paper III, for specifications on biomass estimation from acoustic measurements). The biomass distribution of bottom dwelling fish and other epifauna was sampled during a benthic study consisting of benthic sledge sampling stations (n=49) distributed throughout the fjord in June 2007, 2009, 2010 and 2011 (Figure 1, paper III).

Regression kriging was used to predict the biomass distribution of pelagic, semipelagic and benthic fish species. This consisted in a predictive model with a deterministic and a stochastic component. The deterministic component consisted in a linear regression against environmental variables, such as depth, temperature, salinity, current, and ice cover (Table 2). The stochastic component accounted for the spatial correlation structure present in the data (see Methods and Appendix 3, paper III).

Macroalgal coverage, which is known to be a nursery habitat for juvenile codfish, was predicted from the combination of video observations in the sublittoral zone and direct sampling of macroalgal biomass density in the intertidal zone (see Appendix 4, paper III). A predictive model of cod juveniles biomasses based on macroalgal coverage was used to estimate the density distribution of cod juveniles in the entire fjord (Michaelsen 2012).

2.1.6. *Estimation of harbour seal diet from scat sampling*

Several known haulout sites in the fjord were visited for scat collection in multiple occasions during the falls of 2009 and 2010. From the sampled scats (n = 48), fish otoliths were extracted for taxonomic recognition (see Appendix 1, paper III). The number and size of prey items in each scat were estimated, the latter by means of species-specific regressions found in literature. The autumn diet composition of harbour seals (frequency of occurrence of prey species in scats and size distribution of prey) was used to inform the selection of relevant fish species and size groups in the analyses of resource selection (paper III).

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Table 2 Overview of the data sources from EPIGRAPH, their sampling designs and data ownership. IMR = Institute of Marine Research, UiT = University of Tromsø, FUC = Finnmark University College, Alta.

Data type	Sampling/estimation method	Courtesy	Sampling period	Aim
Oceanographic variables*	Hydrographical model of the fjord	Myksvoll *et al.* (2012)	March, April, May 2009	Predictors for biomass distribution models
Depth*	Depth measurements (resolution), ordinary kriging for extrapolation	Norwegian mapping authority (www.statkart.no/en)	-	Predictor for biomass distribution models
Biomass of pelagic (herring, capelin, etc.) and semipelagic fish (codfish)	Acoustic transect measurements, regression kriging for extrapolation (using the predictors*)	Lindstrøm U (IMR), Pedersen T (UiT)	February, April/May, August 2009 & 2010	Biomass distribution maps of potential prey resources
Biomass of benthic fish (sculpins, etc.)	Benthic sledge samplings and regression kriging for extrapolation (using the predictors *)	Jørgensen LL (IMR)	June 2007, 2009, 2010, 2011	Biomass distribution maps of potential prey resources
Macroalgal coverage**	Video transects, algal biomass sampling and extrapolation with predictive model (using the predictors *)	Steen H (IMR), Sivertsen K (FUC)	summer 2008, 2009, 2010	Macroalgal coverage map, predictor for cod juvenile biomass in sublittoral zone
Biomass of cod juveniles and macroalgal coverage	Video transects	Pedersen T (UiT), Michaelsen C (2012)	summer/autumn 2010 & 2011	Predictive model of cod juveniles from macroalgal coverage (extrapolation is then made using the coverage map for the entire fjord **)

2.2. Hypotheses and approaches

2.2.1. Paper I

(H1) To assess if dives bouts corresponded to independent units of foraging behaviour, the organization of dives in time was compared to the horizontal movements of the animals. In order to test if interbout periods at surface (*i.e.* time lag between two successive dive bouts) had generally higher horizontal speed than dive bouts and therefore if the alternation of dive bouts and surfacing periods corresponded respectively to periods of in-patch foraging and between patch movement, a linear mixed model (LMM) of bout type against HS was fitted with seal individual as a random intercept.

Dive bouts were detected using the method described by Luque *et al.* (2008), an adaptation of log-frequency analysis (Slater & Lester 1982; Sibly, Nott & Fletcher 1990). Events occurring in bouts (*e.g.* dives) can be modelled as if generated by a combination of Poisson random processes operating at progressively larger timescales (Berdoy 1993; Mori, Yoda & Sato 2001; Johnson *et al.* 2002). Log-frequency analysis aims at finding threshold intervals between events, so called bout ending criteria (BEC), able to separate the hierarchically organized processes and identify behavioural bouts at multiple temporal scales (Figure 1 and 2a, paper I). The organization of dives in bouts was assumed to occur at several temporal scales, with individual dives organized into bouts, and bouts into trips. Therefore the occurrence of events was modelled as a mixture of three random processes (for more details on this analysis see Methods in paper I).

The results from dive bout analysis and interpretation, together with the identification of resting behaviour while diving, were then integrated to provide a better estimation of activity budgets in harbour seals.

2.2.2. Paper II

(H2) The hypothesis that changes in search intensity occurred simultaneously in the horizontal and vertical spaces, as the assumed response to resource profitability, was tested by comparing several foraging indices (FIs) derived respectively from the horizontal plane (hFI) and vertical dimension (vFI). A selected vFI, standardized bottom time (stBT), was modelled against three hFIs, respectively HS, MT and RT, by means of LMMs. The best out of three random structures (no random component, individual as a random intercept or as a random slope for the hFI) was assessed by likelihood ratio tests. The effect of additional factors on the relationship between the vFI and hFIs was assessed by the inclusion in the model of covariates and their interactions with the hFI, by forward model selection and likelihood ratio tests. The covariates tested were dive

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depth, trip direction, predatory tactic (*i.e.* benthic or pelagic foraging) and the presence of resting while diving (Figure 1, paper II). Moreover, the effect of the resolution of the movement trajectories on the relationship between indices was inspected by resampling the trajectories at lower resolutions and repeating the modelling exercise. Bootstrapping was used to estimate parameter uncertainties.

2.2.3. Paper III

Resource selection functions (RSFs, Aarts *et al.* 2008) were used to assess preference among potential prey species and size groups by contrasting the landscape of potential prey characterizing used and available locations in space. Harbour seals foraging locations (*i.e.* locations in resident state, MT = 1, excluding resting behaviour) were considered used locations, while different Poisson point processes were used to simulate the locations available to the seals. Logistic regressions were fit to the binomial response (used = 1, available = 0) against the biomass density of different fish species (*i.e.* herring, capelin, two size groups of cod and haddock, respectively < and > 25 cm, sculpins and juvenile cod in the sublittoral zone). Additionally, a variable based on the distance of locations from the three main salmon river estuaries was used as an index for the potential presence of salmon.

Selection was also examined at two different spatial scales. Selection conditional to the haulout site placements (*i.e.* at the level of single trips) was estimated by generating an availability point process with density inversely dependent on the distance from the haulout sites to simulate the decreasing accessibility of points with distance (see Figure 2, paper III). Selection at the level of the home range was estimated by generating an availability point process with constant density in the entire fjord (see Figure 2, paper III).

RSFs were constructed independently for four time periods when both seal movement data and resource sampling were available (August 2009, February, May and August 2010). Only the animal movement data falling within two-months periods closest to the timing of the resource samplings were used, this reduced the number of individual seals used in the analyses to 10 (see Table 1, paper III, for an overview of the data included). The results on resource selection were compared across seasons (*i.e.* across the 4 models) and across months (*i.e.* by means of a monthly interaction factor within each model) to follow the dynamics of ice cover within each season.

The behavioural response to changes in resource availability with time was assessed by testing the presence of a functional response in resource selection (*i.e.* change in selection with changes in resource availability, *sensu* Mysterud *et al.* 1999). This was investigated by regressing the values of resource selection parameters against the total biomass of available resources for different periods

(n=4), independently for each species. Additionally, the movement response in terms of shifts in the location of haulout sites and main direction of the foraging trips across periods was evaluated.

3. Results and discussion

A total of 15 tags were deployed on harbour seals individuals. Six seals were tagged in September 2009, six in 2010, one in 2011 and two in 2012. Four females and eleven males were tagged. All animals were juveniles (1–2 years old), most likely due to the higher likelihood of inexperienced animals to be caught in nets. The duration of the tags was variable with 7 tags lasting between 8 and 10 months, close to their maximum life expectancy (the time between tagging and the subsequent moult, ~10-11 months), 5 lasted between 3 and 5 months, while 3 stopped functioning early (< 2 months, Table 1, paper I).

On average 820 (range 410 – 1 157) GPS positions and 14 672 (range 6372 – 19 237) dives were recorded per month per individual for a total of 77 213 positions and 1 284 695 dives (Table 1, paper I). The seals ranged up to 130 km from the haulout sites in autumn, up to 80 km in winter, and only up to 30 km in spring. Some individuals ranged further than others, for example 5 out of 15 ranged > 70 km during autumn, but all individuals showed seasonality in movements. The animals dived on average 20 m deep and 1.4 min long. The majority of the dives (95%) were less than 67 m and 3.5 min, and the maximum depth registered was 193 m, lasting 6.3 min.

The data on individual harbour seals' movements were first investigated to interpret the animal's behaviour based on theoretical assumptions (chapter 3.1, paper I and II). Then the patterns of foraging of the tagged individuals were compared to the distribution of selected fish species and size groups in different seasons to assess the dynamics of resource selection in the area (chapter 3.2, mostly paper III).

3.1. The interpretation of harbour seals' behaviour from telemetry data (paper I & II)

The data were confronted to different theoretical expectations. The results contributed to an improved interpretation of the harbour seals' diving and movement behaviours, and provided insights in their foraging ecology. Important factors affecting the harbour seals' time budgets, their interpretation and consequently the identification of meaningful units of behaviour were found. These factors may cause significant issues in the identification of foraging behaviour and estimation of related foraging time budgets and need to be taken into consideration when inferring behaviour from movements (see chapter 3.3).

Two major results were found: 1) the usual main characterization of activity budgets in this species, as resting at haulout sites and travelling and feeding during foraging trips, was extended by two types of resting behaviour at sea: at surface

and while diving (paper I); 2) <u>the allocation of time in the horizontal and vertical spaces,</u> usually assumed to be linked to the profitability of the underlying resources, <u>strongly depends on factors such as the presence of resting at sea and the underwater predatory tactic used</u>.

3.1.1. *Does the allocation of time in different activities follow theoretical predictions?*

When analysing the organization of dives in time (paper I), the results indicated that <u>the theoretical framework for the interpretation of dive bouts</u> (see H1, in chapter 2.2.1), <u>which was proved valid for other marine divers</u> (mostly otariids and birds, *e.g.* Boyd 1996; Mori et al. 2002), <u>is not applicable for harbour seals,</u> and most likely not for other phocids either. Dive bouts can therefore not be considered units of in-patch foraging behaviour.

The results indicated the presence of two hierarchical temporal scales of dive organization (Figure 1 and 2a, paper I), with large scale interbout periods at surface having generally lower horizontal swimming speed than large scale dive bouts. For this reason, interbout periods could not be considered travelling periods between patches, suggesting that both travelling and foraging occur within dive bouts. The very low swimming speeds during inter-bout periods at surface (0.06 m/s, see Table 2, paper I) were instead advocating for the alternative explanation of the latter having generally a resting function. These results indicate that the conceptual model of dive bouts being units of foraging behaviour can not be used for testing hypotheses on harbour seals' foraging strategies, as done for example by Mori & Boyd (2004) on Antarctic fur seals (*Arctocephalus gazzella*), where shifts in the durations of dive bouts (in-patch foraging) and interbout periods (between-patch travelling) were used to measure the animals' response to shifts in the distributional characteristics and quality of their resources.

The interpretation of the smaller temporal scale of bout organization was less clear, since horizontal swimming speed differed less between bouts and interbout periods. Small scale interbout periods at surface were associated to slightly slower swimming speed than dive bouts and were also hypothesised to be related to resting behaviour at surface. These were hypothesised to have the function of metabolizing anaerobic by-products progressively accumulated during the preceding dive bout (Boyd 1997; Butler & Jones 1997). This hypothesis should be investigated further by testing if the duration of a dive bout relates to the duration of the successive surfacing period, considering the non linear relationship between the depletion of oxygen during apnea and recovery while breathing at surface (Houston & Carbone 1992). At small scale, transiting and stationary diving behaviours were often detected as separate bouts, but having very similar average

dive depth. This suggests that harbour seals dive to depths of interest also when travelling.

The two independent analyses on dive characteristics resulted in the assessment of the presence of resting while diving in the form of resting dives with a slow and constant descending speed and a faster ascending speed, occurring in prolonged series (see Appendix 3, paper I). The slow and constant descending speed was assumed to be related to the use of negative buoyancy for gliding, as widely described in other phocid species (*i.e.* drift dives, Crocker *et al.* 1997; Page *et al.* 2005). This behaviour has however not been documented in harbour seals previously and represents a novel finding for this species with interesting perspectives to be investigated further (see chapter 3.4). It must be stressed however that in this study it was not possible to determine the actual presence of drifting due to the lack of appropriate data (*e.g.* stroking patterns), but the two independent results both pointed towards this interpretation (see BOX 1). Resting dives were found to occur in series (mean duration 49.5 min, CI = 47.4 – 51.8, Figure 2c, paper I), but the latter did not correspond to independent dive bouts (Appendix 8, paper I).

Paper I concluded that dive bouts and surfacing periods in harbour seals do not correspond respectively to in-patch foraging events opposed to moving between patches, but generally to periods of activity (*i.e.* dive bouts) and inactivity (*i.e.* surfacing periods), with the exception of some cases of resting during diving (on average 7% of the total activity).

To test the hypothesis that changes in search intensity occurred simultaneously in the horizontal and vertical spaces, as the assumed response to resource profitability (see H2, chapter 2.2.2), the indices based on movement in the horizontal and vertical spaces were compared. A positive relationship was found, supporting the original hypothesis (paper II). The strength of this relationship was however higher when accounting for additional covariates, indicating that certain factors affect the allocation of time in space differently in the two spaces (Figure 2, paper II). Bestley *et al.* (2015) recently found similar results when analysing the relationship between vertical and horizontal movements in several pinnipeds species. The weak correlation found in all species was interpreted by these authors as a simplistic interpretation of optimal foraging theory due to the presence of contrasting predictions. In the present study, on the other hand, the cause of the weak correlation was identified in the different and in some cases opposite effects of certain behavioural factors on the trends of allocation of time in the different dimensions. Paper II therefore concluded that the theoretical prediction of the increase in searching intensity in both spaces is

empirically verified when certain important behavioural factors are accounted for (see chapter 3.1.2).

3.1.2. *What are the factors influencing the allocation of time in different dimensions?*

Resting and predatory tactics (*i.e.* benthic or pelagic feeding) had the strongest effect on the vertical foraging index (stBT) based on the allocation of time per unit space (*i.e.* intensity of search). Active benthic dives had the highest values of stBT and the latter was also found to have a stronger positive relationship with the horizontal foraging indices. This result may be explained by the fact that the sea bottom acts as a limiting factor inducing persistence at a given depth layer, concentrating and therefore increasing the time at the maximum depth.

Benthic dives in harbour seals have been previously documented to be generally longer and deeper, have longer bottom times and faster descent/ascent speeds (Coltman *et al.* 1997; Krafft *et al.* 2002), which is in line with the findings in this study. Additionally, a positive relationship was found between bottom time (BT) and its standardized equivalent (stBT). The latter represents the efficiency of the use of the bottom depth and is related to the use of faster vertical speeds (Additional File 2, paper II). Pelagic dives were found to have, on the other hand, generally lower stBT, suggesting a lower efficiency of the use of time at the dive's bottom. The distribution of pelagic prey fish has higher temporal and spatial variability than bottom dwelling fish (Bjørkvoll *et al.* 2012). Pelagic prey patches will therefore necessarily be more motile and harder to relocate than patches of benthic fishes which have a stronger association with the sea bed. Pelagic patches will be less predictable also across the water column, hence, maximizing volume of water swept during a dive can be an advantageous strategy while foraging pelagically (Wilson *et al.* 1991; Tremblay & Cherel 2000).

Harbour seals have been described using prey dependent underwater hunting tactics, which may lead to very different allocation of time at different depths (Bowen *et al.* 2002). Not all tactics needing a prolonged time at the bottom of the dive, however, implied increased energetic costs of diving. A 'sit and wait' technique, in fact, probably results in longer dive durations but less energy spent then pursuing a prey. The time and energetic budgets of underwater predatory behaviour in foraging harbour seals needs further investigation for a better understanding of the metabolic implications of different strategies with respect to the type of prey targeted. Our results support the tendency of benthic dives to be more 'squared' or 'u-shaped' (*i.e.* with steeper vertical descents and ascents, hence higher stBT) than pelagic dives, which tend to be 'v-shaped', but indicate that the

BOX 1 Do harbour seals perform drift dives?

In paper I, two analyses were run to detect potential drift dives using two methods based on slightly different assumptions of the animal's behaviour and physiological characteristics (see chapter 2.1.4). The results from the two methods were compared. The periods of resting while diving (*i.e.* series of skewed dives) obtained from the first analysis were found in 98% of the cases to contain at least one resting dive detected in the second analysis, showing a high degree of agreement between the methods (Appendix 3, paper I). The two methods were based on the assumption of the presence of gliding aided by the seals' buoyancy. The first assumed that, if buoyancy is either strongly negative or positive, gliding would occur in only one of the two vertical phases of the dive (descent or ascent) and, gliding being slower than active swimming, the proportion between descending and ascending speed would be skewed. The second was based on the assumption that, if gliding occurs, the multiple consecutive measurements of vertical speed would be slow and relatively constant (Figure 3).

Despite the high degree of agreement of the two methods, supporting the validity of the assumptions, the presence of gliding during these dives could not be demonstrated due to the lack of appropriate measurements, such as the stroking patterns of the animals and their actual swimming speed (*e.g.* Watanabe *et al.* 2006). Swimming speed in this case was estimated from the vertical speed in the time-depth profiles, which can be considered to be representative of actual swimming speed in case of little horizontal displacement. This was validated by the fact that most of the sequences of identified resting dives had slow horizontal speed. In addition it was found that only the descending phase had the characteristics of gliding, suggesting negative buoyancy, which is a common feature for harbour seals (Bowen, Oftedal & Boness 1992). The use of drifting while diving has also been described as an energy saving strategy while foraging, as a means of reducing the metabolic cost of vertical transport and prolonging dive duration, still maintaining aerobic metabolism (Williams *et al.* 2000). However this is often the case of deep-diving species, but is unlikely to be a valid strategy for relatively shallow divers, such as the harbour seal. The results of this work provided multiple evidence for the presence of resting dives in this species. However, more appropriate measurements (*i.e.* actual swimming speed and stroking patterns) are required to better understand the use of drifting while diving in harbour seals. This may allow future application of methods relating animal buoyancy to condition, which have already been developed and proved useful for other phocid species (Biuw 2003).
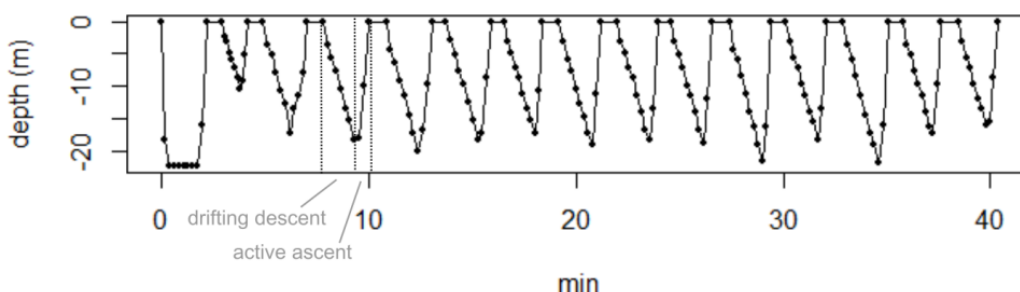

Figure 3 Time-depth profiles of resting dives after one first benthic dive. Dots show the consecutive time-depth measurements. Descending speed is slower than ascending speed and constant.

distinction between these shapes mainly reflects the dives' location in the water column (*i.e.* benthic vs. pelagic), rather than distinguishing between travelling and foraging (*e.g.* Schreer & Testa 1995; Lesage et al. 1999).

Dive depth, had a relatively small but positive impact on the absolute value of the vertical indices, indicating that harbour seals tend to be more efficient in time usage at the bottom of the dives at greater depths. This is in line with the predictions of optimal diving models based on the marginal value theorem (Charnov 1976), where average time in patch (*i.e.* at the dive's bottom) is generally expected to increase with travel time (*i.e.* dive depth), until the animal reaches depths at which it will face oxygen limitations (Carbone & Houston 1996).

The other factors tested (*i.e.* direction of the trip and temporal resolution of the GPS locations) did not show a significant effect on the relationship between the vertical and horizontal foraging indices.

3.1.3. What are meaningful units characterizing the behaviour of harbour seals?

In paper I it was shown that travelling, foraging and to some extent resting, occurred during large scale dive bouts, and that these bouts could not be viewed as units of unique behavioural activities. Small scale dive bouts, on the other hand, were found to be often characterized by consistency in horizontal movement (*i.e.* either fast or slow), therefore displaying units of the same behaviour. At the same time, periods of resting while diving were not found to occur as independent dive bouts, indicating that changes in surfacing patterns (at any scale) could not be used to detect the onset of series of resting dives (paper I).

Harbour seal activity budgets are often simplistically summarised into foraging at sea and resting at the haulout sites (*e.g.* Sharples *et al.* 2012), resting being one of the major constraints of returning to the haulout site outside the pupping and moulting periods. However, the documented presence of significant proportion of time spent resting at sea (13%) challenges the commonly accepted interpretation of trips being units of foraging activity. In paper II for example, an index based on the outgoing and incoming movements of animals from haulout sites was used to represent satiation. This index performed poorly in explaining any pattern in searching intensity, suggesting that trips may not reflect digestion cycles. The use of resting pauses at sea has for example been suggested in other species as a way to reduce transportation costs from and to the central place, but allowing for digestion before a new foraging bout (*e.g.* Cape gannets, *Morus capensis*, Ropert-Coudert *et al.* 2004). These results suggest the need to explore harbour seals behaviour at sea in smaller units than entire trips to investigate the

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presence of behavioural patterns and cycles relative to resource quality and distribution.

3.1.4. *Implications of the findings of resting at sea.*

Energetic implications: The occurrence of resting behaviour at sea was estimated as 13% of the total activity time budget, against a 20% of resting at the haulout sites (paper I). Not considering resting at sea in energetic calculations would therefore highly overestimate field metabolic rates, which has been shown to be of significant importance when estimating total prey consumption in other aquatic predators (*e.g.* harp seal , Nilssen *et al.* 2000). Individuals showed different incidence of the different types of resting behaviour at sea, but had similar cumulative patterns (see Figure A7c in Appendix 9, paper I). This gives rise to speculation on the presence of different behavioural forms with a similar function. Different strategies of resting at sea may imply different energetic savings. For example, the metabolic rate of harbour seals is considerably higher in water than on land at comparable temperatures (Hart, Irving & Mackison 1959), therefore resting on land will be energetically more profitable than at sea. This however will in turn depend on weather conditions (*e.g.* Simpkins *et al.* 2003) and on the distances between haulout sites and feeding grounds. This suggests the need to investigate further the energetic implications of resting behaviour at sea in order to estimate the influence of them on field metabolic rates and behavioural strategies.

Methodological implications: Resting behaviour, which shows prolonged residence in the horizontal plane, inflates the foraging indices based on horizontal movement, leading to a potential biased localization of foraging areas or to an overestimation of the time spent foraging. Resting at surface can easily be accounted for by ruling out periods of little diving activity. Resting while diving, on the other hand, deflates the values of the vertical foraging indices, since the time spent at the dive's bottom when resting is significantly lower than when foraging (paper II). This opposite effect leads to confusion in the relationship between horizontal and vertical foraging indices (paper II), and to a potential misidentification of foraging behaviour if based on horizontal indices only. However, an analysis of the spatial location of foraging and resting areas has shown that the animals often rest close or at the foraging patches (Figure 4). This would not necessarily result in the incorrect location of foraging areas, but most likely in the overestimation of time spent foraging in them (see BOX 2).

BOX 2 Do foraging and resting areas overlap?

Many studies on foraging pinnipeds use a simple dichotomous classification of behaviour at sea based on two categories: travelling (*i.e.* when performing directional fast movements) and foraging (*i.e.* when increasing residence in an area, *e.g.* Breed *et al.* 2009). Resting at sea has not been considered as a major component of the activity budgets of harbour seals up to very recently (McCLintock *et al.* 2013). Ramasco *et al.* (2013) investigated the potential bias induced by the missed identification of resting behaviour at sea (*i.e.* both at surface and while diving, see paper I), when estimating the location of foraging areas and the duration of time spent in each of them. They concluded that resting occurs mostly near or at foraging areas (Figure 4). Not accounting for resting at sea will therefore most likely not bias the location of foraging patches, but will strongly affect the estimates of foraging duration.
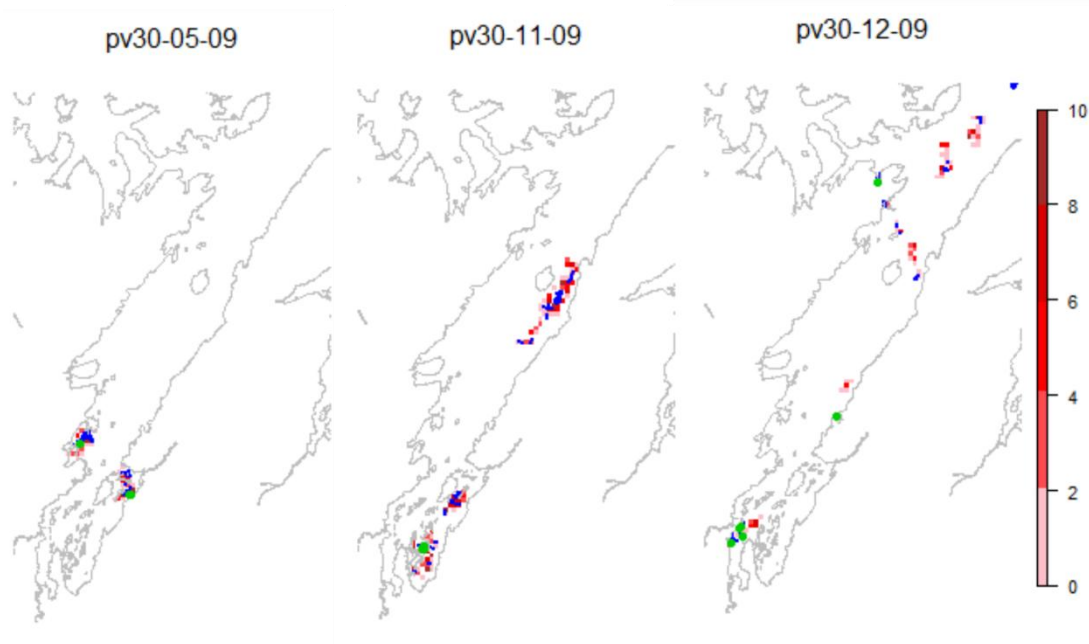

Figure 4 The location of the foraging effort (color scale = number of locations per 1 km² pixel), resting at sea (blue dots) and used haulout site (green dots) for 3 tagged individuals during October 2009.

3.2. The dynamics of harbour seals foraging in Porsangerfjord (paper I, II, III & additional findings)

The following chapter presents and discusses the major results on the relationship between harbour seals' foraging behaviour and the dynamic distribution of their potential prey across seasons in Porsangerfjord. These results are mainly the outcome of the resource selection analysis in paper III. However, some relevant findings on temporal patterns in activity budgets (paper I) and on the presence of different foraging strategies (*i.e.* benthic and pelagic foraging, paper II) are also discussed. Results from an additional analysis comparing the vertical distribution of potential prey and the vertical foraging behaviour of seals are presented to support and develop the findings of paper III.

3.2.1.   Are there temporal patterns in harbour seals' behaviour?

Temporal patterns in the occurrence and duration of the different resting activities were found to be mainly related to daylight, with all individuals showing more frequent or prolonged resting during night-time, in the seasons where night and day alternate (*i.e.* spring and autumn north of the Arctic Circle, Figure 3, 4 and A7, paper I). This suggests that, by exclusion, most of the foraging activity occurred during daylight. Harbour seals are generally considered visual predators, therefore foraging during daylight would be a more favourable strategy. However, these animals possesses sharp underwater visual acuity and can rely on the use of whiskers for movement detection, both of which are adaptations to forage at low light levels (Schusterman 1981; Dehnhardt, Mauck & Bleckmann 1998). The effect of circadian patterns on the activity budgets of harbour seals has in fact been documented to differ between individuals and seasons (Thompson *et al.* 1989). In Svalbard, for example, dominance of nocturnal foraging was observed in juvenile harbour seals (Krafft *et al.* 2002). Despite the presence in certain cases of constraints at the haulout sites potentially influencing these patterns (*e.g.* increased risk of predation from polar bears during daylight, Krafft et al. 2002), it is however more likely that the circadian patterns in activity are to a large extent dependent on the kind of prey targeted and its behaviour, rather than on the sensory capacity of the seals or on constraints at the haulout locations.

Seals were diving deeper and with higher frequency during daylight (Figure 5). The latter was true except for the months with little darkness (April - May). The seals had a dominant benthic diving behaviour from winter to spring (Nov – May), while pelagic diving dominated during autumn. However, while benthic dives were more frequent during daylight in most seasons, the pattern was reversed for early winter (Nov - Dec). The deepest dives were benthic dives during January and

February. The consistent pattern of deeper dives during daylight is most likely a consequence of the downward vertical migration of fish with light (Huse & Korneliussen 2000, see 3.2.5 for further discussion). The use of both pelagic and benthic foraging strategies has been reported in literature (Tollit, Greenstreet & Thompson 1997), as well as in this study (paper II).
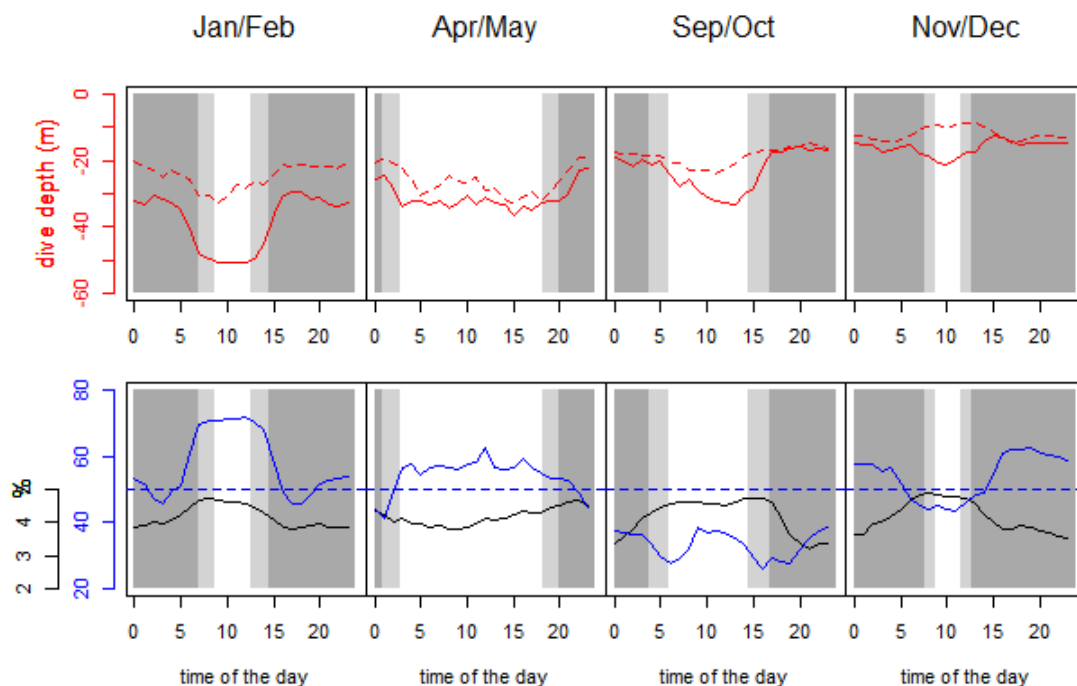
Figure 5 Dive depth (upper plots, solid red line = benthic dives, dashed red line = pelagic dives), % of benthic dives (blue solid line in lower plots, with dashed blue line indicating 50%) and proportion of dives per hour (black line in lower plots) along time of the day and across seasons. The light regime (dark grey shading = darkness, light grey shading = dusk or dawn) varies extensively with season at these latitude, with complete darkness during winter and no darkness during summer.

The relationship between the intensity of search in the vertical and horizontal spaces showed seasonal patterns in residuals for benthic (non-resting) dives (Figure 3, paper II). A higher than average standardized time at the bottom of the dives (stBT) was observed during a defined period of time of around one month (*i.e.* January). This may have two possible explanations: a shift in prey and the need for a new predatory tactic with a different strategy in the allocation of time at depth, or a general decrease in prey quality in the area, requiring longer times spent searching (Stephen & Krebs 1986). Harbour seals have been described to use multiple predatory tactics depending on the targeted species (Bowen *et al.* 2002). A shift to a more cryptic prey or a prey requiring longer handling times would result in increased time at the bottom of the dives (BT) and in higher efficiency in the allocation of time at the bottom (stBT), which are highly

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correlated (see chapter 3.1.2). At the same time, a decrease in the general availability of resources was registered in winter (Figure 3, paper III), with both lower total fish biomasses in the fjord and the formation of ice in the inner areas, rendering part of the resources inaccessible. Both hypotheses are plausible. However, given the patterns of reduced home ranges in winter (Figure 4, paper III), which are opposite than the expected movement response to little food availability (Stephen & Krebs 1986), a prey shift seems a more likely explanation.
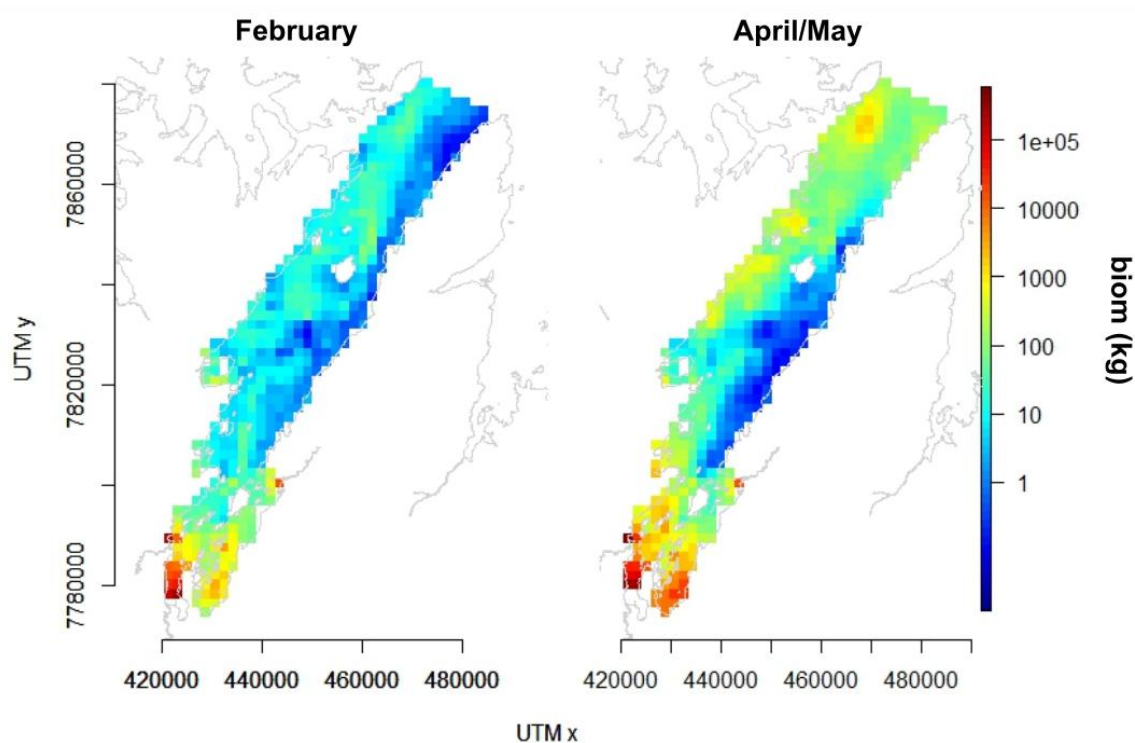
Figure 6 Biomass distribution of herring in winter and spring, predicted through regression kriging and then averaged across 2009 and 2010. The figure shows that higher concentrations of herring are to be expected in the deeper inner eastern basins of the fjord than predicted for 2009 only, when sampling in those areas was impossible due to ice presence (compare to Figure 3, paper III). Latitude and longitude are expressed UTM coordinates (meters).

3.2.2. Are there temporal patterns in the biomass distribution of the main fish resources in Porsangerfjord?

The total biomasses of the main fish species analysed (herring, capelin, cod and haddock) were found to vary in time, with the lowest biomasses in winter and a gradual increase throughout spring and summer for all species (Figure 3, paper III). A general increasing trend in fish size with increasing latitude was found along the main axis of the fjord, with the largest size groups of codfish (> 25 cm) occurring in the outer parts of the fjord, in association with warmer Atlantic water

masses (see S7, paper III, and Myksvoll et al. 2012 for a temperature map), and the highest densities of small sized species (pelagic forage fish and sculpins) occurring in the inner areas. Smaller codfish (< 25 cm, 0-group codfish) was found both in the outer areas and in areas further into the fjord, the latter being probably a result of larval drifting southward from local spawning areas in middle of the fjord (*i.e.* Smørfjorden, see Myksvoll et al. 2012). The high densities of herring found in the inner Arctic areas in winter and early spring (Figure 6) are most likely overwintering juveniles (Fernö *et al.* 1998; Jakobsen & Ozhigin 2011), that concentrate in cold waters as a strategy for energy saving when foraging is at its lowest (Huse & Ona 1996). Figure 6 shows the average biomass density distribution of herring across years (2009 and 2010) for the winter and spring months. In paper III only the data from 2010 were used because of overlapping in time with the seal data. However, ice was present in the inner parts of Porsangerfjord in winter and spring 2010 (Figure 4, paper III), impeding sampling in those locations and generating large prediction uncertainties. It can be noticed that the herring estimates for the inner eastern deep basins of Porsangerfjord used in resource selection analysis in paper III (Figure 3, paper III) were most likely underestimated when compared to the predicted seasonal average across years (Figure 6). This may have had some influence in the preference estimates, most likely underestimating preference for herring in particular in winter as discussed in paper III.

3.2.3.   *Do harbour seals perform resource selection and, if so, at which scale?*

At the large spatial scale, the harbour seals' in this study appeared to select areas with higher densities of either small sized fish species (herring, capelin, sculpins) or small size groups of larger species (codfish), depending on the season (Figure 6, paper III). No clear preference was found in the use of resources with respect to their availability conditional to the haulout sites (*i.e.* selection at the small spatial scale). This can be interpreted as harbour seals being opportunistic feeders at the level of individual trips from the haulout sites, but selective in the location of their home range within the fjord.

Several studies have reported the preference of harbour seals for small sizes of fish (mostly < 30 cm, Olsen & Bjørge 1995; Tollit & Thompson 1996; Tollit *et al.* 1997; Berg *et al.* 2002; Andersen *et al.* 2004; Ramasco 2008), although some have argued for the selection of larger fishes within the young age classes available (Tollit, Greenstreet & Thompson 1997; Brown *et al.* 2001). In Porsangerfjord the preference for smaller size fish was related to the differential size distribution of the fishes along the main axis of the fjord (North-South, Figure 7), with higher densities of small size groups occurring in the inner parts of the fjord and closer to
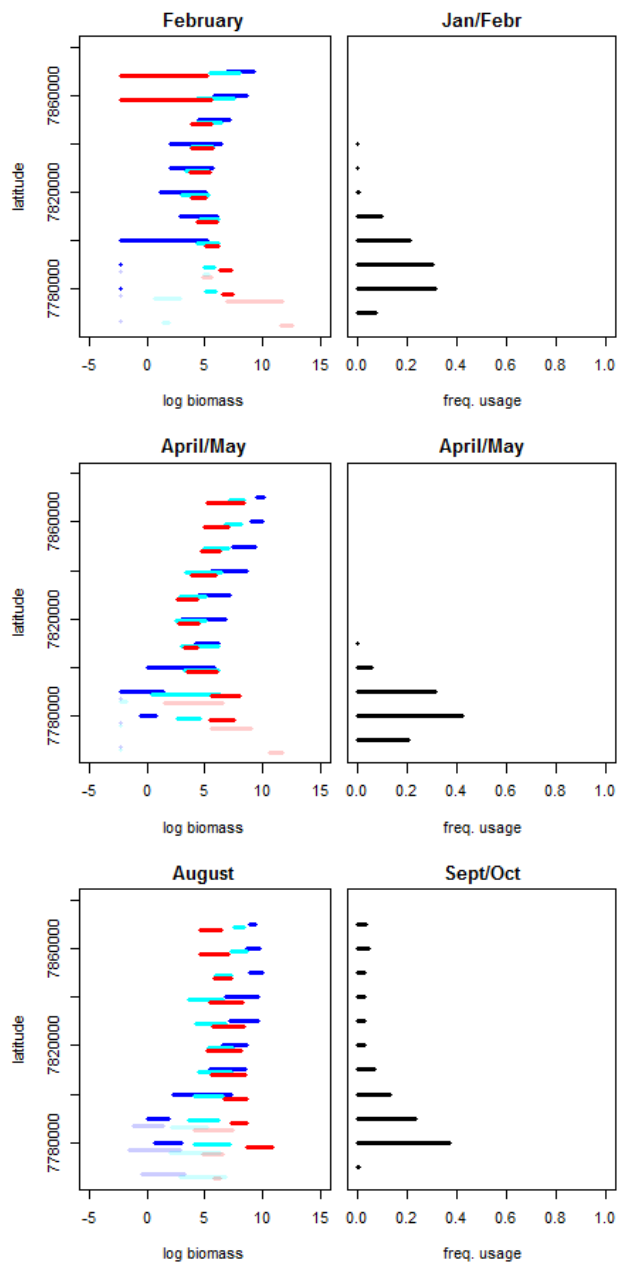
Figure 7 Left column plots: latitudinal distribution of biomass of herring (red), small cod (< 25 cm, light blue) and large cod (> 25 cm, dark blue) in Porsangerfjord across seasons. At lower latitudes the distribution is divided between the inner-east (solid lines) and the inner-west areas (semitransparent lines). Right column plots: frequency of latitudinal usage (% foraging locations per latitudinal interval) of the tagged harbour seals. Horizontal lines in all plots represent the span between the 25 and 75 percentiles of the data. Latitude is expressed in UTM coordinates (meters, see Figure 6 for reference on a map).

the haulout sites. The individuals tagged in this study in fact all foraged mainly in the inner parts of the fjord close to haulout sites, where the larger size groups of codfish occurred in very low densities. The small home ranges were not believed to be due to the young ages of the tagged seals, since younger seals are known to have larger, rather than smaller, home ranges (Lowry *et al.* 2001). Moreover, prey size selection was confirmed in the diet study (see S1), where 99% of all specimens registered were below 25 cm (average 11 cm).

A high variance was observed in the confidence intervals of the selection coefficients, with differences in individual prey preferences being the major source of variance in the population parameters (see S9 and S10, paper III). However, individual preferences were not consistent across seasons (S9, paper III). Seasonal changes at the population level were therefore not due to the slightly different sets of individuals analysed in different periods (see Table 1, paper III), but could rather be attributed to shifts in resource availability.

Changes in vertical and horizontal movement behaviour showed different levels of spatial aggregation (Figure 4, paper II),

suggesting that the spatial scale at which the movement response to resources occurs is smaller for the vertical dimension than on the horizontal plane. This could be partially related to the higher temporal resolution of diving data with respect to GPS locations. However previous findings in other pinnipeds have suggested that the movement changes in the different dimensions occur in response to different kind of stimuli, with horizontal movement responding to large scale environmental cues and diving behaviour to the local presence of prey (Bailleul *et al.* 2008). This may indicate that horizontal movements (on which resource selection analysis was based) may not have had enough resolution to detect small scale preferences. These results, however, suggest that extending resource selection analysis to the vertical dimension may allow for better inference on the presence of selection at the small scale.

Due to the lack of significant population selection patterns at the small scale, prey preference mentioned further in chapter 3 refers to the results from the large scale analysis, if not otherwise specified.

3.2.4. *Are there trends in the population's resource selection across seasons?*

Prey preference at the population level showed seasonal variation (Figure 6, paper III). Pelagic fish was preferred in early winter and late spring, when ice extent was small and overwintering concentrations of those fishes were to be found in the inner cold basins of the fjord (Figure 6). In late winter and early spring, when ice cover was at its highest, the preference was shifted to small codfish, most likely because pelagic forage fish was inaccessible due to the presence of ice covering the areas where these concentrated (see Figure 4, paper III, for ice extent). Small codfish was preferred prey also during autumn, when pelagic forage fish had a more patchy distribution along the fjord (Figure 3, paper III).

Positive selection for sculpins was registered in the same periods as the preference for pelagic forage fish. This could be due to the overlapping distribution of sculpins with pelagic fish in the inner cold areas of the fjord (Figure 3, paper III). Sculpins have in fact generally lower energetic density value compared to herring (Ball, Esler & Schmutz 2007), therefore an increased usage of areas rich in sculpins could be a consequence of targeting an energy rich and generally preferred prey such as herring (*i.e.* incidental prey, see 3.2.8 for more detail). However, the lipid content of herring and capelin decreases drastically during the spring months (January - April) due to the combined effect of reduced feeding during winter and increased energy usage in relation to spawning (the latter is true for capelin only, since only juvenile herring is present in this area, Henderson *et al.* 1984; Mårtensson *et al.* 1996). Since these pelagic species are preferred during a period

of relatively low prey energy content, it can be argued that other characteristics, such as their aggregative behaviour, may play a role in their preference.

3.2.5.   Are the seasonal changes in preference and behaviour consistent in the vertical dimension?

The preference for small codfish during autumn was associated with a dominance of pelagic and shallow diving behaviour during that season (Figure 5). This is counterintuitive, since codfish is generally found closer to the sea bottom (Jakobsen & Ozhigin 2011). However, the acoustic samplings showed that the vertical distribution of the small size group of cod occurred pelagically at around 50 m depth in the middle of the fjord in August (Figure 8). It must be noted that herring and capelin were also abundant in these areas and depths, despite the absence of preference for those species during that season. The opposite reasoning explains the situation in early winter and late spring, when benthic foraging was dominant, but preference was high for pelagic fish. Herring, for example, concentrates in winter in colder waters (Huse & Ona 1996 and Figure 8) and performs daily vertical migrations in the water column by occurring in the upper water layers during the night and schooling in deep waters during daytime to avoid visual predators (Huse & Korneliussen 2000). The dominance of benthic foraging during daytime can be seen as a response to such behaviour. A similar pattern was found for harbour seals feeding on overwintering herring in the Moray Firth, UK (Thompson *et al.* 1991), where the increased diving activity during daytime was related to the higher schooling behaviour of herring with daylight. The presence of a high level of aggregation of prey, even though at depth, was in this case hypothesised to be a factor of higher importance for the seals, than the prey's accessibility from surface. The latter is higher at night time when the fishes migrate upward in the water column but show less aggregative behaviour.
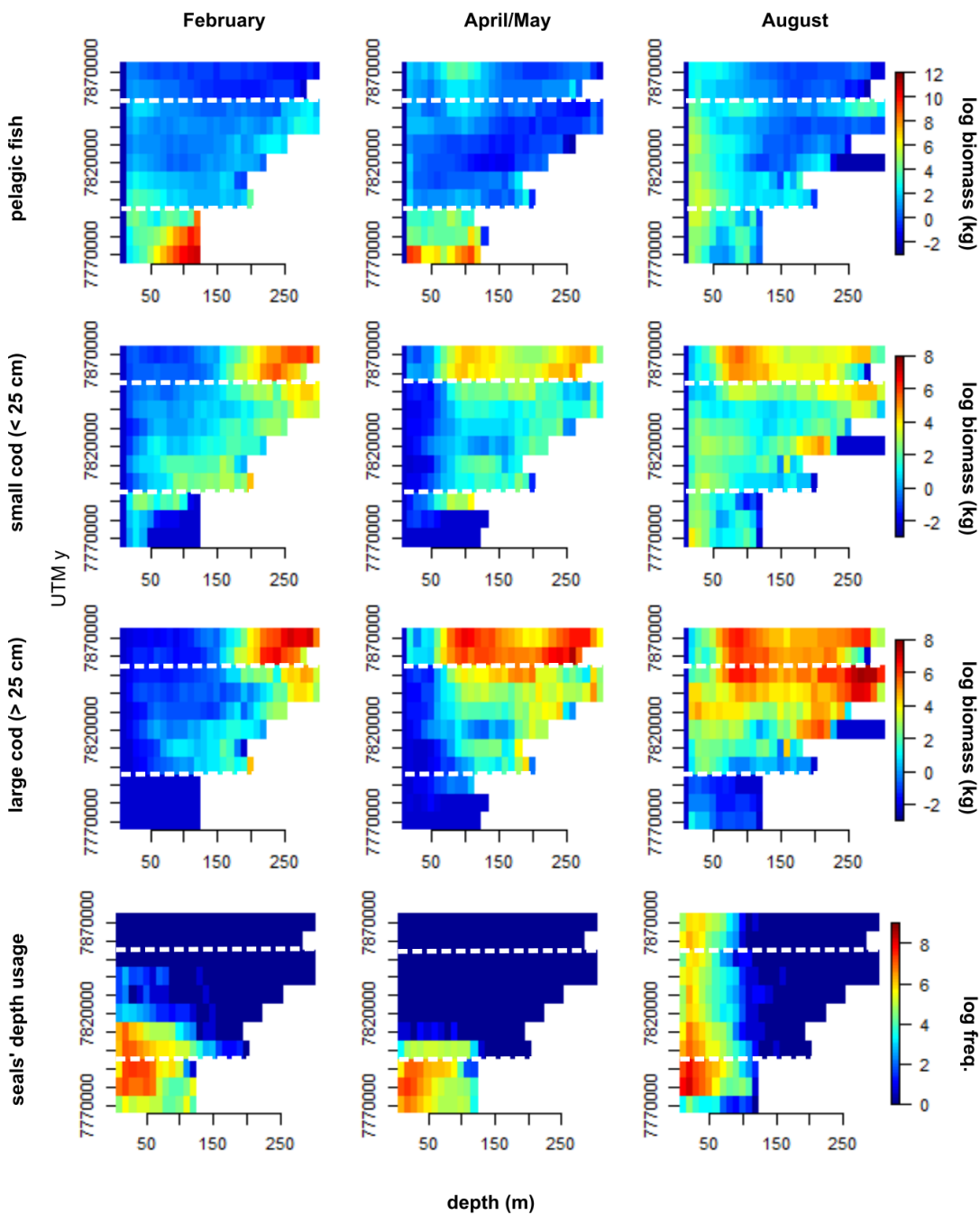
Figure 8 The vertical biomass distribution of 3 main fish groups (pelagic, *i.e.* herring and capelin, small and large cod) and the depth usage (frequency of dives' maximum depth) of the tagged seals along a latitudinal gradient (y axis, UTM coordinates, see Figure 6 for map reference). The horizontal dashed lines show the latitude of the 2 sills that divide the inner, middle and outer areas of the fjord. Fish data are extracted from the acoustic samplings of 2009 and 2010 and averaged. The bimodal distribution of herring and capelin in April/May is due to their benthic distributions respectively in the inner eastern and western parts of the fjord, which have very different depths. The shallow inner western part was not sampled in February, therefore no bimodality is present.
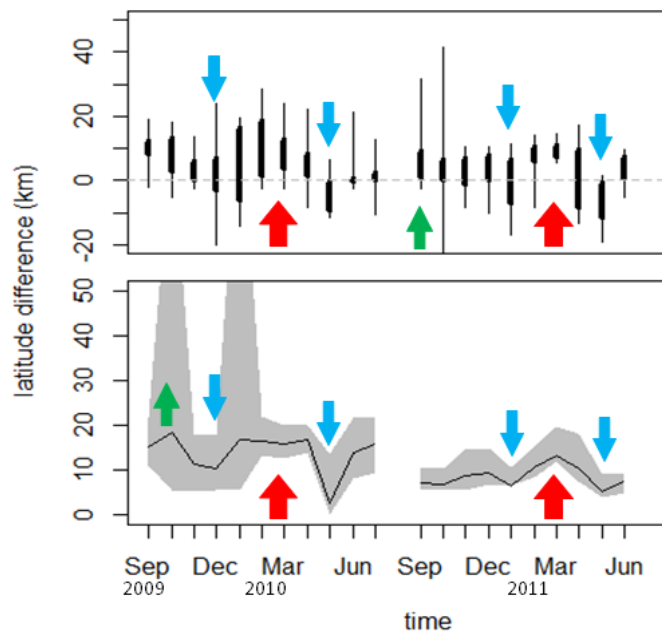
Figure 9 The north-south movement response in trip directionality (upper plot) and haulout site placement (lower plot) at the population level across seasons (2 batches of tagged individuals, n = 6 + 6). Boxplots of trip directionality (upper plot) show the span of 50% (thick lines) and 95% (thin lines) of the distance of each foraging location from the last used haulout site along a latitudinal axis. The horizontal black line (lower plot) shows the mean latitudinal shift with time of used haulout sites (shaded stripe = 95% of the data) from the southernmost used site. Red arrows show the movement response to ice formation, blue arrows to ice retreat, and green arrows the increased home ranges in autumn. The latter were most due to northward shifts of haulout sites in 2009 and to more distant trips in 2010.

3.2.6.   How did harbour seals respond to the dynamics of resources in Porsangerfjord?

One of the clearest behavioural responses of the tagged harbour seals to the dynamics of the fish distribution and environmental conditions in Porsangerfjord was the shifts of both average trip directionality and average haulout location on the latitudinal axis of the fjord (Figure 9). In autumn the seals showed either a northward shift in haulout site location (in 2009) or an increase in northward distances from the haulout sites (in 2010, green arrows, Figure 9). That corresponded to the period when the seals were observed shifting to a pelagic dominant foraging strategy (Figure 5 and Figure 8), ranging further out in the fjord and showing preference for small codfish. These patterns suggest slightly different strategies among individuals, with some choosing to haul out in locations far from the areas usually used by the population to decrease the distances to the foraging areas, while others performed longer trips.

In winter and spring, harbour seals showed a northward shift in haulout placement and trip directionality (red arrows) with increasing ice extent, but a general reduction of the home ranges in early winter and a shift to southward trip directions in late spring coupled with a southward movement of the haulout sites in both periods (blue arrows, see also Figure 4, paper III, for ice extent). This behaviour was found both for the subset of individual movement data with simultaneous ice coverage data (see Figure 4 and 5, paper III, and Figure 9), but

also as a general behaviour for the individuals tagged in the subsequent period (2010 – 2011, Figure 9) and was most likely associated with the retreat of the ice in the inner parts of the fjord and the disclosure of important fish concentrations suddenly made available for the seals (*i.e.* overwintering pelagic fish). A response to the formation of ice has been registered in other areas at high latitude in the Northern hemisphere (Lesage, Hammill & Kovacs 2004; Bajzak *et al.* 2012; Blanchet *et al.* 2014). In all studies the harbour seals were observed to have larger home ranges and travel longer distances from the haulout sites or exhibit a more offshore behaviour, assumed to be due to the ice being a hinder in the movements between feeding grounds and haulout sites. However, in Porsangerfjord the haulout sites are shifted northward in periods of large ice extent (Figure 9) and the ice does not prevent the access to open water at any time; the movements of harbour seals individuals in this area are therefore most likely a reflection of the presence of preferred prey in the areas covered by ice.

3.2.7. *What are the processes driving resource selection for harbour seals in Porsangerfjord?*

The alternation between the northward and southward shifts in trip direction and haulout sites location (see arrows in Figure 9) can be related to the alternation between preference for small codfish (upwards pointing arrows) and for pelagic forage fish (*i.e.* herring and capelin, downward pointing arrows). Despite codfish having been documented to be a major component of the diet of harbour seals in many areas, the shift to preference for schooling prey has been seen in the areas and seasons when pulses of such resources occur (Pierce *et al.* 1991; Brown & Pierce 1998). In the Moray Firth for example, codfish was found to be part of the winter diet only in years of low clupeids abundance (Thompson *et al.* 1996). Based on comparison with other systems, <u>the driving forces determining the shifts in preference, and consequently the movement patterns, of harbour seals in Porsangerfjord, can be argued as being principally the availability of aggregated prey</u>. In Porsangerfjord this occurs in winter and spring, as pelagic forage fish concentrates in cold waters (*i.e.* in the inner parts of the fjord) to overwinter. In addition, the fish is more aggregated during daylight as it migrates towards the sea bottom to avoid predation. Preference for aggregated schooling fish is additionally supported by the dominance of benthic foraging during daylight in winter and spring (see Figure 5). In late winter and early spring, the resources located in the inner areas are rendered unavailable by ice formation, hence the observed shift to preference for small codfish. In autumn pelagic fish, despite being still present in the fjord, has a wider and patchier distribution and becomes most likely less profitable for harbour seals.

3.2.8.   Are harbour seals opportunistic foragers?

Harbour seals are generally described as opportunistic foragers (Bigg 1981). However, several studies, including the present one, have documented certain forms of selection of resources (*e.g.* Tollit & Thompson 1996; Tollit *et al.* 1997). The selection for smaller size fish is widely acknowledged, however some degree of uncertainty still exists on the preference for larger fishes within the small size groups available (Tollit, Greenstreet & Thompson 1997; Brown *et al.* 2001). The preference for pelagic schooling fish has been documented both in this study and several others (Pierce *et al.* 1991; Brown & Pierce 1998). However a preference for certain distributional characteristics of this kind of prey (aggregation) rather than the species has been suggested (Tollit, Greenstreet & Thompson 1997). The findings of this study support this view, in that pelagic forage fish did not have the highest total biomasses or the highest energetic values when preferred by harbour seals (winter-spring, Henderson et al. 1984; Mårtensson et al. 1996), but showed the highest levels of aggregation. Other predators have been found to respond rather to general characteristics of prey distribution than to the specific biomasses of single species (Benoit-Bird *et al.* 2013). Further work should be therefore done in this direction, for example by investigating thresholds of aggregation, distance to haulout sites and other distributional characteristics of prey determining the preference switches.

Another result of interest in this respect was the finding that sculpins were preferred at the large scale in concomitance with high preference for herring (late spring), but slightly avoided at the small scale. This raises the question of the actual presence of preference for sculpins. It may in fact be that their large scale preference was an artefact of the increased usage of the areas with high density of highly aggregated, hence more profitable, prey (*i.e.* herring). However, sculpins were found in high proportions and frequencies in the autumn diet of harbour seals in the fjord (see S1, paper III), suggesting a relatively high degree of predation on these fishes. Sculpins may therefore be used in higher proportions to their general availability, because highly accessible in areas of preferred prey. This type of behaviour has been called incidental predation and has been described in harbour seals foraging on flatfish in the UK (Hall et al. 1998). Extending the analysis of preference to the vertical dimension would most likely allow assessing the validity of this hypothesis in Porsangerfjord, by determining the actual presence of selection for benthic rather than pelagic species.

Individual differences were found as the highest source of variation in preference, potentially suggesting that more significant patterns of selection may be found at the individual rather than at the population level. This study however did not allow for a robust conclusion on the way individual selection strategies

build up to population patterns due to the small sample size. Individual specialization in harbour seals has been documented elsewhere (Tollit *et al.* 1998), but these studies have mostly given a snapshot in time, and cannot therefore conclude on the consistency of such specializations across seasons.

In this study no preference was found at the small spatial scale. <u>It could therefore be concluded that harbour seals are selective in the placement of their home ranges and haulout sites, but not at the level of the single trips</u>. The results of paper I indicated that bouts of foraging and travelling had similar depth ranges, suggesting that harbour seals, not only dive while travelling, but they do so at the same depths as their average foraging patches. This can be interpreted as constantly inspecting the water column while moving. Harbour seals are relatively shallow divers, therefore doing so may increase the chances of finding incidental prey without extensively increasing the cost of transportation.

It must however be remembered that the animals tagged in this study did on average not travel very far from their haulout areas, with respect to maximum ranges observed elsewhere (Lowry *et al.* 2001; Sharples *et al.* 2012). Large differences in home range sizes have been documented depending on the distance between haulout areas and areas of appropriate substrate and depth conditions or due to a high intra-specific competition (Sharples *et al.* 2012). The absence of significant selection patterns at the level of the single trips could be a consequence of the availability of enough prey close to haulout sites for the current size of the harbour seal population.

3.2.9.   What are the general constraints affecting harbour seals foraging in Porsangerfjord? Is there flexibility in the choice of haulout sites?

Harbour seals are able to perform longer trips, farther from their haulout sites, than the ones documented in this study (Sharples *et al.* 2012). However, in Porsangerfjord the seals foraged principally near the haulout sites. As mentioned above, this is not likely to be a consequence of the young age of the tagged individuals, since larger ranges should be expected for juvenile seals (Lowry *et al.* 2001). This suggests that the resources present in the inner areas of Porsangerfjord are enough to support the population all year round, at least at this demographic state. In Porsangerfjord the population, and therefore intra-specific competition, is probably low compared to historical levels as a consequence of severe hunting in the last years (Nilssen *et al.* 2010).

In the periods where the home ranges were slightly larger, the seals used different movement strategies, with some individuals shifting haulout locations northward, while others moving further during single trips (Figure 9). At the population level, the location of haulout sites has been documented to shift in

response to changes in resource distribution and ice (in a range of ~ 20 km, Figure 9 and chapter 3.2.6), which raises a question on the degree of flexibility in the choice of haulout location in harbour seals.

Harbour seals have been described to select their haulout sites in the vicinity of their foraging areas (*e.g.* Bjørge *et al*. 1995). The selection of haulout site is also affected by the availability of suitable sites with respect to tide, exposure to weather, accessibility from and to the sea, disturbance and predation risk (Da Silva & Therune 1988; Grellier, Thompson & Corpe 1996; Lesage, Hammill & Kovacs 2004). Despite the distance to suitable foraging areas being assumed as one of the most important criteria for the choice of haulout sites in harbour seals, the balance between the two major constraints affecting their choice of home range, *i.e.* the suitability of the haulout sites and the distance to appropriate feeding grounds, has not been fully understood yet.

Despite large fluctuations in the population sizes along time, which have been mostly due to hunting pressure (Nilssen *et al.* 2010), the haulout area in the inner part of Porsangerfjord has been known for several decades (Henriksen 1995), suggesting either a high level of site fidelity or the presence of very suitable foraging areas for harbour seals in this region. The fish biomass composition of the fjord, however, has changed drastically in the last decades with a large decrease in codfish especially in the inner parts of the fjords (Lindström U, IMR, pers. comm.). This suggests that the harbour seals population in Porsangerfjord has a high level of site fidelity in the choice of haulout area and that the documented seasonal movements of haulout sites, as a response to prey shifts, occur most likely within a limited set of suitable locations.

The generally low level of constraints that affect the harbour seals population of Porsangerfjord did not allow for the investigation of the balance between the factors influencing the choice of haulout sites and the choice of foraging areas. However, this study suggests a certain degree of flexibility in the use of haulout site up to a certain extent. To which degree this occurs is a question that should be explored further. For this purpose, a large scale analysis could be performed, comparing harbour seals movements across areas with different sets of constraints (*e.g.* resource compositions, environmental characteristics, and population statuses determining competition levels).

3.2.10. *Can harbour seals be a predator pit for cod in Porsangerfjord?*

Given the hypothesised mechanisms driving harbour seals prey preference outlined in chapter 3.2.7, <u>we expect the extent of the impact of the harbour seals on the cod stock in the Porsangerfjord to change with the accessibility of pelagic schooling prey during the winter and spring seasons</u>. That will depend on the

extent of the ice cover, which protects overwintering herring and capelin schools from predation from mammal predators with limited diving capacity, as the harbour seal. In years of little ice cover we hypothesise a larger predation on herring and as a consequence a reduction of predation on cod. On the other hand, predation on cod may increase if the concentration of overwintering herring in the fjord would decrease, as for example in years of low year-classes of herring.

No preference was observed in this study for cod in the sublittoral zone, indicating that kelp forests are not preferred foraging habitats for harbour seals. The seals appeared instead to feed more extensively on small specimen of codfish species that occurred pelagically. Harbour seals are the main predators for cod in the inner areas (south of the innermost fjord sill, see Figure 1, paper III). North of that, several other species (*e.g.* sculpins, halibut, otter, benthic piscivorous birds, and cod itself) have been found to be important predators for juvenile cod (Pedersen *et al. in prep.*). The kelp forest provides not only protection from predators, but also a rich feeding habitat for cod juveniles. The degradation of kelp forests can therefore drive cod juveniles to search for food in the pelagic environment, exposing them to increased predation.

3.3.   Methodological implications

The findings of the present study have highlighted several issues that should be taken into consideration in future works on harbour seals foraging ecology.

Often one of the main reasons for the lack of patterns in the results is assumed to be the low temporal and spatial resolution of the data (respectively frequency of relocations and location error, *e.g.* Robinson *et al.* 2007). With the introduction of GPS over ARGOS technology, relocation errors have been greatly reduced (Cagnacci *et al.* 2010). In addition, the increasing memory and sending capacities of the tags now allow for a high frequency of sampling in time (in this study every 20 min). Several of the analyses performed in this study have evaluated the effect of resolution on the results. In paper II, the temporal resolution of the movement path was not found to be a factor affecting the relationship between indices. In paper III, when examining the sources of error affecting the estimates of resource selection parameters, location error was found to be the smallest with respect to, for example, prediction error in resource distribution. This indicates that an increased precision in resource distribution and prediction would have improved the analysis of resource selection rather than smaller relocation errors.

The data on diving behaviour have generally a much higher temporal resolution (in this study depth was sampled every 4 sec). In addition to that, diving animals have been suggested to respond to larger scale factors in their horizontal

movements (*e.g.* environmental cues), while their diving behaviour would be affected by more localized factors (*e.g.* actual prey presence, (Bailleul *et al.* 2008). In paper II, different levels of spatial aggregation were found in the spatial distribution of the values of the foraging indices, with the vertical ones showing smaller and more defined patches (Figure 4, paper II), supporting this view. This suggests that including the vertical dimension in the analyses of foraging behaviour may already provide one way to increase the resolution of behavioural detection rather than aiming for higher relocation frequency or smaller location errors.

Additionally, combining horizontal and vertical data has been proved important for a better characterization of harbour seal behaviour, and hence the distinction of foraging from other behaviours. In paper I, the combination of horizontal movement and dive characteristics (vertical speed and interdive durations) led to the identification of two forms of resting behaviour, which would otherwise be confounded with foraging because of their similar movement signature on the horizontal plane. In paper II, several factors were found to affect the allocation of time in the two spaces, leading to a more complex interpretation of foraging indices as simple indicators of ARS behaviour. Foraging indices based on the time spent at the bottom of dives, mainly help distinguishing between activity and resting while diving, rather than foraging from other behaviours. On the other hand, looking exclusively at the seals' movements on the horizontal plane does not allow distinguishing between foraging and resting, both having a similar residence signal. Considering only the horizontal movements would most likely allow identifying the location of foraging patches, but lead to an overestimation of the time spent in those areas (see BOX 2). Care should therefore be taken when using the time per unit area as an estimate of foraging effort (*e.g.* Freitas *et al.* 2008).

Switching state-space models have in the last decade emerged as a very good modelling framework to estimate behavioural states in free ranging animals, due to their ability to account for location error and autocorrelation in movement (Jonsen, Flemming & Myers 2005). A recent development of such models was made by introducing ancillary data to improve behavioural characterization (McCLintock *et al.* 2013). The authors specifically tested this by including dive depth for estimating behavioural states in harbour seals and found that seals were, not only either travelling or foraging, but also resting at the surface, in accordance with the results of this study. The results of paper I, however, suggest that this implementation could be taken a step further by including for example dive skewness as an additional variable in the model in order to detect resting while diving as well.

3.4. Conclusions and future work

The present study tested the validity of general theoretical prediction of foraging and movement ecology when applied to harbour seals. The results improved the characterization of time budgets in this species by demonstrating the presence of a significant amount of time spent resting at sea and the presence of different behavioural expressions with a similar function (*i.e* resting at the haulout, at surface and while diving). These in turn may have different energetic implications for the animals. In addition to that, several factors have been identified, affecting the allocation of time in space, commonly used for testing hypotheses of foraging strategies with respect to the distribution of resources. Finally, the results allowed revealing the mechanisms driving the harbour seals response to the dynamics of resources in the Porsangerfjord.

The results have highlighted the need for future research on the energetic implications of different behaviours. The finding of the presence of resting dives (paper I), with slow and constant descending speeds, suggested the use of drifting by means of negative buoyancy. Previous studies on other pinnipeds have shown that changes in buoyancy, due to variability in the condition of the animals (*i.e.* amount of fat), can be determined by analysing changes in drifting speeds (Biuw 2003). Further investigation in this direction should be done by measuring acceleration and stroking patterns, for example by means of accelerometers (Watanabe *et al.* 2006).

The use of accelerometers may additionally improve our understanding of the energetic costs associated to different underwater predatory tactics (Rutz & Hays 2009), the presence of which was highlighted in paper II. This in turn will allow to better estimate field metabolic rates and therefore total energy demands and prey consumption. Different strategies of use of time while diving have been hypothesised to be linked to prey switches or changes in the general profitability of the environment. The question of whether prolonged use of time at depth necessarily leads to increased costs of diving remains, however, partly unsolved and needs further investigation.

When relating the distribution of resources to the location of harbour seals foraging areas, patterns of selection emerged including seasonal switches between prey types (*i.e.* codfish and pelagic forage fish). However, the vertical distribution of both the potential prey species and of the diving effort of the seals was not included in resource selection analysis. Visual examination of the patterns of pelagic and benthic foraging of the seals, together with the vertical distribution of fish, suggested that the inclusion of the vertical dimension in resource selection functions would improve the understanding of different resources which overlap in distribution but are located at different depth layers (*e.g.* herring and sculpins).

The results from these analyses should be then verified by comparing the expected diet of harbour seals, predicted from prey preferences and availability, to the actual diet, investigated through scat analysis. For this purpose, scat sampling across years and seasons should be conducted in the area.

Furthermore, the results of this work, in terms of foraging time budgets, foraging areas and seasonal shifts in prey preferences, should be used to inform the final Ecopath model for the Porsangerfjord, contributing to quantify the effect of this top predator on the different fish stocks of this ecosystem.

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